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REEF FISH MOVEMENTS AND MARINE RESERVE DESIGNS

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Movement patterns and space use by mature fishes are critical in determining the effectiveness of marine reserves in conserving spawning stock biomass and/or providing biomass to adjacent fisheries through ‘spillover’. Home range sizes, activity patterns, site fidelity and habitat preferences were determined for acoustically-tagged snappers and groupers using a rigorously-calibrated array of omnidirectional hydroacoustic receivers deployed in the diverse coral reef environments of a no-take marine reserve (NTMR) network in the Dry Tortugas, Florida. An individual-based localizing tendency model of reef fish movement was parameterized from fine-scale acoustic telemetry data and integrated into a Spatial Management Performance Assessment (SMPA) simulation model for reef fish populations developed to quantitatively evaluate performance of no-take marine reserves in the Dry Tortugas, Florida. Spatially-explicit SMPA models were parameterized for three overfished stocks in the lucrative snapper-grouper fishery: red grouper (*Epinephelus morio*), black grouper (*Mycteroperca bonaci*), and mutton snapper (*Lutjanus analis*). SMPA models were used to evaluate the impacts of a variety of life histories, movement strategies and speeds, and management regulations upon long-term stock sustainability, as measured by annual changes in spawning potential ratio (*SPR*), and long-term stock productivity, as measured by annual changes in fisheries yield-in-weight per recruit (Y_w/R).

Under assumptions of constant regional fishing pressure, constant recruitment, and ‘realistic’ fish movement, SMPA simulation runs from initial conditions in 2000 suggested that by 2014, the Tortugas NTMR network should function to restore red grouper populations to 30% SPR, a Federal management benchmark for sustainability. Mutton snapper were the most mobile of the species investigated; if mutton snapper movements are ignored, their population is predicted to attain 30% SPR by 2014, but given ‘realistic’ mobility, they may not attain this target by 2021 without additional protections. Black grouper are currently fished at over 9 times sustainable levels. SMPA simulations suggest coupling an increase in minimum size at capture of 20 – 25 cm with NTMR implementation would result in substantial short term losses in yield, but would restore both black grouper and mutton snapper populations to 30% SPR by 2021 and lead to increased long-term yields.

Although marine reserve sites are often chosen opportunistically, these findings strongly suggest that reserve designs (e.g. proper sizes and configurations) must take into account the scales and patterns of movement exhibited by the exploited stocks they are intended to protect. These modeling efforts also suggested reserves are not a panacea; in order to promote sustainability for severely depleted stocks, they must be accompanied by an overall reduction in fishing capacity. Although important questions remain concerning the movements of reef fish in response to habitat and density dependent processes, our analyses of realistic reef fish behaviors suggest that the NTMRs of the Dry Tortugas promote substantial gains in SPR, promoting long-term stock sustainability and enhanced egg production. Increased rates of movement diminish these benefits, but may also mitigate short-term losses in yield associated with NTMR establishment.

DEDICATION

To Mom and Dad.

Thank you.

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Chapter 1

Introduction

No-take marine reserves (NTMRs) are a form of marine protected area (MPA) designed to protect coral reef ecosystems and to ensure sustainability of intensely exploited regional fisheries resources (Bohnsack 1990). Theory suggests that buildup of fish biomass, density, and average size in an NTMR due to reduced exploitation (e.g., Ault et al. 2005a) may result in density-dependent emigration of adult fish across reserve boundaries (Crowder et al. 2000). Additionally, increasing spawning stock biomass within reserve boundaries should increase larval production, resulting in advection of eggs and larvae from the reserve to proximal fishable habitats. Although NTMRs are theoretically useful tools for generating sustainable fisheries, the reserve concept has met with considerable opposition and skepticism from recreational and commercial fishing lobbies because available fishing areas are reduced by NTMR implementation.

Although the fisheries benefits of reserves are often sufficient to garner support from local fisherman for spatial closures, empirically demonstrating these benefits is difficult (see reviews in Cote et al. 2001, Russ 2002, Gell & Roberts 2003). Most of the fisheries benefits of NTMRs are contingent upon the build-up of adult fish biomass and spawning potential within their boundaries. Numerous studies have documented increased abundance and/or biomass within reserves (Russ & Alcala 1996, Zeller & Russ 1998, Davidson 2001, Ault et al. 2006). Several empirical studies have suggested increased biomass within reserve boundaries is accompanied by increased catch rates in unprotected areas adjacent to the reserve (Alcala & Russ 1990, Murawski et al. 2000, Davidson 2001, McClanahan & Mangi 2001, Russ et al. 2004, Abesamis & Russ 2005,

Francini-Filho & Moura 2008), and some have documented movement of adults into surrounding areas (Alcala & Russ 1990, Attwood & Bennett 1994, Samoily 1997, Francini-Filho & Moura 2008). Increased reproductive output and subsequent stock enhancement remains largely undocumented (see review in Gell & Roberts 2003).

To ensure protection of a certain percentage of the population from fishing and thus promote the amplification of adult biomass in its boundaries, NTMRs should be designed with considerations towards the scales and patterns of individual movement within the exploited stock; however, for most marine species, this information is extremely limited (Roberts & Polunin 1991, Russ & Alcala 1996; Holland et al. 1996; Zeller 1997a, b; Roberts 1997a, Kramer & Chapman 1999, Lembo et al. 1999, Palumbi 2001, O'Dor et al. 2004). Consequently, most reserves have been implemented on an *ad hoc* basis (Eristhee & Oxenford 2001). Improperly configured reserves that fail to account for the scale of animal movements or the locations of core habitats may lead to high levels of spillover that prevent the reserve from effectively functioning as a buffer against fishing effort (Eklund et al. 2000, Eristhee & Oxenford 2001). Poorly designed NTMRs may generate over-confidence about resource protection, and subsequent failure to generate sustainable fisheries damages their credibility as management tools in a process that is already politically challenging (St. Mary et al. 2000).

Although numerous studies have examined fish movements, few have precisely quantified use of space or examined it in the context of resource protection (Goeden 1978; van Rooij et al. 1996; Shapiro et al. 1994; Zeller 1997a, b; Kramer & Chapman 1999; Bell & Kramer 2000; Eristhee & Oxenford 2001; Bolden 2001; Lembo et al. 2002; Baras et al. 2002; Tremain et al. 2004). It is important to note that the perception of

mobility is dependent upon the scale of time and space over which movement is monitored (Steingrímsson & Grant 2003). Due to technological and financial limitations, most previous studies of fish movement have been of limited spatial and temporal scope and resolution (e.g., Holland et al. 1993, 1996; Zeller 1997a, b; Zeller & Russ 1998; Eristhee & Oxenford 2001; Tremain et al. 2004).

