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research paper

Examining movement patterns of yellowtail snapper, *Ocyurus chrysurus*, in the Dry Tortugas, Florida

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ABSTRACT.—Yellowtail snapper, *Ocyurus chrysurus* (Bloch, 1970), is an important fisheries species in the Florida Keys. In 2008–2009, yellowtail snapper were tagged with acoustic transmitters and tracked through an array of 86 stationary receivers in the Dry Tortugas' network of marine reserves in Florida to determine site fidelity, home range, and temporal patterns of habitat use. Fifteen yellowtail snapper were tracked for 1–427 d [$\bar{x}$ = 188 (SE 39)]. A multistep method for data validation ensured that only the fish with high-quality detection data were selected for data analyses. Brownian bridge models were used to estimate home range rather than more traditional methods because they incorporate not only detection location, but also time between detections, the path between successive detections, and location error. For a species typically described as transient, six of the tagged yellowtail snapper had high site fidelity [$\bar{x}$ = 58.4% (SE 8.4%)], and Brownian bridge models estimated relatively small minimum home ranges [$\bar{x}$ = 5.45 km^2 (SE 1.79)]. Movements were highly variable, but analyses showed that fish displayed diel and seasonal trends, and in general, were more likely to be absent during summer months or during dusk and at night. Tagged yellowtail snapper showed a preference for reef edge habitat, swimming in and out of the marine reserve where the boundary intersected this type of habitat. The knowledge that yellowtail snapper is less transient than previously believed and understanding the habitat preference and temporal movements of this species can help with its future management.

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Yellowtail snapper, *Ocyurus chrysurus* (Bloch, 1970), is a species that occurs year-round in south Florida and has been a component of Florida reef fish landings for more than a century (Lindholm et al. 2005, O'Hop et al. 2012). It supports one of the most profitable commercial reef fish fisheries in the Florida Keys (Waters et al. 2001).

In Florida, about 92.6% of the commercial landings of yellowtail snapper since 2006 have come from Monroe County (which comprises all the Florida Keys), accounting for approximately 8165 t and generating an estimated US$51 million from 2006 to 2016 (FWC 2017). Sustainable management of this species is of critical importance and will depend not only on quantifying the effect of the commercial and recreational fisheries, but also on understanding the life history and behavior of yellowtail snapper.

Yellowtail snapper is unique in the snapper family. It is a semi-pelagic transient species (Harborne et al. 2017, Farmer and Ault 2018), and although its life history and geographic distribution have been well documented, information regarding its movements and migration patterns is limited (Lindholm et al. 2005). Movement occurs on small and large scales, and includes diel habitat shifts, foraging, seasonal migrations, and ontogenetic movements (Friedlander et al. 2013, Pittman et al. 2014). Understanding these movements is imperative for determining habitat connectivity, examining trophic-level dynamics, making management decisions, and even designing marine reserves (Farmer and Ault 2011, Pittman et al. 2014).

The Dry Tortugas region encompasses several multispecies aggregation sites, and recruitment from these spawning sites support the fisheries of the Florida Keys (Farmer and Ault 2011, Ault et al. 2013, Feeley et al. 2018). To protect these important spawning sites, marine protected areas (MPAs) were established in 2001. Ideally, MPA design should incorporate movement data from multiple target species to ensure that sufficient habitat is protected. Little is known about the home ranges of many fish species, or how home ranges vary with age and season. This lack of information on movement and habitat preferences makes it difficult to determine effective MPA size and location. The differences in habitat use between reef fish species highlight that understanding movements of multiple species is crucial for effective MPA design (Lea et al. 2016).

Traditionally, mark-recapture studies have been used to assess movement patterns and habitat use, but for many species recapture rates are low. For example, recapture rates for yellowtail snapper in two mark-recapture studies were 8.3% (Beaumariage 1969) and 0.4% (Feeley et al. 2012). Acoustic telemetry can deliver more detailed information than mark-recapture and can be used to record more extensive fish movements than those perceived only through occasional direct observations (Trefethen et al 1957, Farmer et al. 2013, Hussey et al. 2015). Telemetry data can be used to examine movement behavior, such as home range, patterns of habitat use, and daily activity cycles (Biggs and Nemeth 2016, Herbig and Szedlmayer 2016, Williams-Grove and Szedlmayer 2017). The importance of movement patterns and habitat use has been recognized for other commercially and recreationally important snapper species (Piraino and Szedlmayer 2014, Pittman et al. 2014, Biggs and Nemeth 2016), but few telemetry studies have analyzed yellowtail snapper movements concurrently for home ranges, habitat preference, and seasonal and diel movements (Table 1).

Yellowtail snapper movements have been analyzed in six studies (Table 1), but in three of these, home range could not be estimated due to a limited number of detections or number of days detected (Lindholm et al. 2005, Friedlander et al. 2013, Kendall et al. 2016). Pittman et al. (2014) had enough detections to analyze movement, but this study focused on the connectivity of MPAs rather than on the home range or habitat preference of yellowtail snapper. Farmer and Ault (2011, 2018) were

Table 1. Telemetry studies that have examined yellowtail snapper, *Ocyurus chrysurus*. FL = fork length, TL = total length. The second study resulted in two publications, one which analyzed four yellowtail snapper (Farmer and Ault 2011) and one which analyzed two yellowtail snapper (Farmer and Ault 2018). The third study also resulted in two publications but both analyzed the same number (6) of yellowtail snapper.

Number tagged	Time tracked (d)	Sizes of fish (cm)	Fish analyzed	Receivers	Study location	Telemetry study
14	2–237	21.5–26.5 FL	9	5	Florida Keys, Florida	Lindholm et al. 2005
5	26–153	48.0–55.0 TL	4, 2	32	Dry Tortugas, Florida	Farmer and Ault 2011, 2018
14	0–333	22.5–38.0 TL	6	36	US Virgin Islands	Friedlander et al. 2013, Pittman et al. 2014
5	Slightly >200	25.0–34.0 TL	5	75	St. John, US Virgin Islands	Kendall et al. 2016
18	0–427	37.5–51.4 TL	6	86	Dry Tortugas, Florida	Present study

unable to analyze seasonal movement patterns for yellowtail snapper, but could estimate home ranges using minimum convex polygons (MCPs).

MCPs are a relatively simple method used to calculate home range estimates and are widely used (Abecasis et al. 2009, Farmer and Ault 2011, Biggs and Nemeth 2016, Feeley et al. 2018). However, MCPs are delineated by the outermost detection locations and often overestimate home range, resulting in unreasonable biological assumptions (Börger et al. 2006). Kernel density estimates (KDEs) are another popular method for estimating home range size (Hart et al. 2012, Piraino and Szedlmayer 2014, Herbig and Szedlmayer 2016, Williams-Grove and Szedlmayer 2017, Feeley et al. 2018) and provide more realistic values than MCP estimates (Börger et al. 2006). However, KDEs do not account for the timing of detections and trajectories, which can be important when estimating the home range for a highly mobile species like yellowtail snapper. The Brownian bridge is a more advanced kernel method that takes into account not only the locations of detections, but also the time interval and the path travelled between successive detection locations (Calenge 2006, Horne et al. 2007). The Brownian bridge approach is being used more in acoustic telemetry studies because it incorporates location error, which is appropriate when acoustic receivers detect an animal somewhere within a detection range rather than a specific location (Pagès et al. 2013, Aspillaga et al. 2016).

