Accounting for detection gaps when evaluating reef fish habitat use in an acoustic array

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Abstract

Understanding the relationship between "habitats" and the distribution of fishes is critical to effective survey design and spatial management. Determining reef fish habitat utilization patterns from passive acoustic arrays is challenging because: (1) habitat classifications must be meaningful to the species; (2) the array must contain the species' home range; and, (3) the probability of detection may differ amongst habitats within the array. We conducted a multi-year tracking study in the marine protected areas (MPAs) of Dry Tortugas, Florida, using a calibrated passive acoustic array deployed over habitats classified by type (reef, rubble, sand), rugosity (high, medium, low relief), and patchiness (contiguous, spur-and-groove, isolated). Our design controlled for differences between individuals, diel and edge effects, and detection gaps resulting from the non-linear relationship between acoustic tag detection probabilities as a function of distance from the receiver. We found red and black groupers preferred high relief reef habitats, whereas mutton and yellowtail snappers preferred low-relief contiguous reef habitats. By identifying critical habitats for exploited species, our analysis may facilitate more efficient fishery-independent sampling and MPA designs.

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Introduction

Technological advances in acoustic and satellite telemetry, data assimilation and computational methods have evolved to the point where the dynamic spatial relationships between fishes and their environments are now a standard part of the fisheries management lexicon (e.g., Block et al. 2016). Fisheries management plans in the United States are required to formally define areas of "*essential fish habitat*" and "*critical habitat*" (MSRA 2006). Fish movements within a seascape to satisfy demographic (i.e., growth, reproductive and survivorship) processes may be influenced by the quantity and availability of specific habitats (McIntyre & Wiens 1999; Kahler et al. 2001). Individuals may select for habitats that improve their fitness due to greater food availability, decreased predation risks, or lower metabolic costs (MacArthur & Pianka 1966). Food-value theory (Stenger 1958; Wilson 1975) and animal cost-benefit analyses (Brown 1964) suggest that resource availability plays a major role in determining animal home range size and overlap. A better understanding of habitat use by coral reef fishes is vital to inform scientists and decision-makers, as reef fish are ecologically and economically valuable, but are especially vulnerable to habitat degradation from fishing, coastal development, and climate changes.

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Spatial resource protection strategies such as Marine Protected Areas (MPAs) have been widely employed in coral reef ecosystems to balance competing use interests, protect corals and promote sustainable fisheries (Bohnsack et al. 2004; Meester et al. 2004). In theory, well-designed no-take MPAs will promote the accumulation of spawning biomass and enhance prospects for larval export and the spillover of exploitable fish into adjacent areas open to fishing (Ault et al. 2006; 2013). Failure to align MPAs borders with natural boundaries to movement or include critical habitats may reduce MPA effectiveness by increasing the likelihood of adult fish crossing reserve boundaries and becoming vulnerable to exploitation (Chateau & Wantiez 2008; Farmer & Ault 2011). Fish movements may occur at a range of scales, from small-scale habitat use (100s of m) to broad-scale movements (100s of km). Many reef fish species have broad-scale ontogenetic habitat shifts, often motivated by a desire to balance mortality risk and growth opportunities (Dahlgren & Eggleston 2000; Grol et al. 2014). Increased mating opportunities, especially at spawning aggregation sites, may also lead to broad-scale adult migration (Farmer & Ault 2011; Stump et al. 2017). Although broad-scale movement patterns are somewhat understood within the context of life history demands, our understanding of fish habitat preferences and short term movements within a daily home range are limited (Boström et al. 2011). The presence of preferred benthic habitats (bottom-up control) may have a greater effect on reef fish populations than protection from fishing (top-down effect) in MPAs (Russ et al. 2015). By containing preferred habitats within an MPA, its carrying capacity is maximized, spillover to nearby preferred habitats is reduced, and lost fishing opportunities are minimized.

Acoustic telemetry has become a popular tool for examining in detail fish movements and habitat use at a variety of scales in estuarine, coral reef, and coastal marine environments (review in Heupel et al. 2006). Multiple active tags can be released and passive receiver arrays can be positioned over relatively broad geographic areas such that detection ranges overlap, allowing researchers to expand upon the basic occupancy (presence/absence) statistics recorded by individual receivers (MacKenzie et al. 2006; Topping et al. 2006; Dresser & Kneib 2007; Hedger et al. 2008*a*, 2008*b*; Farmer & Ault 2011). Recent studies have indicated that detection rates are hierarchical non-linear functions of tag distances from receivers (Royle & Dorazio 2009; Welsh et al. 2012; Farmer et al. 2013).

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Many "habitat utilization" studies using acoustic tracking have either: (1) assumed probability of tag detection was equal across habitats (e.g., Farmer & Ault 2011; O'Toole et al. 2011; Munroe et al. 2014; Drymon et al. 2014; Wolfe & Lowe 2015); or, (2) restricted the analysis to subareas assumed to have a 100% detection probability (e.g., Furey et al. 2013). In reality, the tag detection probabilities are largely defined by the position of the tag within the array of receiver's overlapping detection ranges (Farmer et al. 2013). In this study, we tagged and tracked several species of coral reef fishes within an acoustic receiver array in the MPAs of Dry Tortugas, Florida, USA, and developed a novel statistical method that incorporates detection probability as a function of tag distance to evaluate "preferential habitat use" within home ranges.

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Methods

Study Area.—The Florida shallow coral reef ecosystem extends about 400 km southwest from Miami to the Dry Tortugas, and supports lucrative tourism and fishing industries (Ault et al. 2005a; 2013). The isolated reefs of the Dry Tortugas are located upstream of the Florida Keys, where the Florida Current merges into the Gulf Stream (**Fig. 1**). The Dry Tortugas support the Florida Keys reef fishery with recruits from regional spawning and density-dependent emigration of adult biomass (Schmidt et al. 1999; Ault et al. 2006; Bryan et al. 2015). Because of growing stress on regional fisheries and coral reefs (Ault et al. 1998; 2005b; 2009; Hallac & Hunt 2007), in January 2007, the National Park Service implemented a no-take marine reserve (NTMR), or Research Natural Area (RNA), covering 158 km^2 of prime shallow-water reef habitat in the western half of Dry Tortugas National Park (DTNP). The eastern half of DTNP (101 km^2) has been closed to commercial fishing, recreational spearfishing, and lobstering since the 1960s; however, it is open to recreational hook-and-line fishing. The RNA was designed as a shallow-water complement to the Tortugas North and South Ecological Reserves (TNER and TSER), established in 2001 by the National Oceanographic 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 United States (**Fig. 1**).

Depths and benthic habitats were determined using multibeam side-scan sonar, ground-truthing, LIDAR, and aerial photography. Following methods described by Franklin et al. (2003), habitats were categorized within 100 m by 100 m grids as seagrass (SGRS), or contiguous (CONT), isolated (ISOL), spur-and-groove (SPGR; coralline spurs separated by sand grooves), or reef rubble (RUBB) structures with either high (HR; >2 m), medium (MR; 0.5-2 m), or low-relief (LR; <0.5 m) profile based on soundings and diver observations (**Fig. 2**; **Table 2**).