Self-contained passive hydroacoustic monitoring technologies allow scientists to continuously, non-intrusively monitor the presence / absence of tagged fish over long time periods. When arranged in an array, these devices may be used to generate relatively detailed movement paths for acoustically-tagged fish that remain in detection range; and when strategically arranged across reserve boundaries, accurate estimates of flux may also be generated. Although passive acoustic arrays have been used to study fish movements in the past (e.g., Goeden 1978; Holland et al. 1993, 1996; Shapiro et al. 1994; van Rooij et al. 1996; Zeller 1997a, 1997b; Zeller & Russ 1998; Kramer & Chapman 1999; Bell & Kramer 2000; Eristhee & Oxenford 2001; Bolden 2001; Lembo et al. 2002; Baras et al. 2002; Humston et al. 2005), the analysis of movement paths in most studies has been limited to descriptive statistical models which lack theoretical or predictive value. Additionally, quality control of data resulting from acoustic tag detections has been limited, resulting in potential misinterpretation of the biological meaning of tag detection patterns.

In this dissertation, innovative methods for calibrating an array of acoustic receivers are described, and a multivariate model for positioning a coral reef fish within a spatially- and temporally-heterogeneous environment is developed (Chapter Two). This model permits a comprehensive fine-scale analysis of the movements and space use of

groupers and snappers in the marine reserves of the Dry Tortugas, Florida, as recorded over a multi-year period using a broad-scale, rigorously calibrated acoustic array (Chapter Three). The grouper and snapper species investigated represent some of the most lucrative and intensely overexploited fisheries resources in the multibillion dollar Florida Keys / Dry Tortugas ecosystem (Ault et al. 1998).

If empirically demonstrating the fisheries benefits of reserves is difficult (see reviews in Cote et al. 2001, Russ 2002, Gell & Roberts 2003), quantifying these benefits in the context of fisheries productivity and sustainability is even more challenging. A review by Gerber et al. (2003) found that few fisheries reserve models (less than 8%) predict increased landings resulting from reserve implementation. Most of these models grossly oversimplify or ignore the impacts of fish movements across reserve boundaries, which may severely limit their accuracy and predictive abilities. An effective analysis of the impacts of an NTMR on surrounding fisheries requires a high resolution spatial modeling approach, accounting for the rate of flux of exploited individuals across reserve boundaries and residence times inside the NTMR. To simulate reef fish space use, fundamental movement parameters must be quantified from empirical data obtained from advanced movement tracking techniques. Innovative spatially- and temporally-explicit population dynamic simulation modeling is the only viable approach towards evaluation of the complex interactions between reserve implementation, individual fish movements across reserve boundaries, impacts of other non-spatial management measures, and alterations in fisher behavior.

To understand individual coral reef fish movements in the context of a spatially-heterogeneous environment, a predictive model is needed to account for movement paths

that are the product of a vast number of individual movement decisions. In this dissertation, a localizing tendency home range model developed for terrestrial carnivores by Okubo (1970) and Moorcroft & Lewis (2006) is extended to coral reef fish, developing movement responses for a variety of fish species (Chapter Four). This model is driven by distributions of movements and turning angles generated from empirical movement data obtained through two years of passive acoustic monitoring of reef fish movements in the Dry Tortugas, Florida (see Chapter Three).

To address the consequences of fish movement within a spatial management regime, the species-specific movement models developed in Chapter Four are implemented into a spatially-explicit population dynamic model of grouper and snapper stocks in the Dry Tortugas, Florida (Chapter Five). To address the effectiveness of NTMRs, the simulation model is used to evaluate the interactions and impacts of a variety of life histories, movement strategies and speeds, and management regulations upon the long-term sustainability and productivity of simulated grouper and snapper stocks, as measured by annual changes in spawning stock biomass (*SSB*) and fisheries yield in weight (Y_w). Specifically, the model is used to quantitatively evaluate what changes in yields should be expected from reserve establishment, how movement strategies impact these yields, and how these changes vary by species. As such, it permits a quantitative evaluation of reserve performance and provides insights into improved reserve designs and additional management measures necessary to generate sustainable fisheries.

Chapter 2

Interpretation of Coral Reef Fish Movements within an Acoustic Array

Summary

An array of omnidirectional hydroacoustic receivers deployed in a heterogeneous coral reef environment was calibrated to facilitate interpretation of fish acoustic tracking data. Previous studies assumed linear decay in tag detections with distance from receivers and did not incorporate effects of any secondary variables on detection success. Empirical data on detections at known distances from receivers acquired through controlled range tests revealed this assumption leads to systematic underestimation of detections expected within 300 m of the receiver and overestimation beyond 300 m. Multivariate regression analysis objectively determined logistic response functions for the probability of tag detection as a function of tag distance from receiver, regional wind speed, receiver depth, tidal height, and rugosity of the surrounding environment. By incorporating this function as a non-linear weighting term in a data-aggregating mean positioning estimator, we accounted for the spatially- and temporally-diverse environments surrounding each receiver and significantly reduced positioning error compared to previously described methods. Application of this weighted positioning estimator to fish tracking data should generate robust descriptions of movements and spatial habitat requirements.

Background

It is now relatively common practice to arrange stationary omnidirectional hydroacoustic receivers in overlapping arrays over a broad geographic area (Topping et al. 2006, Dresser and Kneib 2007, Hedger et al. 2008) and apply innovative techniques (e.g. Becker et al. 1988, Simpfendorfer et al. 2002) to generate detailed fish movement paths that expand upon the basic presence/absence data recorded by individual receivers. However, the spatial and temporal heterogeneity of the coral reef ecosystem poses significant challenges for the accurate interpretation of fish detection data that must be accounted for to avoid misinterpretation of tag signal detection patterns.