Therefore, we used the Brownian bridge movement model to estimate the home ranges of yellowtail snapper in the Dry Tortugas. In addition, both diel and seasonal movement trends were analyzed. Increasing the vetting of detection data, using the Brownian bridge movement model, and including temporal movement analyses provided more in-depth information than traditional methods to better understand yellowtail snapper movement patterns in the Dry Tortugas region and to provide critical information for management decisions.

Methods

Study Site and Array.—The Dry Tortugas region encompasses 1243 km^2 of ocean approximately 112 km west of Key West, Florida. It comprises three carbonate banks and seven small islands (Ault et al. 2013, Feeley et al. 2018). Within the Dry Tortugas region, there are multiple marine reserves that offer different levels of protection from fishing (Figs. 1, 2). Outside of the Dry Tortugas National Park, the Dry Tortugas North and South Ecological Reserves were established as no-take reserves. Within the park, the National Park Service designated a Research Natural Area, also

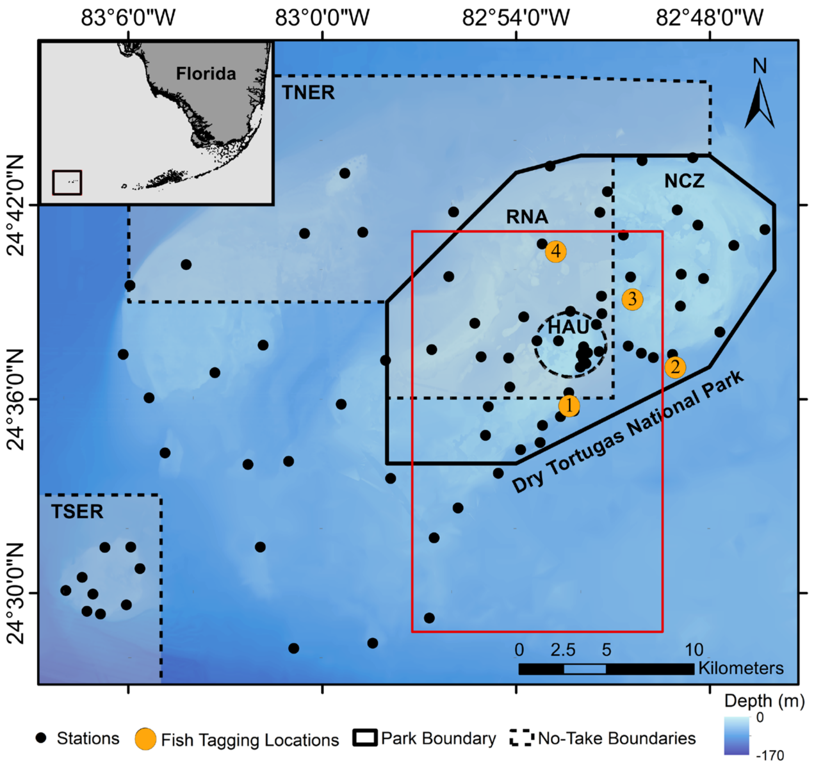

Figure 1. Map of station and fish-tagging locations in the Dry Tortugas. The solid black line represents the Dry Tortugas National Park boundary; dotted lines indicate zones within the Dry Tortugas. Zones include the Tortugas North Ecological Reserve (TNER), the Tortugas South Ecological Reserve (TSER), the Research Natural Area (RNA), the Natural Cultural Zone (NCZ), and the Historic Adaptive Use zone (HAU). Shaded areas indicate no-take reserves. The red box is an extent indicator for Figure 2.

a no-take area. The rest of the Dry Tortugas National Park is limited to hook-and-line fishing and is closed to commercial fishing.

Eighty-six non-overlapping Vemco acoustic receivers (VR2 and VR2W 69 kHz; Vemco Ltd., Amirix Systems, Nova Scotia, Canada) were deployed over approximately 800 km^2 (Fig. 1). This acoustic receiver array was part of a larger acoustic telemetry study by Feeley et al. (2018) to examine movements between management areas. The array was deployed from May 2008 through November 2010 in cooperation between the Florida Fish and Wildlife Conservation Commission (FWC), Mote Marine Laboratory, and the US Geological Survey (Hart et al. 2012, Pratt et al. 2018). To maximize the probability of detecting a tagged fish swimming through the Dry Tortugas, receiver locations were chosen using a variety of data sources, such as reef fish population surveys, benthic habitat and bathymetry maps, management boundaries, and established monitoring sites. Receiver stations were set 600–4000 m apart to ensure maximum spatial coverage of the region rather than to provide 100% detection probability (Farmer et al. 2013). The receiver station depths varied from 1.5 to 50 m. Each acoustic receiver was positioned 1 m above the seafloor housed in a PVC cup with the hydrophone oriented toward the surface of the water, increasing

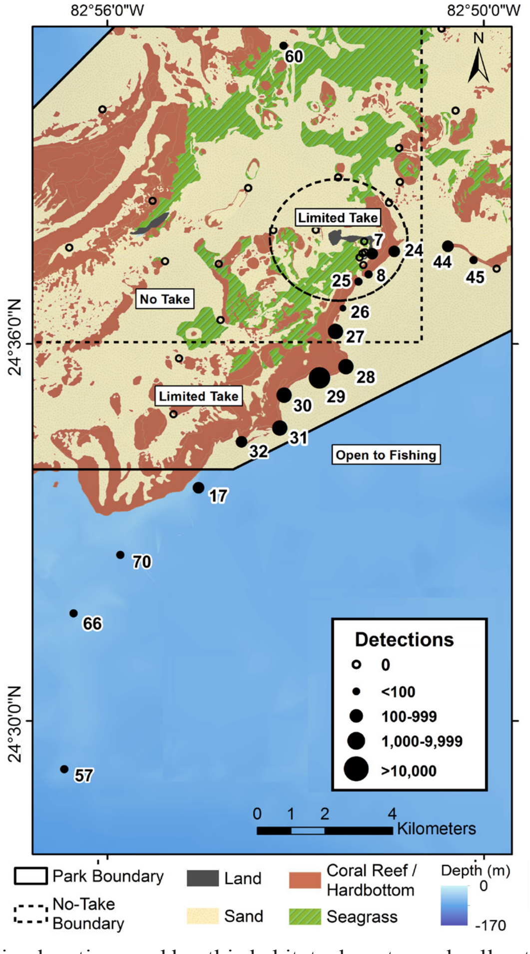

Figure 2. Map of station locations and benthic habitat where tagged yellowtail snapper, *Ocyurus chrysurus*, were detected, showing frequency of validated detections and fishing regulations for the various areas.

the probability of detecting fish like yellowtail snapper that swim higher in the water column. The cup was attached with PVC cement to a 60-cm-long PVC pipe anchored in a square concrete base (approximately 40 × 40 × 25 cm) with a dry weight of approximately 36 kg. The tops of the acoustic receivers, where the hydrophone is located and the only part not inside the PVC cup, were coated with a thin layer of antifouling paint prior to deployment to prevent biofouling. Receivers were retrieved by divers and data were downloaded biannually using VUE software (Vemco Ltd., Amirix Systems Inc., Nova Scotia, Canada).