Acoustic Array.— From March 2006 to January 2007, 25 VEMCO VR2 (VEMCO Ltd., Nova Scotia, Canada; www.vemco.com) hydrophone-receivers were deployed in a 600-1000 m grid array in the Dry Tortugas (**Fig. 3**). From January 2007 to April 2008, the array was expanded and reconfigured to provide better coverage of a range of coral habitats (**Fig. 3**). Receivers provided coverage of the northwestern boundary of DTNP-RNA as well as some areas of TNER and FKNMS. Each omnidirectional VR2 hydrophone functions as a submersed passive listening station, detecting and archiving ID codes, dates and times for acoustically tagged fish that pass within range. Receivers were deployed between 4–34 m depth and mounted 5 m above the seafloor to reduce exposure to benthic noise sources, avoid signal blockage by habitat features, and to maintain a superior listening angle for tagged coral reef fish. Probability of detection within the arrays averaged 75% (Farmer et al. 2013).

Telemetry Tagging and Tracking.— Red grouper (*Epinephelus morio*), black grouper (*Mycteroperca bonaci*), yellowtail snapper (*Ocyurus chrysurus*), mutton snapper (*Lutjanus*

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analis), tiger shark (*Galeocerdo cuvier*), and horse-eye jack (*Caranx latus*) were captured using hook-and-line gear and internally tagged as described in Farmer & Ault (2011) and Farmer (2010). All implanted VEMCO V-16 (www.vemco.com) acoustic tags were 58 mm long and 16 mm diameter and weighed 24 g. Tags were configured with randomized transmission times (**Table 1**), reducing the likelihood of signal collisions with other tagged individuals within the array (Pincock & Voegeli 2002). These relatively short delay times increased the probability of tag transmissions when in range of specific receivers (Løkkeberg et al. 2002). Vicryl undyed 27” Chromic gut line with 2/0 curved needles were used to close incisions with 3-5 individual stitches.

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Prior to analysis, VR2 receiver data were corrected for temporal drift, adjusted for daylight savings time, filtered for spurious detections, categorized by ‘diel period’ (‘Dawn’: within 1 hr of sunrise, ‘Dusk’: within 1 hr of sunset, ‘Day’, or ‘Night’), and batched into short-term movement centers over 5 min intervals. These methods provided a mean positioning resolution of 132 m for stationary tags and 237 m for moving tags (Farmer et al. 2013). Additionally, all detections that occurred after the expected final transmission date for the tag were excluded from analysis to avoid spurious results associated with transmissions from a depleted tag battery.

Habitat Utilization Analysis.—Calibration work by Farmer et al. (2013) indicated that the probability of detecting a tag within a given habitat is primarily dependent upon the distance of the habitat to the passive receiver. Tidal phase played a minor but significant role in detection probability, but inclusion of wind speed, solar phase, receiver depth, and habitat rugosity did not significantly improve model fits (Farmer et al. 2013). We determined the probability of detecting a tag within each 100 m × 100 m habitat cell by computing the distance of each receiver to the midpoint of the cell and solving for the probability (p) of detection at distance (d) from Farmer et al. (2013):

$$p = \frac{e^{7.442-0.0261d+1.47\times10^{-5}d^{2}}}{1+e^{7.442-0.0261d+1.47\times10^{-5}d^{2}}}$$

The number of detections of each individual fish in each habitat cell were computed using the *poly.counts* function in the R v.3.2.3's *spatialEco* package (R Core Team 2013). To ensure that quality position fixes were evaluated, only fish with >150 detections and 5-min activity centers at five or more distinct locations were considered for analysis. Additionally, because edge effects can distort interpretation of observed detection patterns (Farmer & Ault 2014), habitat preferences were only evaluated for fish tagged near the center of the arrays (see **Table 3** and **Fig. 3**). Habitat preferences were evaluated separately for day and night.

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To evaluate preferential habitat use, a generalized additive model for location, scale, and shape (GAMLSS; Rigby & Stasinopoulos 2001; 2005; Akantziliotou et al. 2002) was developed using the R v.3.2.3's *gamlss* package. The GAMLSS function allows modeling of the mean ("location") and other parameters of the distribution of the response variable as linear parametric or additive non-parametric functions of explanatory variables and random effects. Models are fit with maximum (penalized) likelihood functions. A GAMLSS assumes independent observations y_i for $i = 1, 2, \ldots, n$ with probability density function $f(y_i\,|\theta_i)$ conditional on θ_i where $\theta_i = (\theta_{i1}, \theta_{i2}, \ldots, \theta_{ip})$ is a vector of p parameters. We implemented a GAMLSS with 3 distribution parameters, denoted as μ_i, σ_i, and v_i. The first two parameters, μ_i and σ_i, are characterized as location and scale parameters; the final parameter, v_i, is characterized as a shape parameter. Let $y^{T} = (y_1, y_2, \ldots, y_n)$ be the *n* length vector of the response variable. Also for k = 1, 2, 3, 4, let $g_k(.)$ be known monotonic link functions relating the k^{th} parameter θ_k to explanatory variables by semi-parametric additive models given by

$$g_1(\boldsymbol{\mu})J{=}J\boldsymbol{\eta}_{1J}{=}J\mathbf{X}_1\boldsymbol{\beta}_{1J}+\sum_{j=1J}^{1J}\mathbf{Z}_{j1}\boldsymbol{\gamma}_{j1J}$$

$$g\ \ (\boldsymbol{\sigma})J{=}J\boldsymbol{\eta}2=J\mathbf{X}\ \ \boldsymbol{\beta}2+\sum_{j=1J}^{2J}\mathbf{Z}_j\ \ \boldsymbol{\gamma}_{j2}$$

$$g_3(\boldsymbol{\nu})J{=}J\boldsymbol{\eta}_{3J}{=}J\mathbf{X}_3\boldsymbol{\beta}_{3J}+\sum_{j=1J}^{3J}\mathbf{Z}_{j3}\boldsymbol{\gamma}_{j3J}$$

where μ, σ, ν and η_k and γ_{jk}, for $j = 1, 2, \ldots, J_k$ and $k = 1, 2, 3$, are vectors of length n. Also $\boldsymbol{X}_k$, for $k = 1, 2, 3$, are fixed design matrices while $\boldsymbol{\beta}_k$ are the parameters vectors. The random effects parameters $\boldsymbol{\gamma}_{jk}$ have independent (prior) normal distributions.

To avoid biasing analytical results towards the fish with the highest number of detections, the percentage of each individual's detections within each habitat grid cell was used as the regression response variable μ. Individual fish were modeled as random effects γ_{jk}. Depth and habitat type within each cell were used as explanatory variables for g_1 and g_2. To account for the unequal probabilities of detecting a fish at different sites within the passive arrays, the sum of the probabilities of detection across all receivers (Σ[P(Detection)]) was used as an explanatory variable for g_1, g_2, and g_3. As this weighting term was the sum of probabilities across receivers, its value could exceed one in areas of high overlap of detection ranges.

Because the response variable was a percentage and the vast majority of habitat cells had no detections for each individual, the GAMLSS model was fit with a zero-inflated beta distribution. Estimation of additive terms was accomplished using the RS (Rigby & Stasinopoulos 1996) backfitting algorithm. A total of 24 reasonable GAMLSS models were explored for each species and diel period (**Table S-1**), with the best GAMLSS *mu*, *sigma*, and *nu* formula expressions selected through AICc (Akaike 1974; Burnham & Anderson 2002). Selected models satisfied

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model assumptions as evidenced by residual plots and normalized randomized quantile residual plots. Significant preferential habitat use was evaluated by visually inspecting the mean and 95% confidence intervals of term plots for the habitat class additive term.