Within the structurally complex coral reef environment, each receiver in an array is exposed to a unique suite of bathymetric and oceanographic conditions that result in spatially- and temporally-distinct signal reception patterns. Ambient environmental noise is relatively high on a coral reef (Kingsford et al. 2002), and rises with increased snapping shrimp activity (Cato 1980; McCauley 1994), and wind and rain (Kingsford et al. 2002, Hobday and Pincock 2009). For a single omnidirectional hydroacoustic receiver, the probability that a signal from a transmitter will be detected decreases with distance between receiver and transmitter out to some maximal distance (Lacroix and Voegeli 2000, Pincock and Voegeli 2002). Acoustic sound generated by a transmitter diminishes through spreading loss across three-dimensional space and absorption by seawater (Pincock and Voegeli 2002). Signal reception is additionally complicated by scattering, reflection, and refraction due to bathymetric features, oceanographic conditions such as thermoclines, and air-sea interface interactions (Pincock and Voegeli 2002). For a detection to be logged by a receiver, the tag signal must exceed a critical

threshold relative to the ambient environmental noise across the receiver bandwidth (D. Pincock, VEMCO Ltd., pers. comm.).

In this chapter, empirical data are presented on detections at known distances from receivers acquired through several controlled range-tests performed within an array of hydroacoustic receivers in Dry Tortugas National Park, Florida. From this data, a multidimensional function is developed describing the probability of tag signal detection at distance from receiver given a broad suite of environmental and bathymetric factors. Finally, the utility of this regression relationship to account for the impacts of environmental variability upon the non-linear decline in detections with distance is explored through the introduction of a weighting term into the arithmetic and harmonic mean positioning estimators described by Simpfendorfer et al (2002).

Methods and Analysis

During these experiments, the interactions of VEMCO VR2 hydroacoustic receivers with V16-3H ('3H', transmission strength = 158 dB re 1 μ Pa @ 1 m) and V16-4H ('4H', transmission strength = 153 dB re 1 μ Pa @ 1 m) acoustic tags (VEMCO Ltd., Nova Scotia, Canada) were calibrated under a variety of oceanographic and atmospheric conditions in a variety of locations. The various acoustic receiver calibration experiments performed in this study are summarized in Table 2.1 and Figure 2.1. Three different acoustic arrays were tested. Controlled experiments were performed in a homogeneous benthic environment using five VR2 receivers deployed along a line between two finger slips in Bayboro Harbor, St. Petersburg, Florida ('Bayboro'). Receivers were spaced 1 m apart and suspended 1.5 m from the bottom in water 5 m

deep. Field experiments were performed in a heterogeneous suite of benthic reef habitats in the northwestern quadrant of Dry Tortugas National Park, some 112 km west of Key West, FL, along the border of Tortugas North Ecological Reserve ('Tortugas I': Fig. 2.1A; 'Tortugas II': Fig. 2.1B). Spacing between receivers ranged between 600 – 1,200 m. Receivers were mounted 5 m above the seafloor to reduce exposure to benthic noise sources that may interfere with tag signal reception, avoid signal blockage by habitat features (e.g. large blocks of coral reef), and to maintain a superior listening angle for tagged animals moving within 5 m of the seafloor (Voegeli and Pincock 1996). Vinyl-coated wire ('Tortugas I') and 3-strand nylon ('Tortugas II') mooring line was used to reduce acoustic noise from the anchorage (see Clements et al. 2005).

Time between acoustic signal transmissions is a function of a programmed 'offtime' and the time to transmit the coded pulse identifying the tag (Pincock and Voegeli 2002). Some *3H* tags tested were configured to ping randomly every 60 – 180 sec with a mean 'offtime' between transmission cycles of 120 sec (*120s*); others had a fixed 'offtime' of 5 seconds (*5s*). All *4H* tags tested were *5s* tags.

Logistic Regression Analysis

Preliminary analyses suggested a traditional linear modeling approach to evaluate the impacts of impacts of tag distance from receiver and a variety of secondary variables upon number of tag signals detected would fail to meet assumptions of normality and heteroscedasticity of residuals, even after transformations. Due to the high percentage of zeroes (e.g. no detections during interval) present in the data and the need to easily extrapolate findings to tags with different ping rates, the data were modeled

probabilistically. Through the logit function, logistic regression modeling provides the power and statistical robustness of generalized linear modeling while providing an appropriate functional fit to probabilistic data. A multivariate logistic regression analysis was conducted on data from Test #9 using SAS software (SAS Institute, Cary, NC, USA). Each 90+ min drop was divided into 30 min intervals. As no detections during this test were obtained beyond 915 m from any receiver, this was designated as the threshold detection radius, and all interval-receiver subsets within this range were analyzed (n = 1513).

Predictor variables evaluated using SAS 'Proc Logistic' are listed in Table 2.2. Bathymetry data used to compute rugosity variables were obtained from a projected (UTM NAD83 Zone 17N) combination of NASA LIDAR data and USGS multi-beam bathymetry data for the Dry Tortugas, FL region, with a horizontal grid resolution of 10 m (see Fig. 2.1). Bathymetry data for depth of tag and depth of receiver were obtained from boat-based soundings using a DS600X FishFinder (RayMarine Inc., Merrimack, NH). Wind speed time series were obtained from National Data Buoy Center's C-MAN Station at 'Pulaski Shoal Light, FL' (*PLSF1*; 24°41'36" N 82°46'24" W), approximately 12 km east of the receiver array (www.ndbc.gov).

All variables selected for evaluation in the logistic models had reasonable physical explanations for their impact upon observed detection patterns. Increased distance from signal origin to receiver results in reduced signal strength through spreading loss and absorption (Clay and Medwin 1977, Voegeli and Pincock 2002). Increased wind speed creates increased ambient noise in the water which may interfere with signal detection (Wenz 1962, 1964; Hobday and Pincock 2009). Increased receiver

depth reduces the impact of topographical features relative to available water. Increased tidal height reduces probability of detection, as increased tidal height may increase spreading loss by shifting it from a cylindrical (e.g. shallow water) to a spherical (e.g. deep water) process. Tides may also create reflective barriers and eddies that may interfere with acoustic spreading. It is possible that the falling tide may advect these turbulent tidal bores and associated acoustic barriers off the topography or promote mixing within the water column (Leichter et al. 1996, 2003). Habitat rugosity creates obstacles for tag signals along their path to the receiver, and may reflect signals either towards (e.g. an amphitheater effect) or away from the receiver. The variable ‘Rugosity11’ (e.g. presence of a reef edge) accounted for an observed amplification of sound by large reef walls (e.g., an amphitheater effect) by increasing the probability of detection for receivers located in a flat habitat (e.g. low-relief hardbottom or sand) near a substantial reef edge. Chi-square likelihood ratios and AIC values (Burnham & Anderson 2002) were used to determine parameters for inclusion in final model.