Tagging.—Fish were tagged from May 2008 through September 2009. Eighteen yellowtail snapper were surgically tagged with coded acoustic transmitters. Two of the fish were captured using fish traps and 16 were captured using hook and line, all in depths of 5–11 m. All fish were brought to the boat and anesthetized with Aqui-S™ (0.449 ml L^{-1}). Vemco V9 low-powered tags (frequency 69 kHz, with a random

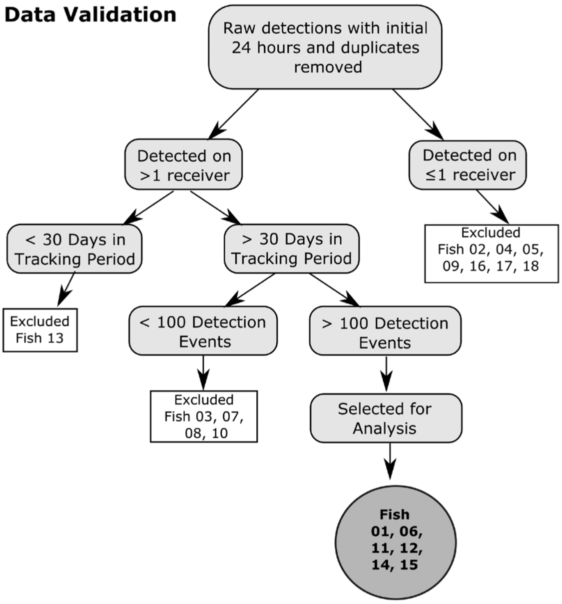

Figure 3. Flow chart of the steps taken to select yellowtail snapper, *Ocyurus chrysurus,* used for analysis. The number of receivers the fish was detected on, the total tracking time period, and number of detection events were considered during this process.

delay of 50–130 s and an estimated tag life of 375–432 d; Vemco Ltd., Amirix Systems Inc., Nova Scotia, Canada) were implanted in each fish's abdominal cavity via an incision made along the midline posterior to the pelvic girdle. The incision was closed using sterile synthetic absorbable sutures (Vicryl Plus, Ethicon Inc., Somerville, New Jersey) with an antibacterial coating and a size-0 cutting needle. The fish were then measured and placed in a holding tank on board until they demonstrated signs of recovery, when they were taken by divers to their initial capture sites and released at the bottom.

Data Validation Analysis.—All detection data were validated and all analyses conducted in R (R Core Team 2016) unless otherwise noted. Acoustic detections were checked for validity by filtering the data in a multistep process (Fig. 3). The initial 24 hrs of detections were removed before analysis to reduce effects of tagging (Farmer and Ault 2011). Detection data were checked to ensure that no single fish was detected at two stations at the same time and that two fish were not detected at the same station at the exact same time.

Using the validated detections, a total detection period (TP) was calculated for each fish as the total number of days the fish was at liberty from 24 hrs after tagging until the tag was detected for the last time. The number of days on which a fish was detected (DD) was calculated as the total number of days on which a fish was detected on a receiver at least once. Using these two values, a residency index (R_i) was calculated for each tagged fish as follows: R_i = DD/TP, with values between zero and one (Abecasis et al. 2009).

The remaining detections were filtered by creating detection events using the V-Track package (Campbell et al. 2012). A detection event was defined as any set of two detections occurring within the time that it would take a fish to leave the detection range of a given receiver (Biggs and Nemeth 2016). There have been few range tests performed for V9 acoustic tags (Singh et al. 2009, Bacheler et al. 2015; J Renchen, Florida Fish and Wildlife Conservation Commission, pers comm), and some have used V9 high powered tags instead of low power or used external attachment methods instead of internal. Therefore, 200 m was chosen as a conservative estimate for the detection radius of acoustic receivers based on these studies. Transit speed was estimated for each fish as the time between two detections divided by the linear distance between two different detecting receivers. Fish with low R_i values (i.e., $R_i \leq 0.10$) or with artificially inflated R_i values (high R_i values but a low number of detections) were not included in the calculation of transit speed. After estimating the mean transit speed for fish in the present study (559 m hr^{-1}), it was determined that it would take approximately 21 mins on average for a tagged yellowtail snapper to swim outside the detection radius of a receiver (200 m). Therefore, a detection event was defined as having at least two detections within a 21-min window.

Not all fish were used in the analysis of site fidelity, home range, or temporal patterns. Many fish were detected for short periods or were not detected regularly. Therefore, only fish that were detected at more than one receiver, that had a tracking period longer than 30 d, and for which there were more than 100 detection events were included in the following analyses (Fig. 3). Using validated detections, animated tracks (Keyhole Markout Language files, Online Appendix 1) of individual fish movements were created using the V-Track package and imported into Google Earth.

Site Fidelity and Home Range Analyses.—Fish were typically tagged between receiver locations (Fig. 1), so site fidelity could not be calculated based on tagging location. Therefore, site fidelity was calculated as the number of detections at the receiver most frequented by a fish divided by the total number of detections for that fish. Brownian bridge movement models were used to estimate the utilization distributions, or home ranges, of each fish. Brownian bridge home range estimates were calculated using the adehabitatHR package (Calenge 2006) for 50% and 95% utilization distributions. Contours from the output of the model were exported to ArcGIS, and 95% contours were used as home range borders. Empirical Bayesian Kriging available in ArcGIS 10.3 (Esri 2014) was used to create interpolated probability surfaces for each fish within its 95% home range contours based on the number of times it was detected at each station. To examine correlation between fish size and home range size, a linear regression was used to compare Brownian bridge estimates and site fidelity to fish total length.

Temporal Pattern Analysis.—Seasonal and diel activity patterns for yellowtail snapper were characterized by grouping the detection data into 1-hr time bins. Each detection was given a value of one. When a fish was not detected within a 1-hr period, a value of zero was given to that time bin. All detections were assigned a diel period and a season. Diel periods were dawn (30 mins before to 30 mins after sunrise), day (30 mins after sunrise to 30 mins before sunset), dusk (30 mins before to 30 mins after sunset), and night (30 mins after sunset to 30 mins before sunrise). Sunrise and sunset times were calculated daily at each receiver location using the StreamMetabolism package (Sefick 2016). Seasons assigned to detections were winter (December, January, February), spring (March, April, May), summer (June, July, August), and fall (September, October, November).