Results

Data for acoustically tagged fish are provided in **Table 3**. A total of 45 red grouper were tagged, producing over two million detections with a mean of 46,731 detections per fish over a mean tracking duration of 111 days. Three black grouper were tagged; one was never detected. The two black grouper that were tracked averaged 44,055 detections over 135 tracking days. Five yellowtail snapper were tagged, with a mean of 17,755 detections per fish over a mean tracking duration of 83 days. Four mutton snapper were tagged but two were never detected; one was tracked for 168 days and produced 21,805 total detections. One tiger shark was tracked for 47 days and was detected 4,978 times. One horse-eye jack was tracked for 218 days and was detected 21,856 times.

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Habitats were distributed non-uniformly within the detection range of the acoustic array. From March 2006 through January 2007, the detection range of the array contained mostly contiguous low relief reef habitats and sand. Three receivers were located in sand habitats off the reef shelf (see **Fig. 3**). These three receivers were the only receivers never to register reef fish detections. From January 2007 through April 2008, the array contained more contiguous low relief reef habitats.

Total percent use of habitats across individuals, without controlling for detection probabilities, is provided in **Table 4**. Of the 45 tagged red grouper, 24 met criteria for the habitat utilization analysis. During the day and night, red grouper were detected primarily in contiguous low relief and sand habitats. Red grouper habitat use differed substantially amongst individuals.

Of the three tagged black grouper, two met criteria for the habitat utilization analysis. They were detected primarily in sand habitats regardless of time of day. Of the five tagged yellowtail snapper, two met criteria for the habitat utilization analysis. They were detected primarily in contiguous low relief habitats regardless of time of day; detection patterns were relatively consistent across individuals. Of the four tagged mutton snapper, one met criteria for the habitat utilization analysis. It was detected almost exclusively (>99%) in contiguous low relief habitats. The tagged tiger shark and horse-eye jack met criteria for inclusion in the analysis by virtue of their high mobility and substantial use of habitats within the core of the acoustic array. The tagged tiger shark was detected primarily in contiguous low relief and sand habitats regardless of time of day. By day, the tagged horse-eye jack was detected primarily in isolated medium relief, contiguous low relief, and sand habitats. At night, it was detected primarily in sand and isolated medium relief habitats.

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The percent detections described in the previous paragraph are, in part, a byproduct of the configuration of the acoustic array relative to habitats. Probability of detection in a passive acoustic array is non-uniform (**Fig. 4**). Tags in locations close to individual receivers or within the detection range of multiple receivers have the highest probability of detection (**Fig. 4**). Receivers were configured to have overlapping detection ranges at around the 50% probability of detection (**Fig. 3**). Detection ranges overlapped in both array configurations, with the nearest receiver 787 m away, on average, in Mar 2006-Jan 2007, and 832 m away, on average, in Jan 2007-Apr 2008. Inclusion of a weighted term for the cumulative probability of detection improved GAMLSS habitat utilization model fits for all species (**Table 5**).

After controlling for probability of detection and depth (**Table 5**, **Figs. S1-S12**), some clear habitat preferences were evident amongst the species tested (**Figs. 5-6**). In many cases, these preferences were different from what might be inferred from the raw percentage of detections in each habitat, and some differed from habitat preferences reported previously in the literature. By day, red grouper preferentially utilized shallow (<25 m) contiguous and sand habitats over isolated and spur-and-groove high relief habitats (**Fig. 5**). By night, red grouper preferentially utilized contiguous high relief and isolated high relief habitats (**Fig. 6**). By day, black grouper preferentially utilized contiguous medium relief habitats (**Fig. 5**). Black grouper appeared to preferentially use sand habitats at night; however, no black grouper were detected at more than two locations at night (**Fig. 6**). Yellowtail snapper preferentially utilized deeper (>17 m) contiguous low relief habitats (**Figs. 5-6**). Mutton snapper preferentially utilized contiguous low relief habitats (**Figs. 5-6**). The tiger shark preferentially utilized shallow (<17 m depth) contiguous high-relief habitats, and underutilized medium relief habitats (**Figs. 5-6**). Although the tagged horse-eye jack was tagged near an edge of the acoustic array, it appeared to be highly mobile and not subject to edge effects. By day, it preferentially utilized isolated medium relief and unclassified habitats on the edges of the array (**Fig. 5**). At night, it preferentially utilized isolated medium relief and sand habitats and underutilized low relief habitats (**Fig. 6**).

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Discussion

In this study, we evaluated preferential habitat use within the home ranges of a variety of reef fish. In Farmer & Ault (2011), following methods presented in Winter & Ross (1981) and Lowe et al. (2003), a habitat selection "suitability" index (HSI) 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 m by 200 m cells containing that identified habitat type within the fish's MCP home range. However, like most previous studies on reef fish habitat use inferred from passive acoustic monitoring, Farmer & Ault (2011) failed to account for differences in the probability of detection amongst habitats within a passive acoustic array can generate misleading conclusions about habitat preferences. By doubling the resolution of our habitat categorizations and accounting for the non-uniform probability of detection across habitats we have provided more robust estimates of “preferential habitat use” for a broad suite of reef fish species in and around a network of no-take MPAs. Due to limitations on sample size, our results are most robust for red grouper. Other reef fish species were more difficult to obtain at sizes large enough to allow internal tagging.

Red grouper

Previous studies of red grouper habitat use have found they are strongly associated with karst topography, especially limestone solution holes formed by past freshwater incursion (Coleman et al. 1996). Adult red grouper expose rocky habitat at these “grouper holes” by excavating with their mouths and fanning with their fins to clear away surficial sediment (Coleman et al. 2010). This “ecosystem engineering” provides habitat for themselves as well as other reef-dwelling organisms. Coleman et al. (2010) also found that red grouper preferentially utilized sites with the greatest amount of architectural structure (e.g., greater spatial extent, number of entrances, and the presence of large encrusting corals).

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Red groupers and black groupers are opportunistic apex predators in reef community food webs (May et al. 1979). Red grouper are strongly associated with the bottom, and their diets may include many types of invertebrates including xanthid and portunid crabs, spiny lobster, snapping shrimp, stomatopods, octopus, and squid and penaeid shrimp, especially the pink shrimp (*Penaeus duorarum*), as well as lutjanid and sparid fishes (Gudger 1929; Longley & Hildebrand 1941; Moe 1969; Costello & Allen 1970). Our passive acoustic monitoring found diel differences in red grouper habitat preferences. By day, red grouper preferentially used contiguous reef and adjacent sand habitats. By night, red grouper preferred high-relief and contiguous reef habitats. High quality habitats (e.g., containing abundant food and shelter) 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 are believed to be territorial (Moe 1969), and the authors have witnessed repeated conspecific interactions involving buccal flaring, dynamic color changes from red to a pale almost white color pattern with pronounced striation, and booming vocalizations. These interactions, which appear to take place on territorial edges as indicated by cruising/patrolling patterns by individuals, are typically resolved quickly with the smaller individual moving away from the territorial boundary. Such territorial behavior may force smaller individuals into less desirable habitats. Red grouper home range overlap was higher in high profile habitats relative to low profile habitats, and higher in isolated habitats than in contiguous habitats (Farmer & Ault 2011). High profile coral reef habitats provide higher prey densities for red grouper (Ault et al. 2007), and likely contain more locations for shelter. Contiguous habitats may provide a greater density of shelters and foraging areas than isolated sites. Visual observations may be needed to determine the reasons for diel shifts in habitat preference for red grouper.