Weighted Mean Positioning Estimators

Over time the number of signal receptions logged by a hydrophone will be higher if the transmitter is close by than if it is distant. Simpfendorfer et al. (2002) exploit this observation to improve estimates of tag position by batching detections over short time intervals (Δt), then computing a short term center of activity as the mean of the receiver locations weighted by the number of detections during Δt .

Aggregation of tag data over short time intervals provides numerous benefits. By weighting the mean location of the animal by the number of detections at each receiver,

these methods reduce the relative influence of infrequent singular tag detections at distant receivers resulting from signal ducting or ‘false detections’. Signal ducting occurs when water conditions such as presence of a thermocline function to reflect a tag signal along a greater distance than usually possible (Fabrizio et al. 2005). ‘False detections’ occur when a receiver incorrectly codes a recorded signal, and should be expected to comprise at least 1% of a large tracking dataset (Heupel et al. 2005). By generating position estimates between receivers, the mean positioning algorithms also generate more relocation positions for tagged organisms, facilitating a more comprehensive description of home range use. By aggregating detections across appropriate time intervals (Simpfendorfer et al. 2002), the level of autocorrelation between detections is reduced, which helps the telemetry dataset meet the assumptions of several statistical models developed to convert spatial distributions of telemetry relocations into estimates of home range size (Odum and Kuenzler 1955, Jennrich and Turner 1969, Dixon and Chapman 1980, Worton 1989).

As actual and estimated positions were expressed as (*longitude, latitude*) coordinate sets, positioning errors associated with each method were computed as distance between estimated and actual position using Great Circle methods (Vincenty 1975). Position estimates were expressed as either arithmetic means or harmonic means (see Table 2.3; note corrected formula).

Simpfendorfer et al. (2002)’s arithmetic and harmonic mean positioning methods are constrained by assumptions that the relationship between probability of detection and distance is linear, constant, and identical among receivers. Environmental heterogeneity results in extreme variability in this relationship (Giacalone et al. 2005, Hobday and

Pincock 2009), both across time and between receivers; especially when signals are aggregated (e.g. ‘batched’) over time. The utility of a logistic regression between the percentage of tag signals detected and several environmental covariates to generate improved positioning estimates over previously available methods was explored through the introduction of a nonlinear weighting term into Simpfendorfer et al. (2002)’s equations.

As the maximum detection range for a receiver might reflect the acoustic properties of its surroundings, we developed a weighted positioning estimator (Table 2.3) for analysis of field data obtained using *3H* tags using empirically-estimated maximum detection radii for that receiver (d_i) relative to maximum detection radius for any receiver recording detections during that interval (d_{max}). For receiver sites that were not tested empirically, detection radius was estimated using the regression relationship between maximum range and receiver depth.

We also developed an estimator that would accept a weighting term input from either the basic, reduced, or full logistic probability of detection models (Table 2.3). The weighting term for each receiver in this formulation is computed from the ratio of estimated distance between tag and receiver for that receiver (d_i) relative to the farthest estimated distance of the tag from any receiver (d_{max}). Estimates are computed from the relevant logistic response model using the number of detections registered at the receiver.

To investigate positioning error associated with the simple assumption that the tag was located at the site of the receiver (e.g. ‘VR2’) and positioning estimates generated by the arithmetic and harmonic mean positioning estimators discussed above, a computer program was written in Java 6.10 (Sun Microsystems, Inc., Santa Clara, CA) to enable

the application of each method to field data from Tests #5, 8, and 9. All positioning estimators were applied to each data series using batching intervals (Δt) of 1, 5, 10, and 30 minutes. To determine appropriate batching interval, we compared accuracy of mean positioning estimates generated at 1 min intervals between 1 – 30 min for different speeds of tag movement from Test #5. Movement speed at time of tag signal detection was computed using the archived GPS track.

Results

Differences between receivers

During Test #1, there were no obstructions present between receivers and transmitters, and all hydroacoustic equipment was at least 7 m from any solid object (e.g. pier or shore). Analysis of tag detection data revealed that 5s tags required approximately 3.5 sec to transmit their unique identification code; when added to a fixed 5 sec offtime, this resulted in detections every 8 – 9 seconds. As such, any detection recorded by the same receiver at a time interval of less than 8 seconds (e.g. an echo) was eliminated from analysis. Receiver performance for 5s tags was analyzed as detects·10 min⁻¹. Receiver performance for 120s tags was analyzed as detections·30 min⁻¹. One-way ANOVA revealed no significant differences in receiver performance between receivers for either 5s tags ($F_{4,55} = 0.22, p > 0.05$) or 120s tags ($F_{4,52} = 0.17, p > 0.05$).

Differences between tags

One-way ANOVA of 'detects·30 min⁻¹' between 120s tags in Test #1 revealed no significant differences ($F_{1,22} = 3.98, p > 0.05$). A paired t-test for means comparing

‘detects·time⁻¹’ for 120s tags in Test #2 also revealed no statistically significant differences (*means* ± *SE*: 10.76 ± 0.37 detections·30 min⁻¹, 10.76 ± 0.40 detections·30 min⁻¹; *t* = 0.00, *df* = 131, *p* > 0.05). By contrast, a significant difference was found in ‘detects·10 min⁻¹’ for the four 5s tags ($F_{3,56} = 55.62$, *p* < 0.01). Additional analysis of average intervals between detections for 5s tags using one-way ANOVA revealed significant differences ($F_{3,56} = 82.41$, *p* < 0.001), with a posteriori tests (Tukey HSD) suggesting each tag had a significantly different mean time between detections; however, these differences were minor (< 0.31 s). For subsequent analyses, we accounted for differences in tag ping rates by using a divisor (expected pings·time⁻¹) unique to each tag.

Depth of tag

For Test #1, a paired t-test of mean detection rates for tags at different depths in a harbor a 15% higher detection rate for a tag at 1.5 m (8.4 ± 1.2 detections·30 min⁻¹) versus a tag at 2.4 m depth (6.2 ± 1.3 detections·30 min⁻¹). This difference was statistically significant (*t* = 5.28, *df* = 14, *p* < 0.001). For Test #3, a paired t-test of mean detection rates for tags at different depths in a coral reef habitat revealed a 7% higher mean detection rate for a tag at 10.1 m depth (12.2 ± 0.3 detections·30 min⁻¹) versus a tag at 11.1 m depth (11.1 ± 0.4 detections·30 min⁻¹). This difference was statistically significant (*t* = -3.50, *df* = 130, *p* < 0.05). Differences in linear distance between the two tags and the receiver was less than 1 cm; as such, differences in detection rates may be explained by partial signal blockage by a reef feature for the deeper tag. Tag signal collisions may have confounded this analysis, as in the harbor, detection rates were significantly higher for the shallow tag on its own in the same location shortly after Test

#1 ($t = 5.18$, $df = 25$, $p < 0.001$), although environmental conditions were also slightly different during this period.