To analyze detection data, a generalized linear mixed model (GLMM) was fit using a two-part hurdle model to account for zero-inflation of the data (Zuur et al. 2009, Bilder and Loughin 2015, Harborne et al. 2017). The first part of a hurdle model analyzed the data as a binary response to determine which factors affect the presence or absence of a fish. To determine which factors affect how many times a fish is detected, the second part of the model analyzed the data as a truncated response. A binomial regression with a logit link function was used for the first part of the hurdle model, and a truncated negative-binomial regression with a log link function was used for the second part of the hurdle model. In the models, diel period and season were fixed effects and fish ID was a random effect. GLMM hurdle analyses were performed using the glmmADMB package (Skaug et al. 2016) and the lme4 package (Bates et al. 2015). Model selection was based on an information-theoretic approach using the corrected Akaike information criterion (AIC_c), which provides an objective means of ranking a model based on explained deviance and the number of parameters in the model (Burnham et al. 2011). Model fit was checked by examining residual diagnostic plots (Online Appendix 2) using the DHARMa package (Hartig 2017). To estimate effect size, odds ratios were calculated for parameter estimates for the presence-absence portion of the hurdle model and rate ratios were calculated for parameter estimates for the count portion of the hurdle model.

Results

Tagging.—Eighteen yellowtail snapper were tagged and measured 37.5–51.4 cm in total length [$\bar{x}$ = 42.4 (SE 0.8) cm; Table 2]. Throughout the study, 38,332 raw detections were recorded on the array. The recorded number of detections per fish varied from 1 to 15,994 [$\bar{x}$ = 2513.0 (SE 933.4); Table 2]. Three fish were never detected after release, whereas 15 fish were tracked for 1–427 d [$\bar{x}$ = 188 (SE 39); Table 2, Fig. 4]. After detections had been validated, 36,332 detections remained (95% of the total raw detection) and the six fish that met the criteria for analysis had been detected 1088–15,417 times [$\bar{x}$ = 5881 (SE 2400)] and tracked for 244–427 d [$\bar{x}$ = 365.0 (SE 23.8) d; Fig. 5]. Although only six of the 18 tagged fish were analyzed, these six fish were responsible for 99.9% of the raw detections and 97% of the validated detections.

Site Fidelity and Home Range.—Yellowtail snapper were detected only by the receivers at stations shown in Figure 2. The receiver at station 29 had the most validated detections (19,907) and the largest cumulative detection time (1098 hrs). Site fidelity for the six fish analyzed ranged from 32.8% to 93.8% [$\bar{x}$ = 58.4% (SE 8.4%); Table 3], and home ranges varied in size from 0.22 to 1.20 km^2 [$\bar{x}$ = 0.42 (SE 0.14) km^2] at 50% contours and from 1.59 to 11.79 km^2 [$\bar{x}$ = 5.45 (SE 1.79) km^2; Table 3] at 95% contours. For four of the fish (01, 06, 14, and 15), home ranges were similar in size and shape, whereas fish 11 and 12 had larger and more spread out home ranges (Fig. 6). There was no significant relationship between fish total length and site fidelity ($F_{1,4}$ = 0.148, P = 0.720, R^2 = 0.036) or Brownian bridge estimates (50% $F_{1,4}$ = 0.132, P = 0.737, R^2 = 0.032; 95% $F_{1,4}$ = 0.828, P = 0.414, R^2 = 0.172). Four of the non-analyzed fish (Fish 03, 07, 08, and 10) were tracked from 122 to 332 d after their release, but did not have consistent detection data for analysis (Table 2).

Table 2. Summary information for acoustically tagged yellowtail snapper, *Ocyurus chrysurus*. Fish denoted with an asterisk (*) are those that met the criteria for analysis for habitat use and temporal patterns. The table includes the number of days detected (DD), the total tracking time period (TP), and the residency index (R_i = DD/TP).

Fish ID	Date tagged	Tagging site	TL (cm)	DD	TP	R_i	No. validated detections	No. detection events	No. stations visited	Station numbers
01*	5/16/2008	1	43.2	123	350	0.35	1,814	161	5	28, 29, 30, 31, 32
02	5/17/2008	1	38.1	6	6	1.00	93	25	1	29
03	5/17/2008	1	43.2	23	287	0.08	100	18	3	29, 30, 31
04	5/19/2008	2	37.6	0	0	0.00	0	0	–	–
05	5/19/2008	2	40.1	1	1	1.00	0	0	1	45
06*	10/10/2008	1	43.8	191	334	0.57	8,571	476	4	28, 29, 30, 31
07	10/10/2008	1	40.6	48	332	0.14	155	35	2	28, 29
08	10/10/2008	1	44.5	49	310	0.16	86	33	4	27, 29, 30, 31
09	10/11/2008	3	41.9	0	0	0.00	0	0	–	–
10	10/11/2008	3	51.4	12	122	0.10	591	47	2	44, 45
11*	5/7/2009	1	40.1	193	420	0.46	1,088	200	14	7, 8, 17, 24, 25, 26, 27, 29, 30, 31, 32, 57, 66, 70
12*	5/7/2009	1	42.7	238	400	0.60	3,799	491	11	17, 24, 26, 27, 28, 29, 30, 31, 32, 57, 66
13	5/7/2009	1	37.5	3	22	0.14	3	1	1	30
14*	9/24/2009	1	44.0	197	244	0.81	4,597	437	7	17, 27, 28, 29, 30, 31, 32
15*	9/24/2009	1	40.6	398	427	0.93	15,417	1,438	6	26, 27, 28, 29,30, 31
16	9/25/2009	4	40.6	3	5	0.60	22	4	1	60
17	9/25/2009	4	43.2	7	16	0.44	10	1	1	60
18	9/25/2009	4	50.8	0	0	0.00	0	0	–	–

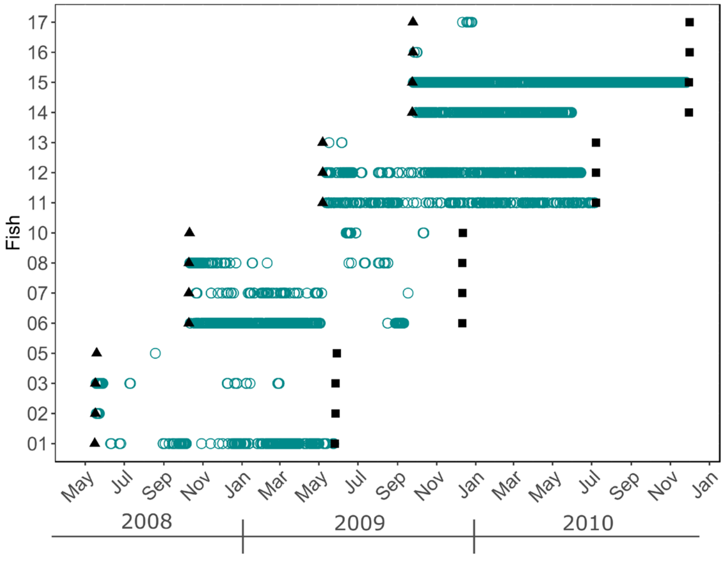

Figure 4. Dates of raw detections of tagged yellowtail snapper, *Ocyurus chrysurus,* from date of first detection until last detection. Fish 04, 09, and 18 were removed due to zero detections. Triangles indicate the tagging date and squares indicate the expiration date of the tag.