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Black grouper

Black grouper are also opportunistic feeders, although they are more piscivorous than red grouper and are less associated with the bottom (Randall 1967). Farmer & Ault (2011) previously reported black grouper utilized isolated and contiguous low-relief habitats; however, by doubling the resolution of our habitat classifications and controlling for the probability of detection, we found that black grouper preferentially utilized contiguous medium relief habitats. Our sample size was limited and makes it difficult to generalize this finding; however, it is supported by hundreds of hours of underwater observations in the Dry Tortugas with black grouper most commonly observed at reef/sand interfaces, typically in areas with ledges or abundant gorgonian cover (N.A. Farmer, pers. obs.). Nocturnal sheltering in or near structure that obstructed tag signal transmission (Farmer et al. 2013: Figure 2) may have been responsible for the limited black grouper movements observed at night, as no movements were detected at receivers near the edge of array that may have indicated movements beyond detection range.

Yellowtail snapper

Yellowtail snapper are semi-pelagic wanderers over the reef habitat (Moe 1972). Muller et al. (2003) reported that adult yellowtail snapper typically inhabit sandy areas near offshore reefs. In the Dry Tortugas, yellowtail snapper preferentially utilized contiguous low relief reef structures. The reasons for this habitat preference are unclear; however, it may provide them with access to fish, crustaceans, and mollusks (Randall 1967; Piedra 1969) as well as holoplankton such as larval stages, pelagic mollusks and polychaetes, and gelatinous invertebrates (Schroeder 1980; Parrish 1987).

Mutton snapper

Mutton snapper are known to associate with a wide variety of habitats, including reef, sand, seagrass, and coral rubble (Randall 1967). They are relatively mobile reef predators (Farmer & Ault 2011), cruising over many habitats and foraging actively throughout the day (Mueller et al. 2005). In this study, a tagged mutton snapper preferentially utilized contiguous low relief habitats and underutilized contiguous high relief habitats. Our sample size was limited, making it difficult to generalize this finding; however, it is supported by hundreds of hours of underwater observations of mutton snapper cruising along low relief reef and sand interfaces (N.A. Farmer, pers. obs.).

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Tiger shark

The tiger shark is among the largest (maximum size >800 kg, up to 5.5 m total length, TL) apex predatory fish found throughout tropical seas (Springer 1938). Hawaiian juvenile tiger sharks appear to forage over very large areas (>100 km^2) to obtain sufficient resources (Meyer et al. 2009); visits to specific receiver sites were typically brief (mean duration 3.3 min) and interspersed with absences of weeks, months, or years. By contrast, the tagged tiger shark in this study demonstrated high short-term (47 d) residency in an approximately 25 km^2 area. Its detection frequency was similar to that of reef fish tracked in the same location, although it was more mobile and less strongly affiliated with a home range center than groupers and snappers (Farmer & Ault 2011; Farmer & Ault 2014). Receiver detection patterns were consistent with previous findings that tiger sharks use short-term home ranges containing important foraging grounds, and their movements in these shallow water habitats (< 300 m) are characterized by frequent loops and turns (Holland et al. 1999; Heithaus et al. 2007). The tiger shark was detected most frequently during crepuscular hours, suggesting increased movement during periods of reduced light.

In this study, the tiger shark preferentially utilized shallow (<17 m) contiguous high-relief habitats and underutilized medium relief habitats. Tiger sharks undergo an ontogenetic shift in diet, with small individuals primarily feeding on fish and large individuals consuming fish and a variety of large-bodied species (Lowe et al. 1996; Heithaus et al. 2001). High-relief habitats in the Dry Tortugas contain some of the highest fish densities on the Florida reef tract (Ault et al. 2007). Increased sampling is needed to allow generalization of these findings and to determine if the Dry Tortugas MPA network contains important intergenerational nursery habitats or foraging grounds for tiger sharks (Castro 1993).

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Horse-eye jack

The horse-eye jack is a poorly studied pelagic fish that is commonly found schooling in the subtropical Atlantic Ocean near reefs and offshore oil rigs (Claro 1994; Lieske & Myers 1994). Previously tagging studies have been unsuccessful and inferred horse-eye jacks to be highly mobile with low site fidelity (Randall 1962; Chapman & Kramer 2000). Adults feed on fishes, shrimps, and other invertebrates (Berry & Smith-Vaniz 1978). Our tagged horse-eye jack was broadly ranging, moving over sand between isolated medium relief reef habitats. Our sample size was limited, making it difficult to generalize this finding; however, it is supported by hundreds of hours of underwater observations of horse-eye jacks moving across sand and schooling above isolated reef pinnacles (N.A. Farmer, pers. obs.).

Management Implications

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Knowledge of the distribution of fish abundance to habitats, or what are "preferential or essential habitats" for fishes, is critical to the efficient and cost-effective design of fishery-independent surveys, evaluation of spatially-explicit management performance, and MPA design (Meester et al. 2004; Farmer & Ault 2011). Accurate and precise fishery-independent surveys designed to assess multispecies reef fish stocks often strategically employ habitat as an environmental covariate in their stratified sampling designs. An improved understanding of fish-habitat relationships will allow cost-effective refinements of survey sample allocations (Smith et al. 2011; Bryan et al. 2016). Efficient spatial management strategies require protected areas to contain critical habitats and to have boundaries aligned with natural barriers to movement, reducing the spillover of spawning stock biomass into fishable areas. Sufficiently large MPAs that contain critical habitats can provide substantial protection, even to highly mobile predators (White et al. 2017). To maximize fisheries benefits, no-take MPAs should contain important habitats that allow organisms to maximize growth and reduce risk of predation (MacArthur & Pianka 1966).

Summary

Obtaining robust estimates of habitat utilization from a passive acoustic array is challenging. The array must be large enough to contain the home range of the tagged fish (Farmer & Ault 2011), but with receiver spacing sufficient to provide position fixes within the resolution of the habitat categorizations (Farmer et al. 2013). Centers of activity should be determined with sufficient temporal resolution to provide meaningful categorizations of habitat use, and should consider the non-linear spatial relationship between detection probability and distance of the acoustic tag to the receiver (Farmer et al. 2013). Similarly, the analysis of habitat utilization should control for edge effects (Farmer & Ault 2014) and account for the non-uniform probability of detection at different habitats within the acoustic array. Most analyses of habitat use by reef fish have ignored these factors, and have also aggregated across individuals and time periods. By accounting for all of these potentially confounding factors in a nested, zero-inflated beta regression analysis, we have provided robust estimates of diel habitat use for red grouper and additional information for black grouper, yellowtail snapper, mutton snapper, tiger shark, and horse-eye jack. Evaluations of habitat use for these species could be further improved through: (1) increased sample size, (2) greater overlap among receiver detection ranges, (3) use of co-located tags to improve positioning resolution, (4) signal arrival time computations to triangulate position (e.g., VEMCO Positioning System), (5) higher resolution habitat identification including biotic cover (e.g., gorgonians and sea fans), and (6) better accounting for environmental (e.g., wave state, tidal phase) factors that may also influence movement patterns.

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There are several emergent patterns from our analysis of reef fish preferential habitat use that could be used to guide sample allocation in fishery-independent surveys as well as the design and evaluation of spatial management strategies such as no-take MPAs. Not surprisingly, large sand channels appear to function as natural barriers to movement for many reef fish. Fishery-independent surveys designed for reef fish should allocate the bulk of sampling to the habitats with the highest variability, with few samples allocated to sand habitats (Smith et al. 2011). Similarly, aligning MPA boundaries to land and large sand channels is recommended to naturally reduce reef fish spillover into fishable areas. The tagged red and black groupers studied demonstrated preferences for high relief habitats. By contrast, the tagged mutton and yellowtail snappers studied demonstrated preferences for low-relief contiguous reef habitats. Prey biomass (Ault et al. 2007) and available shelter (N.A. Farmer, pers. obs.) are often highest in high-relief habitats, and they may maximize opportunities for growth for large-bodied species. Our findings suggest that high-relief areas (contiguous and isolated) should receive the highest sample allocation in fishery-independent surveys and should be well-represented within no-take MPAs designed to conserve grouper spawning stock biomass; however, low-relief contiguous reef habitats play a critical role in maintaining snapper biomass and movement pathways for a variety of species. These findings reinforce the importance of protecting a mosaic of reef habitats across a broad spatial domain (Parrish 1989; Friedlander et al. 2006).