Distance and Rugosity

For Test #4, exact tag position and distance from receiver was computed both for detected and undetected transmissions through examination of the GPS track. Examination of digital video records from time of transmission was used to determine probable cause for missed detections by identifying potential signal blocking objects (e.g. reef habitat features of > 1 m height; diver between tag and receiver) within 3 m of the tag at time of transmission. Distance of tag from receiver appeared to explain the majority of missed detections; of 334 total missed transmissions, 238 (71.2%) originated beyond 150 m from a receiver. Of the additional 96 missed detections that occurred within 150 m of a receiver, 49 (51.0%) originated within close proximity of a high-profile reef feature, and an additional 5 (5.2%) originated with a diver between the tag and the receiver.

Depth of receiver

By synchronizing time of tag signal detection at a receiver with tag position from archived GPS tracks for Tests #5 and 6, we were able to calculate distance of tag from receiver at time of detection. Linear regression analysis of *3H* tags revealed that receivers in deeper water had significantly larger maximal detection ranges ($\beta = 12.7$, $F_{1,17} = 4.88$, $p < 0.05$), with depth of receiver accounting for 22% of the variance in observed maximum range. Receiver depth was not predictive of maximum range for the

V16-4H tag; however, a paired sample t-test for means between maximum ranges observed at sites tested with both tags found average maximum range to be significantly greater for 3H tags versus 4H tags (3H: 750.1 ± 63.0 m, mean \pm SE; 4H: 608.7 ± 70.1 m; $t = 2.33$, $df = 15$, $p < 0.05$).

Presence – Absence

To investigate the effects of selected computation time interval upon estimates of presence – absence from Test #7, estimates of percent time “present” in the array were calculated using time intervals ranging from 1 min to 1 d following:

$$\text{Percent Perceived 'Presence'} = \frac{\text{Total Intervals with Detections}}{\text{Total Intervals}}$$

Analyses revealed that intervals shorter than 120-min would result in several perceived ‘absences’ for the majority of tags permanently anchored at 300 m from the receiver (Fig. 2.2).

Wind Speed, Time of Day

Upon controlling for temporal changes in ambient noise due to biological activity by partitioning detection rates from Test #2 into two diel categories: Day (1 hr after sunrise to 1 hr before sunset); and, Night (1 hr after sunset to 1 hr before sunrise), we found detection rates were relatively constant across wind speeds during the day ($F_{1,49} = 0.13$, $p > 0.05$), but at ‘Night’, detection rates showed a decline best expressed as a quadratic function (Fig. 2.3; $F_{1,58} = 56.3$, $p < 0.001$) at wind speeds above 4 knots, suggesting a combination of biologically-induced ambient noise and wind-related noise contributing to reduced detection rates. At night, wind speed explained 66% of the

variance in detection rate. A linear regression model overestimated detection rates at lower wind speeds and showed an overall poorer fit.

Logistic Regression Analysis

A plot of detections per 30 min vs. transmitter distance from receiver from Test #9 illustrates similarly unsatisfactory fits of for a linear model (Fig. 2.4A), with systematic underestimation of number of detections near the receiver and overestimation at further distances. We next considered a log-linear fit using the sonar equations (Urick 1983) for spreading loss and absorption:

$$\text{Transmission Loss} = 20 \log (\text{Distance}) + a(\text{Distance})$$

where ‘Distance’ denotes distance between tag and receiver and a denotes absorption coefficient for sound in seawater (0.02 dB/m). Theoretically, detections should be registered if the signal strength at the receiver is higher than the receiver threshold:

$$\text{Receiver Threshold} > (\text{Initial Signal Strength} - \text{Transmission Loss} - \text{Ambient Noise})$$

This explicitly computational approach to predicting detection rates was problematic due to our inability to measure ambient environmental noise levels at each receiver through time, and would not be useful for interpreting fish detections as distance from the receiver would be unknown.

As traditional approaches to modeling signal detections failed to meet critical assumptions, logistic regression analysis of Test #9 was conducted to control for the impacts of tag distance upon detection rate and parse out the multivariate impacts of temporal and spatial heterogeneity upon the probability of tag signal detection. Logistic regression analysis indicated tag distance from receiver was the most significant predictor

of probability of tag detection (Table 2.4; ‘Basic’); however, significant additional variability was explained by environmental factors. The following variables were included in a reduced model (Table 2.4; ‘Reduced’) excluding rugosity: (1) tag distance from receiver; (2) the square of tag distance from receiver; (3) wind speed; and, (4) receiver depth.

The following additional variables were included in the full model (Table 2.4; ‘Full’): (1) tidal height; (2) Rugosity2 (‘Surface Area Ratio’); (3) Rugosity5 (‘coefficient of variation for Elevation’); and, (4) Rugosity11 (‘Presence of Reef Edge’). Direct path rugosity values (e.g. values along a line) were not selected for inclusion in the final model because as the angle of approach of a tag signal to an omnidirectional receiver would be unknown for any tagged organism, a model including these variables would have limited predictive value. The rugosity variables selected permit model application to data where the actual tag location is unknown. Although the ‘Full’ model included four additional variables, it was the best-fitting model per the AIC. The maximum and minimum logistic response curves for probability of detection fit to data from Test #9 are presented in Figure 2.4B-C, illustrating the models’ relative abilities to account for the range of observations in the data. Note that the inclusion of rugosity and tidal height variables in the ‘Full’ model (Fig. 2.4C) expands the range of observations that may be accounted for by the ‘Full’ model relative to the ‘Reduced’ model (Fig. 2.4B).

Weighted Mean Positioning Estimators

As expected, both number of detections and number of receivers logging detections were positively correlated with increased batching interval. Average speed

during Test #5 was 1.3 m/s. In general, a five minute batching interval appeared to provide the best positioning estimates for most methods, with the arithmetic mean maximum range weighted model and both the harmonic and arithmetic mean ‘Reduced’ logistic weighted models providing the most accurate position estimates (Table 2.5).