Temporal Patterns.—The diel period, season, and the interaction between factors had an effect (confidence intervals not spanning zero) on the presence-absence of tagged fish (Tables 4 and 5, Fig. 7). The odds ratio provided for each parameter provides an effect size. An odds ratio less than one means that, while holding all other variables constant in the model, fish were more likely to be absent from the array while an odds ratio greater than one means fish were less likely to be absent from the array. For example, when all other parameters were held constant, fish were 3 times more likely to be absent during the summer while fish were 1.06 times less likely to be absent during the spring.

Predicted probabilities of "jumping the hurdle," or fish being present, were estimated based on parameter estimates from the best approximating model (Fig. 7). In general, fish were more likely to be present during dawn and day periods, but more likely to be absent at night for all seasons. Fish were also more likely to be absent during dusk for all seasons except for during the summer, when fish were more likely to be present at dusk than dawn and as likely to be present during the day. In general yellowtail snapper were less likely to be present in the summer than other seasons. Fish 01 and 06 were both present within the array during winter months, but were present only occasionally during the summer months (Fig. 5). Fish 11 and 12 moved more during the summer and were detected farther south than where they were detected the rest of the year. Fish 11 showed a similar pattern two summers in a row, traveling to receiver 57, located 16.1 km south of station 8, the station at which fish 11 was most often detected. Fish 14 and 15 showed different patterns. Fish 14 left during the summer and was not detected again whereas fish 15 was detected regularly throughout all seasons.

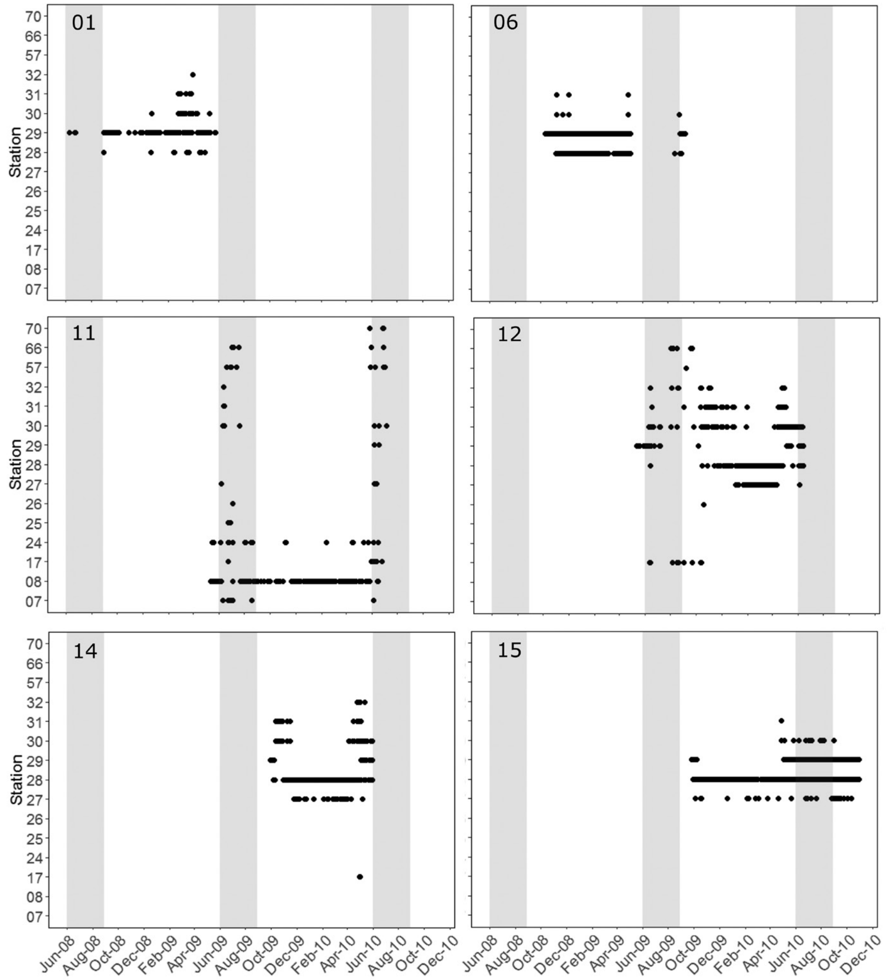

Figure 5. Dates and locations of validated detections from analyzed yellowtail snapper, *Ocyurus chrysurus*. Numbers in the upper left of each plot are fish IDs; shaded bars indicate summer months (June–August).

There was support for two models for the count portion of the hurdle model (Table 4). The best approximating model included diel and season and based on AICc weights was 1.6 times (0.61/0.39) more plausible than the next model which also included the interaction term. The rate ratio provided for each parameter for the best approximating model provides an effect size (Table 5). A rate ratio less than one means that, while holding all other variables constant in the model, the variable of interest will have fewer detections per hour while a rate ratio greater than one means that the detections per hour will be higher. Predicted detections per hour for each diel period were plotted based on the parameter estimates for the best approximating model (Fig. 8). For all seasons the number of detections per hour was higher during the day and night than during dusk and dawn. Fall had the highest number of detections per hour, while summer had the fewest.

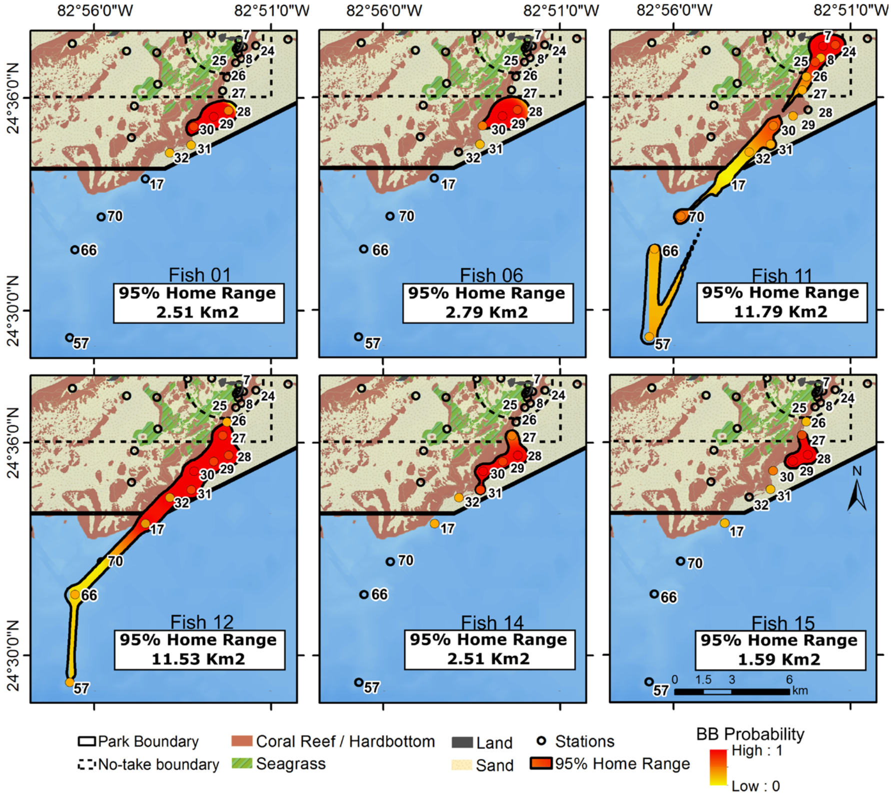

Figure 6. Brownian bridge 95% home ranges of yellowtail snapper, *Ocyurus chrysurus,* with benthic habitat data and the Dry Tortugas National Park boundary. Brownian bridge (BB) probability scales inside the home range boundaries indicate probability of a fish being detected.