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Table . Specifications for 69 kHz VEMCO V16a coustic tags utilized in this study. Note 3H tags have higher transmission strength but shorter battery life**.**

Fish IDs	**Year**	**n**	**Type**	**Power output (µPa @ m)**	**Random delay (s)**
862–872	2006	33	3H	158	20–69
170–194	2006	23	3H	158	30–79
32–59	2007	20	3H	158	60–180
873–884	2007	12	4H	153	20–69

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Table 2. Characteristics of habitat categorizations used in this study, adapted from Franklin et al. (2003).

Category	**Type**	**Habitat Type**	**Relief Code**	**Characteristics**
Unclassified	UNK	Unknown	n/a	Unclassified habitat
Sand	SAND	Sand	n/a	Predominantly sand; no hardbottom present.
Seagrass	SGRS	Seagrass	n/a	Predominantly seagrass; no hardbottom present.
Contiguous	CONT	Low-relief hard-bottom	LR	Contiguous hard-bottom substrate Low structural complexity and relief Usually dominated by gorgonians
		Medium-profile reef	MR	Contiguous reef substrate Moderate vertical relief and complexity
		Reef Terrace	HR	High-relief (>2 m), contiguous reef habitat Abundant large mushroom and platy corals Primarily located on western sides of banks
Spur and Groove	SPGR	Low-relief spur and groove	LR	Low-profile coralline spurs separated by sand grooves Broad spurs up to 5 m wide with low vertical relief
		Rocky outcrop	MR	Hard-bottom aggregations bounded by sand Moderate vertical relief (0.5 to 2.0 m)
		High-relief spur and groove	HR	High-profile coralline spurs separated by sand grooves High vertical relief (>2 m) and complexity Diverse assemblage of reef benthos
Isolated	ISOL	Patchy hard-bottom in sand	LR	Sand plains with patches of hard-bottom Low vertical relief (<0.5 m) and complexity
		Patch reef	MR	Aggregate or clusters of dome-shaped reefs Interspersed with sand Moderate vertical relief and substrate complexity
		Pinnacle reef	HR	High-complexity patches rising to 15 m depth

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Table 3. Data for fish fitted with acoustic transmitters. 'Tag': type of VEMCO tag (see Table 1); 'Code': unique identification code; 'Species': fish species (RG: Red Grouper, BG: Black Grouper, MS: Mutton Snapper, YTS: Yellowtail Snapper, HEJ: Horse-eye Jack, TS: Tiger Shark); 'TL': total length in cm; 'W': weight in kg; 'Tagged': date of capture; 'Last Detect': date of final detection; 'Days': days between capture and final detection; 'Tag Life': anticipated battery life of tag; 'Detects': total recorded detections; 'Rec': number of receivers registering detections; 'Edge': likelihood of edge effects based on tagging location relative to edge of array. Note dates follow mm/dd/yy format.

Tag	Code	Species	TL	W	Tagged	Last Detect	Days	Tag Life	Detects	Rec.	Edge
3H	36	RG	64	3.6	1/7/07	1/25/07	18	130	2,051	15	
3H	37	RG	47	1.4	1/7/07	7/5/07	179	130	64,672	3	
3H	41	RG	47	1.1	1/7/07	7/5/07	179	130	75,732	3	
3H	42	RG	48	1.8	1/7/07	7/5/07	179	130	21,823	4	
3H	47	RG	48	1.8	1/7/07	1/18/07	11	130	1,534	17	
3H	51	RG	66	5.4	2/27/07	8/3/07	157	130	12,329	6	
3H	170	RG	61	9.0	3/7/06	6/8/06	93	62	708	2	
3H	171	RG	60	6.5	3/7/06	6/13/06	98	62	2,359	4	
3H	172	RG	49	4.0	3/7/06	3/10/06	3	62	471	8	
3H	173	RG	49	4.0	3/7/06	6/7/06	92	62	613	5	
3H	175	RG	53	6.0	3/7/06	6/11/06	96	62	5,190	2	Y
3H	176	RG	55	6.5	3/7/06	6/8/06	93	62	4,512	4	
3H	177	RG	50	4.5	3/7/06	6/4/06	89	62	373	2	
3H	178	RG	65	10.0	3/7/06	6/5/06	90	62	2,466	2	
3H	179	RG	57	6.0	3/27/06	4/19/06	23	62	229	14	
3H	180	RG	55	6.0	3/27/06	5/6/06	40	62	382	5	Y
3H	181	RG	49	4.0	3/27/06	4/9/06	13	62	880	9	Y
3H	183	RG	48	4.5	3/28/06	7/4/06	98	62	8,491	3	Y
3H	186	RG	51	6.0	3/27/06	6/26/06	91	62	12,077	8	
3H	187	RG	50	4.5	3/27/06	6/27/06	92	62	4,806	8	
3H	189	RG	59	8.0	3/7/06	6/9/06	94	62	28,035	1	Y
3H	190	RG	62	9.0	3/6/06	6/15/06	101	62	55,092	2	Y
3H	191	RG	51	4.0	3/6/06	6/7/06	93	62	36,324	4	Y
3H	194	RG	54	6.5	3/6/06	6/8/06	94	62	12,928	4	Y
3H	863	RG	51	6.5	3/5/06	6/8/06	95	56	6,728	3	Y
3H	864	RG	55	6.0	3/6/06	6/6/06	92	56	44,890	2	Y
3H	867	RG	55	5.5	3/5/06	6/2/06	89	56	42,058	4	Y
3H	868	RG	49	4.5	3/5/06	6/1/06	88	56	24,533	2	Y
3H	869	RG	60	-	3/6/06	6/1/06	87	56	21,703	2	Y
3H	870	RG	45	2.5	3/5/06	3/30/06	25	56	2,530	7	
3H	871	RG	57	8.0	3/5/06	5/20/06	76	56	402	2	Y
3H	872	RG	53	4.5	3/5/06	5/23/06	79	56	70,316	4	Y
4H	873	RG	48	1.8	1/4/07	10/11/07	280	570	199,933	2	
4H	874	RG	60	2.9	1/5/07	10/10/07	278	570	313,237	5	
4H	875	RG	52	2.0	1/4/07	10/11/07	280	570	205,442	5	
4H	877	RG	57	2.7	1/4/07	10/11/07	280	570	124,104	4	
4H	878	RG	48	1.8	1/4/07	2/17/07	44	570	21,144	9	
4H	880	RG	49	1.8	1/4/07	9/30/07	269	570	35,439	3	
4H	881	RG	50	1.8	1/4/07	10/11/07	280	570	261,025	7	
4H	884	RG	53	2.0	1/4/07	10/11/07	280	570	272,798	5	
3H	184*	RG	55	6.5	3/27/06	5/9/06	43	62	4,915	7	
3H	185*	RG	55	5.0	3/27/06	5/9/06	43	62	8,895	7	
3H	862*	RG	54	4.5	3/6/06	5/31/06	86	56	73,704	3	Y
3H	865*	RG	56	8.0	3/5/06	4/7/06	33	56	14,616	6	