In nearly all comparisons, use of a mean positioning estimator generated superior estimates compared with the simple assumption that the tag was located at the position of the receiver making the detection (e.g. ‘VR2 assumption’, Table 2.6). As mean positioning methods only generate unique positioning estimates when multiple receivers record detections within a batching interval, comparisons between methods were restricted to these cases. Accuracy of positioning estimates ranged was significantly different between methods ($H = 27.4$, $df = 10$, $p < 0.01$), with the harmonic mean ‘Reduced’ logistic weighted model providing the best overall estimates for 5 of the 6 range-tests examined (Table 2.6, Fig. 2.5). Post-hoc Mann-Whitney U-test comparisons suggested the ‘Reduced’ model provided significantly reduced positioning error compared to the Simpfendorfer et al. (2002) and ‘Max Range’ methods (e.g., ‘Reduced HM’ vs. Simpfendorfer et al. 2002 AM: $U = 4.5$, $p < 0.05$). Mean positioning estimates generated by the harmonic and arithmetic mean ‘Reduced’ logistic weighted model were essentially identical. Positioning accuracy increased as the number of receivers registering detections within the batching interval increased (Fig. 2.6).

Discussion

Although arrays of passive receivers are a broadly used tool for observing the movements of acoustically-tagged fish in coastal and continental shelf ecosystems, the

extensive coral reef environments of Dry Tortugas National Park pose significant challenges for the accurate interpretation of presence/absence data. Our results indicate that probability of tag signal detection is a function of not only distance of the tag from the receiver, but also bathymetric features such as receiver depth and surrounding habitat rugosity and environmental factors such as wind-generated noise.

In a shallow (< 35 m) coral reef environment, percent tag signal detections at distance are best predicted by a logistic model accounting for the unique bathymetric and oceanographic conditions surrounding each receiver. Our observations suggest that a linear regression model underestimates detection rates for tags close to the receiver and overestimates detection rates for tags far from the receiver (Fig. 2.4A). The innovative mean positioning methods described in Simpfendorfer et al. (2002) are predicated upon the explicit assumption that the probability of tag signal detection decreases linearly with distance, and the implicit assumption that this rate of decline is constant across receivers. By accounting for non-linear spatial and temporal variability in tag signal detections at distance, the weighted positioning estimators described in this paper represent a significant improvement in our ability to determine a coral reef fish's position within an array of omnidirectional receivers. Additionally, the probabilistic formulation of the logistic model is advantageous for the interpretation of tag data because it allows for easy extrapolation from rapidly-pinging tags commonly used in receiver calibration to the more slowly pinging tags typically implanted in reef fish.

Although the introduction of terms for rugosity and tidal height in the 'Full' logistic regression model result in a better fit to observed detection data relative to the 'Reduced' model, the 'Reduced' model mean positioning estimator consistently

generated comparable or superior positioning estimates relative to all other models. Our available rugosity data was aggregated over 10 m blocks, and may have been too coarse to detect important barricades to tag signals. Acoustically-impermeable structures (e.g. coral reef, wrecks, etc.) near a transmitter can result in signal blocking, which severely impacts the accuracy of positioning algorithms and may also lead to erroneous conclusions regarding animal presence/absence (Giacalone et al. 2005). Future studies should attempt to quantify these factors and their impacts at a finer scale.

The relationship between maximum detection range and receiver depth may be used to help guide receiver spread in the array, though consideration must be given to the fact that maximum detection distance varies both among receivers and through time. The common practice of using an estimate of maximal distance from a range-test of one receiver over a limited set of environmental conditions to determine spacing for an entire array may lead to a configuration that under many conditions does not ensure the detection of a tagged fish. Broad spacing of receivers is appropriate when quantification of overall space use is a priority; however, for research where missing detections within the array is unacceptable, such as studies of directional movement or passage through a checkpoint, tight receiver spacing (< 200 m) may be required to raise probability of signal detection to near 100%. Increased overlap between receivers will also provide increased positioning resolution (Giacalone et al. 2005).

The detection rates at distance predicted by our logistic model appear to be in good concordance with other studies (Fabrizio et al. 2005, Giacalone et al. 2005); however, an examination of output from the microtopography test suggests that detection rates would be reduced by the cryptic movement patterns of many reef fish. For an

acoustically-tagged SCUBA diver moving in a deliberate path between receivers while using cover like a reef fish (Test #4), the probability of detecting a tag signal dropped to 20% between 100 – 150 m, then to 10% between 150 – 200 m. These signal detection rates are significantly lower than those predicted by the logistic model (see Fig. 2.4B). During this test, a combination of the shallow depths of the receivers tested, diver depth, additional ambient noise from the SCUBA equipment, and the sheltering effects of the reef may have contributed to the reduced detection ranges observed. These observations suggest detection rates below 50% for fish spending 100% of their time within the receiver arrays depicted within Figure 2.1.

For researchers to accurately interpret data from reef-affiliated tagged organisms, assumptions must be made regarding the movement speeds and sheltering behaviors of the organisms. Our findings strongly indicate that failure to detect any single tag transmission does not imply that the tag is beyond the maximum detection range of the receiver. Indeed, in our broadly-spaced array, a sampling interval between 2 – 24 hrs appears necessary to accurately assess presence – absence for a tag 300 m from a receiver. The goal of the researcher should be to interpret when a gap in detection is due to movement into or behind topographical features of the reef as compared to movement out of the receiver array; requiring inferences about the movement speed of the organism, its behavior, and its proximity to an edge of the array.

Our finding that increased tag depth reduces the probability of tag signal detection has important implications for the interpretation of data from tagged reef organisms. Fabrizio et al. (2005) reported similar findings, and suggested that reflections of sound waves off of the sea surface may serve to increase the propagation of the transmitted

signal. An increase in tag depth may also function to mitigate the blocking effects of benthic topography by lifting the tag signal over the reef and providing a direct line-of-sight transmission to the receiver. A change in tag depth may also put the receiver and tag on the same side of a thermocline, increasing the likelihood of tag signal detection (Fabrizio et al. 2005). These findings all suggest that an increased number of detections from a tagged organism may be associated with it either moving closer to the receiver or moving up in the water column.

In this study, we have attempted to account for the impacts of environmental variability upon the non-linear decline in detections with distance through the introduction of a weighting term into the arithmetic and harmonic mean positioning estimators of Simpfendorfer et al (2002). The ‘Maximum Range’ weighted mean model essentially gives added weight to detections occurring at receivers with limited maximum ranges, as the tag is more likely to be near these receivers when it is detected. This simple formulation provides a crude method to account for spatial variability in receiver detection patterns.