Table 3. Site fidelity and Brownian bridge home range estimates for six yellowtail snapper, *Ocyurus chrysurus*. Site fidelity was calculated as the percentage of the detections at the most-frequented station.

Fish ID	Station most frequented	Site fidelity (%)	95% home range (km^2)	50% home range (km^2)
01	29	74.7	2.51	0.24
06	29	93.8	2.79	0.34
11	8	49.7	11.79	0.23
12	30	40.8	11.53	1.20
14	30	32.8	2.51	0.29
15	29	58.9	1.59	0.22

Table 4. Set of ranked models for the generalized linear mixed model hurdle analyses on yellowtail snapper, *Ocyurus chrysurus*. Models were ranked based on the number of parameters (k), the corrected Akaike information criterion (AIC_c), the change in AIC_c from the top ranked model (ΔAIC_c), and the model weight.

Presence-absence model	k	AIC_c	ΔAIC_c	Weight
diel + season + diel:season	17	27,899.54	0.00	1.00
diel + season	8	28,001.57	102.03	0.00
diel	5	28,097.96	198.42	0.00
season	5	29,565.92	1,666.38	0.00
null	2	29,645.67	1,746.13	0.00
Count model				
diel + season	9	27,849.24	0.00	0.61
diel + season + diel:season	18	27,850.14	0.90	0.39
diel	6	27,905.62	56.38	0.00
season	6	28,056.02	206.78	0.00
null	3	28,106.60	257.37	0.00

Table 5. The model parameters (Estimate) from the top-ranked models for the hurdle analyses on yellowtail snapper, *Ocyurus chrysurus*. The reported estimates for the random effects are the standard deviation. Sigma is the overdispersion parameter estimated in the truncated negative binomial regression. To approximate effect size, odds ratios were calculated for the presence-absence portion of the hurdle model and rate ratios were calculated for the count portion of the hurdle model.

Presence-absence parameters	Estimate	Lower CI	Upper CI	Odds ratio
Intercept	−1.72	−2.42	−1.03	
Random effect	0.82	0.46	1.44	
dielday	−0.17	−0.41	0.06	0.84
dieldusk	−0.61	−0.95	−0.26	0.56
dielnight	−1.45	−1.70	−1.20	0.23
seasonspring	0.06	−0.26	0.37	1.06
seasonsummer	−1.09	−1.53	−0.66	0.34
seasonwinter	−0.18	−0.51	0.14	0.83
dielday:seasonspring	−0.19	−0.52	0.14	0.83
dieldusk:seasonspring	−0.29	−0.80	0.21	0.74
dielnight:seasonspring	−0.23	−0.59	0.13	0.79
dielday:seasonsummer	0.54	0.09	0.99	1.72
dieldusk:seasonsummer	0.91	0.31	1.51	2.49
dielnight:seasonsummer	0.98	0.51	1.45	2.67
dielday:seasonwinter	0.11	−0.23	0.45	1.11
dieldusk:seasonwinter	0.05	−0.45	0.56	1.05
dielnight:seasonwinter	−0.65	−1.03	−0.27	0.52
Count parameters				
Intercept	1.31	1.07	1.55	
Random effect	0.26	0.14	0.47	
Sigma	1.39	1.29	1.49	
dielday	0.64	0.53	0.75	1.90
dieldusk	0.11	−0.06	0.28	1.12
dielnight	0.84	0.71	0.97	2.31
seasonspring	−0.14	−0.21	−0.07	0.87
seasonsummer	−0.34	−0.42	−0.25	0.71
seasonwinter	−0.14	−0.22	−0.06	0.87

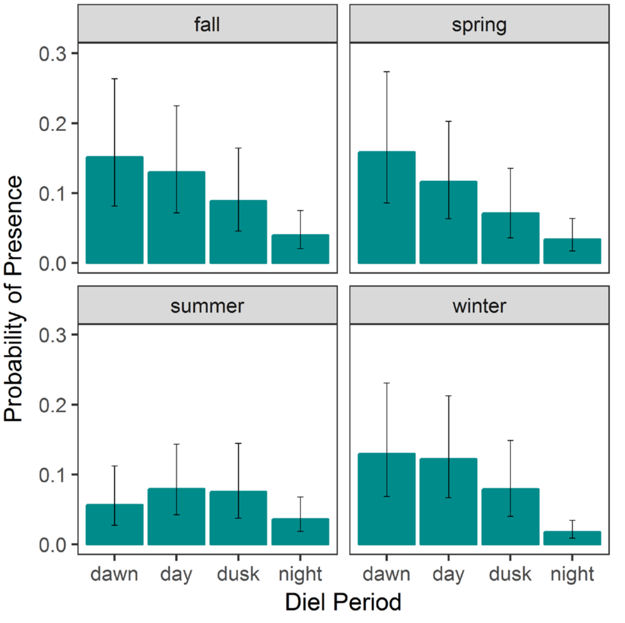

Figure 7. The predicted probability of yellowtail snapper, *Ocyurus chrysurus,* presence calculated using parameter estimates from the best approximating model (Table 5). The best approximating model included diel period, season, and an interaction between diel period and season (Table 4). Error bars represent the 95% confidence intervals.

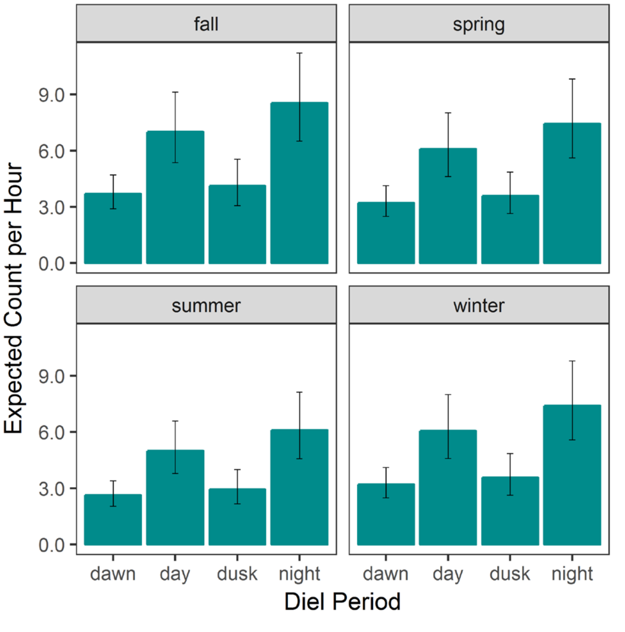

Figure 8. The predicted number of detections per hour for each diel period when yellowtail snapper, *Ocyurus chrysurus,* were present calculated using parameter estimates from the best approximating model (Table 5). The best approximating model included diel period, season, but not an interaction between diel period and season (Table 4). Error bars represent the 95% confidence intervals.