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3H	866*	RG	53	5.0	3/6/06	5/11/06	66	56	426	2	Y
3H	55	YTS	55	1.8	4/24/07	9/24/07	153	130	10,566	6	Y
3H	57	YTS	52	1.4	7/11/07	10/11/07	92	130	31,804	7	
3H	58	YTS	48	0.9	4/24/07	7/1/07	68	130	2,238	3	Y
3H	59	YTS	52	0.9	4/24/07	7/10/07	77	130	4,791	5	
3H	182	YTS	52	2.5	3/28/06	4/23/06	26	62	39,374	9	Y
3H	40	MS	53	4.5	4/25/07	NA	0	130	0	0	
3H	50	MS	43	2.5	10/9/07	10/13/07	4	130	183	6	
3H	52	MS	49	2.0	10/9/07	NA	0	130	0	0	
3H	53	MS	70	5.4	4/25/07	10/10/07	168	130	21,805	18	
3H	35	BG	57	4.5	10/9/07	NA	0	130	0	0	
3H	43	BG	75	6.6	1/7/07	7/5/07	179	130	72,644	6	
3H	174	BG	50	5.5	3/7/06	6/6/06	91	62	11,466	4	
3H	54	HEJ	71	3.6	4/24/07	11/28/07	218	130	21,856	16	Y
3H	48	TS	274	X	2/28/07	4/16/07	47	130	4,978	21	

----Denotes fish tracked by 2006 (above) and 2007 receiver configurations (below). (*) denotes recaptured. *TL*= Total Length (cm), *W*= Weight (kg), *Rec.*= Receivers detecting fish.

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Table 4. Mean percentage of total detections by habitat type, by species. Habitat composition within detection range of receivers provided for reference. Habitat grids were categorized as unknown (UNK), sand, seagrass (SG), contiguous reef (CONT), isolated reef (ISOL), spur-and-groove reef (SPGR; coralline spurs separated by sand grooves), or reef rubble (RUBB) with high (HR; >2 m), medium (MR; 0.5-2 m), or low-profile relief (LR; <0.5 m) following Franklin et al. (2003).

Mean Percent of Total Detections by Habitat Types (%)

Species	**Period**	**CONT_ LR**	**CONT_ MR**	**CONT_ HR**	**ISOL_ LR**	**ISOL_ MR**	**ISOL_ HR**	**SPGR_ LR**	**SPGR_ HR**	**RUBB_ LR**	**SGRS**	**SAND**	**UNK**
Red grouper	Day	68	1	1	0	0	0	9	0	0	0	21	0
	Night	52	2	1	0	0	0	9	0	0	0	35	0
Black grouper[1]	Day	1	0	0	0	0	0	0	0	0	0	99	0
	Night	0	0	0	0	0	0	0	0	0	0	100	0
Yellowtail snapper	Day	93	0	1	0	3	1	0	0	0	0	2	0
	Night	96	0	1	0	1	1	0	0	0	0	1	0
Mutton snapper	Day	99	0	0	0	0	0	0	0	0	0	1	0
	Night	100	0	0	0	0	0	0	0	0	0	0	0
Tiger shark	Day	63	1	2	9	0	0	0	0	0	0	21	4
	Night	59	1	4	11	1	1	0	0	0	0	21	1
Horse-eye jack[2]	Day	29	0	0	0	44	0	0	0	0	0	22	5
	Night	11	0	0	0	40	0	0	0	0	0	44	4
Detectable Range (Mar 2006-Jan 2007)		35	30	4	4	5	6	3	3	0	1	3	23
Detectable Range (Jan 2007-Apr 2008)		53	47	5	4	4	4	2	2	0	0	2	18

[1] No black grouper were detected at >2 locations at night

[2] No horse-eye jack were tracked without potential edge effects

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Table 5. AICc-selected GAMLSS model fits explaining non-uniform diel habitat utilization preferences. Note: 'pDetectSum' denotes the cumulative probability of detection at a particular grid-cell summed across all receivers; 'cs' denotes a cubic spline, and 'p' denotes a penalized spline.

		GAMLSS Model Parameters		
Species	**Diel Period**	**μ**	**σ**	**ν**
Red grouper	Day	ps(Depth) HabitatType pDetectSum	HabitatType pDetectSum	HabitatType pDetectSum
	Night	Depth HabitatType pDetectSum	HabitatType pDetectSum	HabitatType pDetectSum
Black grouper	Day	cs(Depth, df = 5) HabitatType pDetectSum	Depth HabitatType pDetectSum	pDetectSum
	Night	Depth HabitatType pDetectSum	pDetectSum	pDetectSum
Yellowtail snapper	Day	cs(Depth, df = 3) HabitatType pDetectSum	HabitatType pDetectSum	HabitatType pDetectSum
	Night	Depth HabitatType pDetectSum	Depth HabitatType pDetectSum	pDetectSum
Mutton snapper	Day	Depth HabitatType pDetectSum	Depth HabitatType pDetectSum	pDetectSum
	Night	Depth HabitatType pDetectSum	HabitatType pDetectSum	HabitatType pDetectSum
Tiger shark	Day	Depth HabitatType pDetectSum	Depth HabitatType pDetectSum	pDetectSum
	Night	Depth HabitatType pDetectSum	Depth HabitatType pDetectSum	pDetectSum
Horse-eye Jack	Day	cs(Depth, df = 5) HabitatType pDetectSum	HabitatType pDetectSum	HabitatType pDetectSum
	Night	cs(Depth, df = 5) HabitatType pDetectSum	HabitatType pDetectSum	HabitatType pDetectSum

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FIGURE CAPTIONS

Figure 1. Location map of the Dry Tortugas, Florida (star), showing fishable and management zones including fishable waters in Dry Tortugas National Park (DTNP) and Florida Keys National Marine Sanctuary (FKNMS); and, no-take Research Natural Area (RNA) Tortugas North and South Ecological Reserves (TNER and TSER). Passive acoustic receiver deployment locations for March 2006 to January 2007 (open crosses) and January 2007 to April 2008 (black crosses) are shown relative to bathymetry. Inset also shows location of Dry Tortugas, Florida, relative to regional oceanographic currents measured by satellite drifters in the Gulf of Mexico (gray track lines). Drifter data from Atlantic Oceanographic and Meteorological Laboratory Global Drifter Program. Bathymetric data from NOAA National Ocean Service and United States Geological Survey Light Detection and Ranging (LIDAR) surveys.

Figure 2. Habitats categorized by vertical relief and degree of patchiness following Franklin et al. (2003) as seagrass (SGRS), contiguous reef (CONT), isolated reef (ISOL), spur-and-groove reef (SPGR; coralline spurs separated by sand grooves), or reef rubble (RUBB) with high (HR; >2 m), medium (MR; 0.5-2 m), or low-profile relief (LR; <0.5 m).

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Figure 3. Passive acoustic receiver deployment locations for March 2006 to January 2007 and from January 2007 to April 2008 with 50% probability of detection ranges relative to benthic habitats. Habitats categorized at 100 m resolution as unknown (white), sand, seagrass (SGRS), contiguous reef (CONT), isolated reef (ISOL), spur-and-groove reef (SPGR; coralline spurs separated by sand grooves), or reef rubble (RUBB) with high (HR; >2 m), medium (MR; 0.5-2 m), or low-profile relief (LR; <0.5 m) following Franklin et al. (2003). Labels correspond to tag codes for tagged red grouper (red), black grouper (gray), yellowtail snapper (yellow), mutton snapper (pink), horse-eye jack (blue), and tiger shark (light blue).