In the formulation of the ‘Full’ logistic mean model, we accounted for spatial variability in receiver depth and surrounding rugosity, as well as temporal variability in wind-generated ambient noise and tidal flow around the receiver. Previously, Giacalone et al. (2005) applied a variant of the Simpfendorfer et al. (2002) arithmetic mean method in which the observed number of detections during a given time block is replaced with the mean value of the ‘number of detections’ group, giving equal weight to groups whose variability is due to the impact of environmental ‘noise’ upon recorded detections as opposed to a change in transmitter position. Rather than excluding samples from tests

carried out under various thermocline or high turbidity conditions from our analysis per Giacalone et al. (2005), we have attempted to account for these dynamic conditions using data readily available to most researchers through boat-based soundings and data from remote meteorological buoys.

A major criterion for proper model selection is the choice of a batching interval (Δt) appropriate to the mobility of the organism. Selection of a Δt that is too short reduces the probability of detections at multiple receivers and the utility of mean positioning methods for generating unique centers of activity. Selecting a Δt that is too long can result in large positioning errors by averaging out detections at distant locations. An organism's net mobility is a function of its movement speed and its turning frequency; if an organism moves quickly but turns often, its positional displacement may be minimal. For average movement speeds less than $2 \text{ m}\cdot\text{s}^{-1}$, we found a Δt of 5 min provides the best positioning estimates given our receiver spacing of 800 – 1000 m (see Table 2.4). Future studies should evaluate the performance of these methods when extrapolated to transmitters commonly used in reef fish, typically characterized by infrequent pings on semi-random intervals.

In this study, we have shown that the depth of a tag and its distance from a receiver, spatial differences in the depth of each receiver and the rugosity of its surrounding environment, and temporal differences in wind-generated noise all play a significant role in determining the likelihood of a tag transmission being detected. Figure 2.5 illustrates retroactive application of this method to data from Test #9 at a location where between 1 – 3 receivers registered detections during each 5 minute batching interval. The density contours plotted around the position estimates from the two

Simpfendorfer et al. (2002) positioning estimators and our ‘Reduced’ logistic weighted harmonic mean positioning estimator illustrates the enhanced overall positioning resolution and reduced spread of error in positioning estimates generated through the inclusion of a logistic weighting term. Our findings suggest that failure to account for spatial and temporal variability in receiver detection patterns increases the probability of misinterpretation of detection data from tagged organisms. We have described and explored the dynamics of several data-aggregating positioning estimation methods that help mitigate the impacts of this variability. Application of these methods with an appropriately selected batching interval should assist researchers in the interpretation of data collected from tagged organisms. In addition, the logistic model of detection probability described within this paper may be useful in the context of validating simulation models by generating a simulated time series of detections from simulated animal movements for comparison to empirical datasets.

Table 2.1. Summary of acoustic receiver calibration experiments.

Test	Variables	Location	Tags	Duration	VR2	Depth _{rec}	Method
1	Tag Receiver Depth _{tag}	Bayboro	2·120s 4·5s	90 min·120s ⁻¹ 30 min·5s ⁻¹	5	2.5	Tags sequentially mounted 1 m from bottom, 5.5 m from center of receiver curtain
2	Tag Wind Speed TOD	Tortugas II	2·120s	164 hrs	1	14	Tags simultaneously mounted, 2 m from bottom, 300 m from receiver
3	Depth _{tag}	Tortugas II	2·120s	3 d	1	13.1	Tags simultaneously mounted; one 2 m and one 3 m from bottom, 300 m from receiver
4	Distance Rugosity	Tortugas I	1·5s	8 hrs	8	6 – 11	Tag suspended 3.5 m above bottom swum between receivers by diver carrying GPS-synched video camera
5	Depth _{rec}	Tortugas I	1·5s (1·3H, 1·4H)	16 hrs	19	6 – 28	Tag suspended ~5 m from bottom slowly pulled behind vessel between receivers
6	Depth _{rec}	Tortugas II	1·5s (4H)	10 hrs	13	4 – 16	Tag suspended ~5 m from bottom slowly pulled behind vessel between receivers
7	Presence	Tortugas II	7·5s	12+ hrs	7	4 – 35	Tags individually mounted, 2 m from bottom, 300 m from receiver
8	Distance	Tortugas II	1·5s	8+ min·drop ⁻¹ (2 overnight drops)	14	4 – 26	Tags individually mounted, 2 m from bottom, dropped at 150 m intervals between receivers (42 drop sites)
9	Distance Wind Speed Depth _{rec} Tidal Phase Rugosity Meteorological Depth _{tag}	Tortugas II	5·5s (4·3H, 1·4H)	90+ min·drop ⁻¹ (8 overnight drops)	12	4 – 35	Tags individually mounted, 2 m from bottom, dropped at 150 m intervals between receivers (66 drop sites)

where ‘VR2’ denotes number of receivers tested; ‘120s’ and ‘5s’ denotes tags with mean 120 sec and fixed 5 sec offtimes between pings, respectively; and, ‘Depth_{rec}’ and ‘Depth_{tag}’ denote water depth (m) at receiver site and tag drop site, respectively.

Table 2.2. Predictor variables investigated in logistic regression analysis of percentage of tag transmissions detected under varying spatial and environmental conditions.

Predictor	Units	Description
Distance	m	Distance between tag and receiver
Depth of tag	m	Water depth surrounding tag anchored 2 m off bottom
Depth of receiver	categorical	Water depth surrounding receiver anchored 5 m off bottom; takes positive value above, negative value below 17 m (median value of receiver depth)
Tidal phase	categorical	Divided into low, high, rising, and falling categories
Tidal height	m	Expressed as deviation from lower low water, computed as half-cosine function extrapolating between known high and low tide values from archive at Fort Jefferson National Monument, Garden Key, Dry Tortugas National Park, FL
Wind speed	knots	Continuous wind speed data averaged over interval
Barometric pressure	mBar	Barometric pressure averaged over interval
Air temperature	°C	Air temperature averaged over interval
Rugosity1*	ratio	Surface to flat area ratio around receiver at radius of distance to tag
Rugosity2*	ratio	Surface area : flat area ratio around receiver radius of 900 m
Rugosity3*	m	Elevation range (e.g. difference between max and min elevations) around receiver at radius of distance to tag
Rugosity4*	m	Elevation range at radius of 900 m
Rugosity5*	m	Coefficient of variation (CV) of elevation range around receiver at radius of 900 m
Rugosity6**	m	Coefficient of variation for elevation range along line between tag and receiver
Rugosity7**	ratio	Surface to flat length ratio along line between tag and receiver
Rugosity8**	degrees	Average slope of a line between drop site and receiver
Rugosity9**	degrees	Maximum slope between drop site and receiver
Rugosity10**	m	Elevation range along line between drop site and receiver
Rugosity11**	categorical	Presence of a reef edge; determined using bathymetric maps to identify large (>2 m), continuous reef slopes. Resulted in positive values for receivers located along the northwestern edge of the array, negative for other receivers