Discussion

The acoustic receiver array (Fig. 1) was designed to assess the connectivity between management zones by capturing large movements throughout the regions of the Dry Tortugas. Large movements between management areas were documented for mutton snapper, *Lutjanus analis* (Cuvier, 1828), in the Dry Tortugas (Feeley et al. 2018) and similar movements were expected for yellowtail snapper due to their description as a semi-pelagic transient species (Harborne et al. 2017, Farmer and Ault 2018). However, yellowtail snapper in the present study were generally not detected making larger movements, and the stations were not set up for fine scale tracking. An array arranged in a grid with receivers spaced closer together would have provided better resolution of fish movement (Farmer and Ault 2014). Even though Brownian bridge was used to calculate more accurate home range estimates, due to the design of the study array and the unanticipated behavior of yellowtail snapper, the home range estimates presented here are considered to be minimal home ranges.

Site Fidelity and Home Range.—High site fidelity was not expected for yellowtail snapper, but was seen in the six fish analyzed (Table 3). This analysis revealed that tagged yellowtail snapper also had relatively small 50% [$\bar{x}$ = 0.42 (SE 0.14) km^2] and 95% [$\bar{x}$ = 5.45 (SE 1.79) km^2] home ranges for a species considered highly mobile (Friedlander et al. 2013). The difference between the 50% and 95% home ranges indicates that the tagged yellowtail snapper remained within an area no larger than 1 km^2 for much of the time, but occasionally made larger movements. Feeley et al. (2012) also found that although most recaptured yellowtail snapper were caught in the same area in which they had been tagged, some (25%) were caught farther (18.5–100 km) away.

Of the yellowtail snapper not analyzed, three fish (Fish 04, 09, and 18) were never detected, which could be due to tag failure, or immediate emigration from the array due to tagging stress. Five of the yellowtail snapper (Fish 02, 05, 13, 16, and 17) were only “heard from” soon after release (Fig. 3), and it is unclear whether predation, removal by fishing (in areas open to fishing, Fig. 2), or the non-overlapping receiver station array was the cause of the limited data. In addition, fish were baited into the area during tagging, so it is possible that some fish were baited in from outside the array and returned to their original locations shortly after tagging. Yellowtail snapper may also show partial migration, with some members of the population displaying high site fidelity and others being more migratory (Chapman et al. 2012). Most of the fish with few or no detections were tagged on sand and seagrass habitat (Table 2, Figs. 1, 2) and these fish could be more transient than those tagged on the reef. Tagged silver seabream, *Pagrus auratus* (Forster, 1801), showed partial migration; those that were tagged on reef habitat had higher site fidelity and were less mobile than those tagged on soft bottom habitat (Parsons et al. 2011). Like silver seabream, the yellowtail snapper that we analyzed on the reef could be the more resident portion of the population. Yellowtail snapper may also switch strategies depending on its life stage.

Detection data for four fish (Fish 03, 07, 08, 10) were not robust enough for home range calculations or incorporation into the GLMM. However, they likely had high site fidelity due to detections on receiver stations close to each other for almost a year and no detections on other receivers (Table 2, Fig. 2). Fish 10 was tagged in the middle of the array, and considering that 86 active receivers were spread out over

800 km^2, it is probable that if it had traveled an extended distance it would have been detected by another receiver.

Tagged fish might have emigrated from the array toward the east or could have been using the sand habitat east of the park where there were no receivers. However, Farmer and Ault (2011) hypothesized that open sand habitat was a barrier to fish movement because their receivers never detected tagged yellowtail snapper in sand habitat. In addition, although earlier ecological studies often described yellowtail snapper as a semi-pelagic wanderer (Moe 1972, Thompson and Munro 1974), Lindholm et al. (2005) also documented high site fidelity and Farmer and Ault (2011) report 95% home range sizes [$\bar{x}$ = 4.17 (SE 1.75) km^2], similar to those in the present study. Fish 11 and 12 had larger home ranges (>11 km^2 each) than the other four fish, but these fish had small 50% home ranges (Table 3) and the interpolation of detections by station indicate that these two fish spent most of their time farther north in the array near the stations frequented by the other four fish (Fig. 6).

Fish size is known to influence home range size and site fidelity (Kramer and Chapman 1999), with more migratory members of the population being larger than the more resident members of the population (Chapman et al. 2012). However, the present study discerned no relationship between either fish size and site fidelity or fish size and home range size. Although the fish tagged here were representative of those typically captured in the Dry Tortugas and were all of reproductive size, smaller or larger fish may display different movement patterns or behaviors.

The receivers with the most detections were located along the reef edge (Fig. 2), which may indicate a preference for this type of continuous habitat or that it provides a good planktonic food source from upwelling. The only fish with enough data for analysis (Table 2) were all tagged at site 1 (Figs. 2, 3), which is located along this reef edge. These fish may have been the only individuals tagged at their preferred habitat, or they could be the more residential fish of the population. The two most frequented receiver stations, 28 and 29, were located at depths of 21.3 and 22.6 m, respectively, similar to depths at nearby sites. But these two stations were located next to a reef promontory (Fig. 2) that has higher relief than the rest of the reef edge. Spawning aggregations often form near promontories, which have unique oceanographic characteristics that may be more favorable for larval dispersal than those for the rest of the reef tract (Kobara et al. 2013). Yellowtail snapper aggregates to spawn, and some studies have reported that it has a protracted spawning season (Figuerola et al. 1998, Cummings 2004). All tagged fish were likely capable of spawning (L_{50} = 23.2cm TL; O'Hop et al. 2012) and could frequent this promontory if it were a potential spawning site. Fish traveling near this feature were usually detected (by consecutive receiver stations 27, 28, and 29) traveling around the promontory. Tagged fish rarely moved directly from station 27 to 29 or 30, preferring to go around the feature, not to cross over the top, possibly to avoid the shallower water (approximately 5 m deep). This is further demonstrated when displaying animated tracks (Keyhole Markout Language files, Online Appendix 1) exported from the V-Track package in Google Earth. This behavior indicates that the tagged yellowtail snapper are likely following this reef edge as they swim over the hardbottom habitat and may prefer medium-to-high–relief promontories.

Temporal Patterns.—Understanding the temporal patterns of yellowtail snapper movement can help clarify how the fish use habitat within their home ranges.