Figure 4. Cumulative receiver detection probabilities relative to March 2006-January 2007 and January 2007-April 2008 receiver deployments. Note that not all locations in a passive array have an equal probability of detection, and different array spacing can result in different cumulative probabilities.

Figure 5. Species habitat utilization during the day, indicated by GAMLSS term plots showing mean and 95% confidence limits (gray box) and residuals (open circles).

Figure 6. Species habitat utilization during the night, indicated by GAMLSS term plots showing mean and 95% confidence limits (gray box) and residuals (open circles). Note no black grouper were detected at greater than two locations at night.

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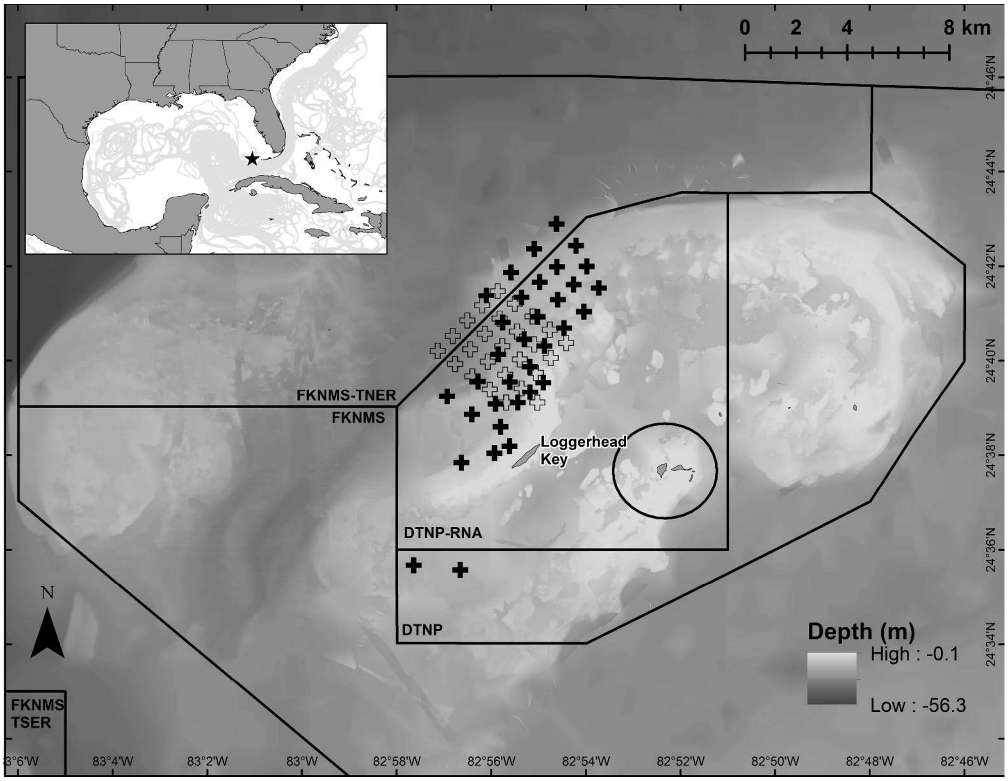

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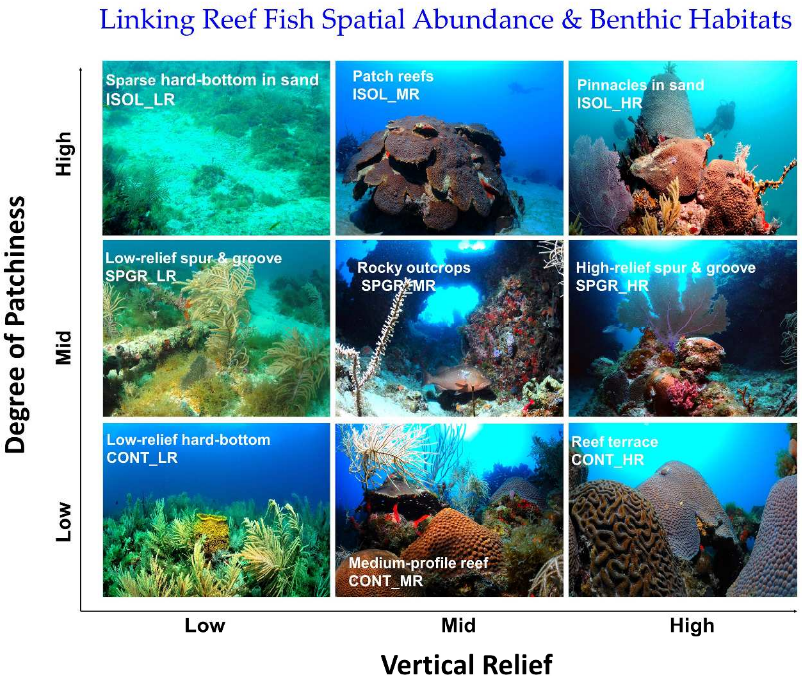

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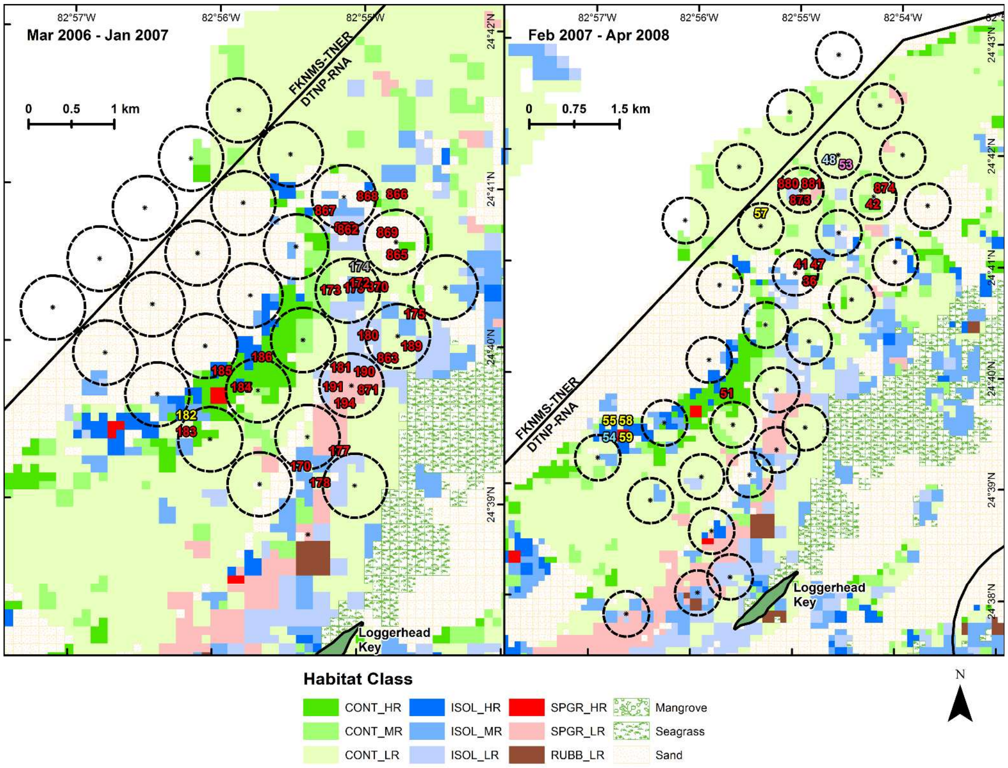

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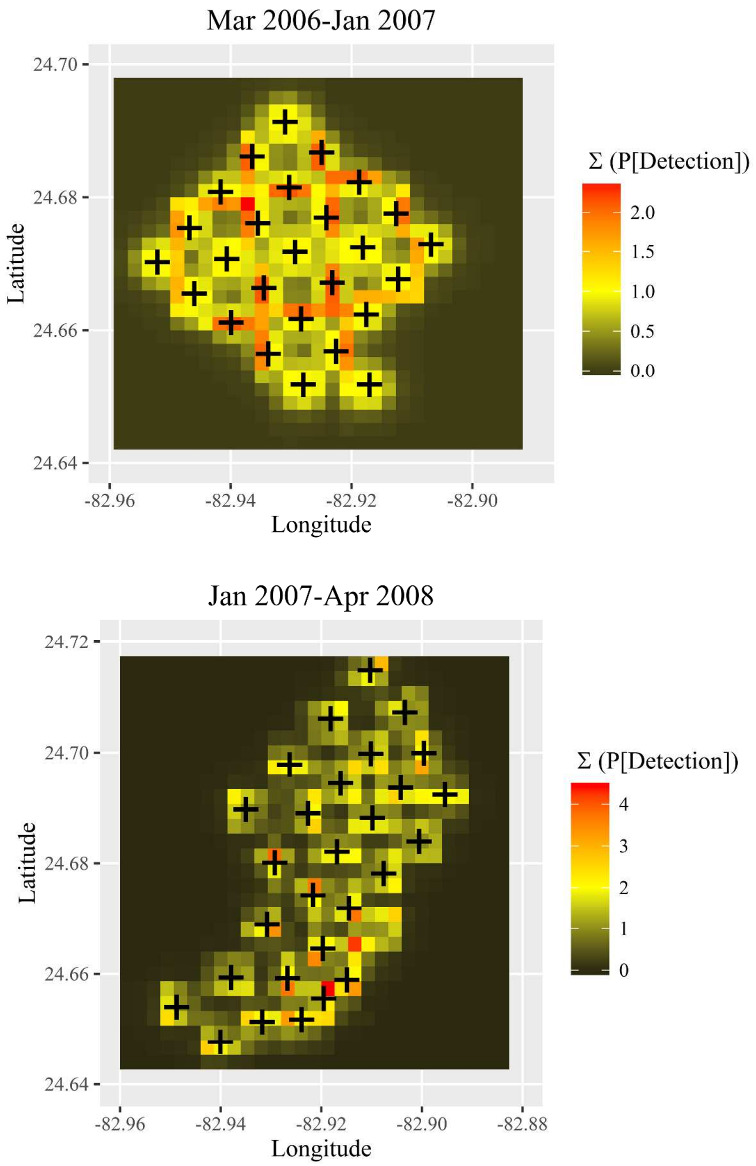

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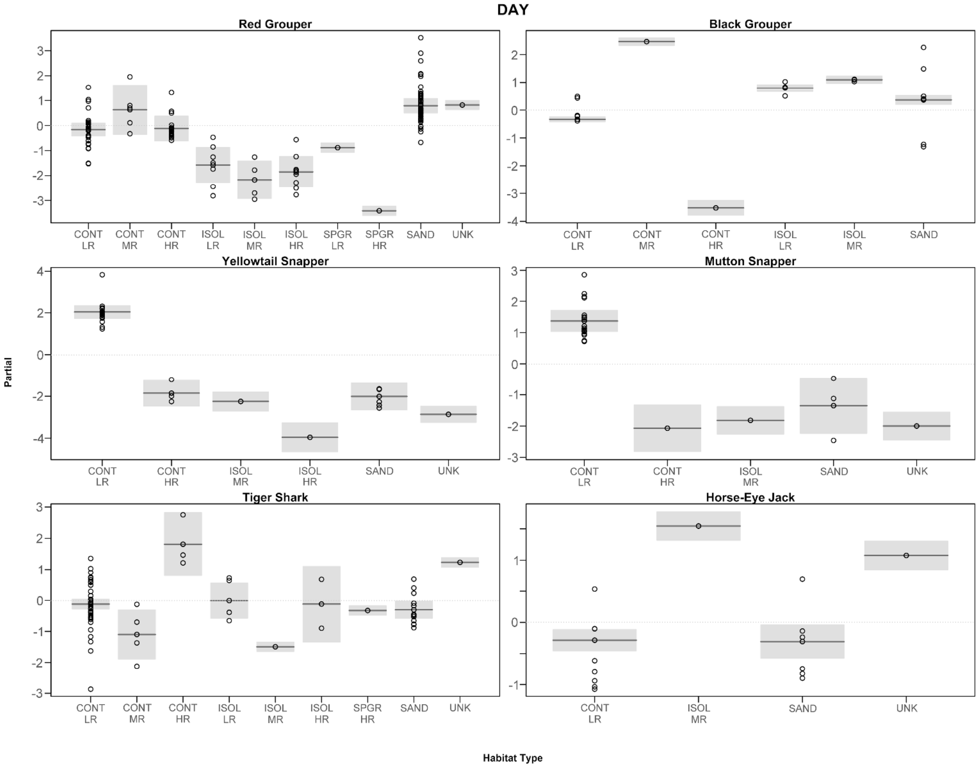

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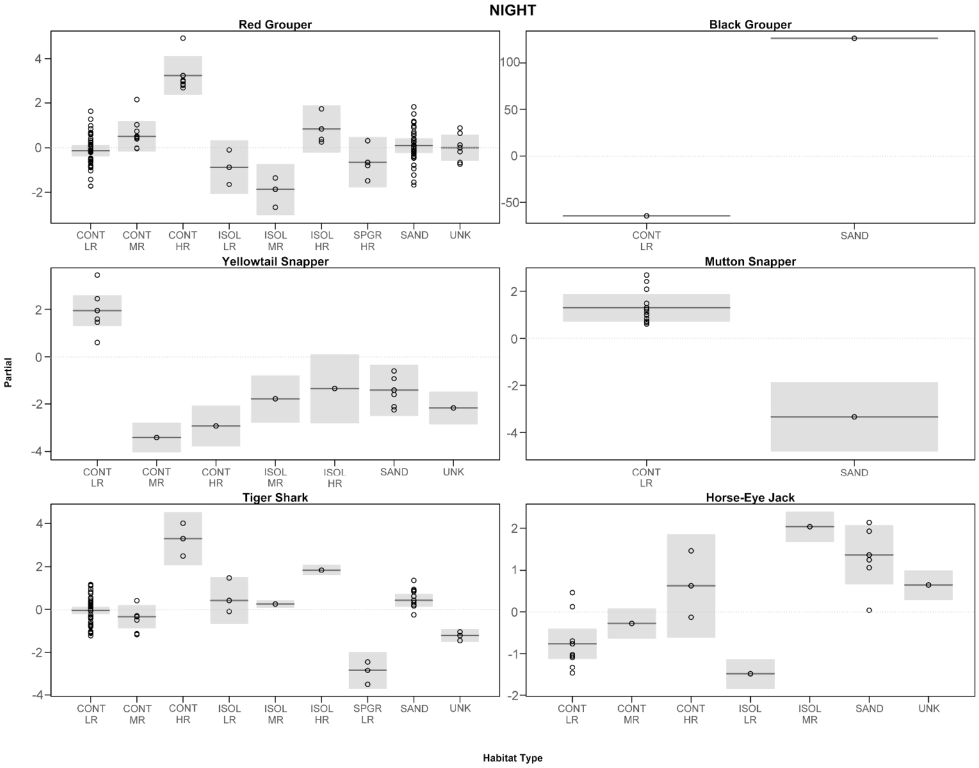

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