Individual variability (*see* Fig. 5 and Online Appendix 1) can make such patterns difficult to discern. However, although analyzed yellowtail snapper showed high site fidelity, they were more likely to be absent during the summer and were rarely detected on their most frequented station during this time (Figs. 5, 7). The longest gaps between detections also occurred during the summer months, which coincides with hypothesized peak spawning times for yellowtail snapper in the Florida Keys (Cummings 2004). Although a yellowtail snapper spawning aggregation site has been reported within the South Ecological Reserve, approximately 20 km southwest of the Dry Tortugas National Park (Lindeman et al. 2000), none of the tagged fish were recorded at receivers located there. During summer months, fish 11 and 12 were detected on receivers outside of park boundaries on isolated medium-relief patches (stations 57, 66, and 70), whereas fish 01, 06, and 14 were not detected for most, or all, of the summer. In fact, the only time fish 11 and 12 made these longer movements outside the park (which contributed to their larger home ranges) was in summer. The absence of some yellowtail snapper in the summer and the detection of other individuals by stations 57, 66, and 70 could suggest that during the summer, fish were traveling to spawning aggregations outside the array. Unlike mutton snapper, which also forms spawning aggregations (Feeley et al. 2018), tagged yellowtail snapper did not show synchronized movement from one area to a specific spawning aggregation site. Little information exists about yellowtail snapper spawning aggregation sites, but they are reported to be smaller with less predictable timing and location than those of other snapper species (Lindeman et al. 2000).

Temperature also might have affected movement of yellowtail snapper in our study. As water temperature increases in summer, the metabolic rate of fish increases (Johnston and Dunn 1987). In summer, they could be absent from the reef edge because they are foraging over a larger area to meet these increased metabolic demands. Other reef fish have also shown larger home ranges in the summer correlated with increased water temperatures (Piraino and Szedlmayer 2014, Herbig and Szedlmayer 2016). In addition, anecdotal evidence suggests that predation rates might be lower when the water is warmer. Some of the predators that prey on yellowtail snapper, such as king mackerel, *Scomberomorus cavalla* (Cuvier, 1829), migrate into the area during the winter (Barile 2013). When temperatures increase in the late spring through summer, king mackerel move farther north or into deep water and are far less abundant along the reef tract. If there are fewer predators during the summer, yellowtail snapper could be moving farther from the protection of the reef.

Threat of predation is high in the Dry Tortugas National Park (Farmer and Ault 2011), and yellowtail snapper may alter behavior at dusk and night to avoid predation. Red snapper, *Lutjanus campechanus* (Poey, 1860), typically a nocturnal predator, has also been shown to use smaller areas during crepuscular periods and at night when its own predators are more locally abundant (Piraino and Szedlmayer 2014). Tagged yellowtail snapper were less likely to be present within the array at dusk and even less likely to be present at night (Fig. 7). Lindholm et al. (2005) reported that, although there was no significant difference in the number of detections by diel period, 58% of their detections for tagged yellowtail snapper occurred during daylight hours, 25% occurred during nighttime hours, and 17% occurred during crepuscular periods. Farmer and Ault (2011) also reported that tagged yellowtail snapper were detected more during the day than during other diel periods. If tagged fish are not in the water column at night but rather remain close to the reef floor, detection efficiency could decrease due to shadowing from the reef or if fish are in the shadow zone of the upward facing receivers (Farmer et al. 2013). However, when fish were present at night, the number of detections per hour was equal to or greater than it was during the day (Fig. 8), so it is unlikely that a change in fish behavior or biological noise masked the presence of fish. Biological noise during crepuscular periods, the dawn-dusk chorus, could account for the decreased number of detections per hour during dusk and dawn (Fig 8). However, it is unlikely that it affected the probability of detection since fish were more likely to be present at dawn when the number of detections per hour was lower than night when the number of detections per hour was higher.

Although some studies suggest that yellowtail snapper feeds opportunistically throughout the day (Cummings 2004), others suggest it feeds primarily at night (Friedlander et al. 2013). Therefore, rather than sheltering at night, fish could be spending more time actively foraging away from the reef edge (Lindholm et al. 2005). Tagged fish could be using the hardbottom/coral reef and seagrass habitats to the west of the reef edge between receiver station detection ranges (Fig. 2) to forage from dusk through the night and then return at dawn to forage along the reef edge throughout the day. However, foraging in seagrass habitat has previously only been associated with juvenile or subadult individuals (Cummings 2004, Verweij et al. 2008) and the fish in this study were mature adults. Yellowtail snapper has also been shown to eat the eggs of other spawning fish (Cummings 2004) and may leave the area to take advantage of the many species of fish that spawn in the evening.

Implications in MPA Management.—Four of the six fish analyzed had home ranges that crossed over different management zones, with fish 03 and 04 crossing into three zones: no-take, limited take, and open to fishing (Fig. 6). Although the tagged yellowtail snapper in the present study were detected a majority of the time within limited take or protected areas, some traveled out into areas open to fishing during the summer. Benthic habitat maps did not extend beyond park boundaries; however, yellowtail snapper showed a preference for a reef/sand interface within the park. Understanding the movement of fish like yellowtail snapper can influence MPA design and factors other than habitat type and reserve size should be acknowledged. Habitat connectivity should be considered by management as MPAs could completely enclose certain habitats or intentionally cut across them depending on the objective of the MPA.

Conclusions

Acoustic telemetry proved to be a successful method for assessing the movements and behaviors of yellowtail snapper over distances as great as 10s of kilometers. The movement of tagged yellowtail snapper was not completely random, but rather was methodical as fish visited the same sites during most of the year, and some fish demonstrated similar seasonal differences. Yellowtail snapper demonstrated movement patterns based on diel activity (fewer detections at night) and seasonal patterns (fewer detections and longer movements in summer). The information generated in this study enhances the understanding of the movement patterns of yellowtail snapper, information that is crucial for identifying the proper scale and strategy for its management.

To date, the present study represents the most comprehensive research using telemetry to analyze home ranges, and diel and seasonal patterns of yellowtail snapper. The methods used to filter detections were rigorous and led to a robust data set so that only fish with the best detection data were analyzed. A stricter method of data selection meant that fewer fish were analyzed; however, the benefit was a high-quality data set for more comprehensive analyses than in previous studies. Additionally, the spatial behavior of yellowtail snapper was tracked for a longer period of time than in earlier acoustic research. Although not all fish had data robust enough for analyses, the ones that were analyzed revealed higher site fidelity and smaller home ranges than expected. It is also possible that yellowtail snapper experiences partial migration and that these fish were the residential members of the population while the fish with limited detections were the migratory members. Fish tagged were all large enough to be spawning capable, but differences in movement behavior indicate the lack of well-defined spawning aggregations. Since some of yellowtail population is less transient than previously believed and has relatively small home ranges, the marine reserves in the Dry Tortugas are likely an effective way to protect this species. Eventual spillover from the reserve will likely be restricted to the continuous reef-edge habitat adjacent to the protected areas, with the possibility of occasional larger migrations.

Marine protected areas, like those in the Dry Tortugas, have been proposed as a tool for protecting important fisheries species. The design of MPAs is considered one of the most important determinants of the areas' success. Therefore, the knowledge of individual fish movements, habitat preference, and connectivity among populations should play a critical role in development of an MPA. For this reason, the most recently available and appropriate methods should be used to improve the analysis of acoustic telemetry, and the statistical models used should be robust enough to account for the inherent limitations of telemetry data (e.g., zero-inflated, limited detections). These improved methods generate more reliable estimates of fish movement patterns and home ranges. This valuable information can be used to explain habitat use of reef fish across different time scales and the effectiveness of the spatial protection provided by the marine reserves in the Dry Tortugas region.

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