*computed by applying Surface Tools extension for ArcView® (Jenness 2008) on buffered circles created at 150 m radial intervals around each receiver

**computed by applying Surface Tools on polylines between receivers and tag drop sites

Table 2.3. Formulae for calculating weighted mean positions ($\bar{X}_{\Delta t}, \bar{Y}_{\Delta t}$) using arithmetic and harmonic approaches within an X- and Y-coordinate system.

Mean Type	Arithmetic		Harmonic	
Simpfendorfer et al. (2002)*	$\bar{X}_{\Delta t} = \frac{\sum_{i=1}^n R_i X_i}{\sum_{i=1}^n R_i}$	$\bar{Y}_{\Delta t} = \frac{\sum_{i=1}^n R_i Y_i}{\sum_{i=1}^n R_i}$	$\bar{X}_{\Delta t} = \frac{\sum_{i=1}^n R_i}{\sum_{i=1}^n \left(\frac{R_i}{X_i} \right)}$	$\bar{Y}_{\Delta t} = \frac{\sum_{i=1}^n R_i}{\sum_{i=1}^n \left(\frac{R_i}{Y_i} \right)}$
Maximum Range Weighted	$\bar{X}_{\Delta t} = \frac{\sum_{i=1}^n \left(\frac{R_i X_i}{W_i} \right)}{\sum_{i=1}^n \left(\frac{R_i}{W_i} \right)}$	$\bar{Y}_{\Delta t} = \frac{\sum_{i=1}^n \left(\frac{R_i Y_i}{W_i} \right)}{\sum_{i=1}^n \left(\frac{R_i}{W_i} \right)}$	$\bar{X}_{\Delta t} = \frac{\sum_{i=1}^n \left(\frac{R_i}{W_i} \right)}{\sum_{i=1}^n \left(\frac{R_i}{W_i X_i} \right)}$	$\bar{Y}_{\Delta t} = \frac{\sum_{i=1}^n \left(\frac{R_i}{W_i} \right)}{\sum_{i=1}^n \left(\frac{R_i}{W_i Y_i} \right)}$
Non-linear Probability of Detection Weighted	$\bar{X}_{\Delta t} = \frac{\sum_{i=1}^n \left(\frac{X_i}{W_i} \right)}{\sum_{i=1}^n \left(\frac{1}{W_i} \right)}$	$\bar{Y}_{\Delta t} = \frac{\sum_{i=1}^n \left(\frac{Y_i}{W_i} \right)}{\sum_{i=1}^n \left(\frac{1}{W_i} \right)}$	$\bar{X}_{\Delta t} = \frac{\sum_{i=1}^n \left(\frac{1}{W_i} \right)}{\sum_{i=1}^n \left(\frac{1}{W_i X_i} \right)}$	$\bar{Y}_{\Delta t} = \frac{\sum_{i=1}^n \left(\frac{1}{W_i} \right)}{\sum_{i=1}^n \left(\frac{1}{W_i Y_i} \right)}$

* Harmonic mean estimator corrected from original manuscript (C. Simpfendorfer, personal communication, 2008).

Note: n = number of receivers in the array; R_i , the number of receptions at the i^{th} receiver during Δt ; X_i , the X-coordinate of the i^{th} receiver; Y_i , the Y-coordinate of the i^{th} receiver; and W_i , a relative weighting factor.

Table 2.4. Parameter estimates for logistic regression models of probability of tag detection.

Variable	'Basic'		'Reduced'		'Full'	
	Value	Sig.	Value	Sig.	Value	Sig.
Intercept	4.916	<i>p</i> < 0.0001	8.088	<i>p</i> < 0.0001	563.542	<i>p</i> < 0.0001
Distance (m)	-0.0133	<i>p</i> < 0.0001	-0.026	<i>p</i> < 0.0001	-0.027	<i>p</i> < 0.0001
Distance²	<i>n/a</i>		0.00001	<i>p</i> < 0.0001	0.00001	<i>p</i> < 0.0001
Wind Speed (knots)	<i>n/a</i>		-0.087	<i>p</i> < 0.0001	-0.077	<i>p</i> < 0.0001
Receiver Depth (m)	<i>n/a</i>		0.107	<i>p</i> < 0.0001	0.103	<i>p</i> < 0.0001
Tidal Height (m)	<i>n/a</i>		<i>n/a</i>		-0.399	<i>p</i> < 0.0001
Surface Area Ratio	<i>n/a</i>		<i>n/a</i>		-553.91	<i>p</i> < 0.0001
CV of Elevation (m)	<i>n/a</i>		<i>n/a</i>		-0.193	<i>p</i> < 0.0001
Presence of Reef Edge	<i>n/a</i>		<i>n/a</i>		-0.317	<i>p</i> < 0.0001
AIC	105472.8		102933.4		99965.1	

Table 2.5. Mean positioning error (m) for harmonic (HM) and arithmetic (AM) mean positioning estimators applied to data from Test #5 at tag movement speeds greater than 0 and less than 1.5 m/s. Estimators computed using batching intervals of 5 minutes. Methods are sorted by precision, with paired t-test comparisons for means shown for method in row versus method in row immediately below.

Method	N	Min	Max	Mean	SE	SD	t	df	p < 0.05
Reduced Logistic HM	2287	6	794	231.8	2.9	139.9	-6.96	2286	*
Reduced Logistic AM	2287	6	794	231.8	2.9	139.9	2.88	2286	*
Full Logistic HM	2287	6	779	233.9	3.0	144.7	-0.11	2286	NSD
Max Range AM	2287	5	691	234.1	3.0	143.5	-0.06	2286	NSD
Full Logistic AM	2287	6	785	234.2	3.0	145.5	0.81	2286	NSD
Simpfendorfer et al. (2002) AM	2287	2	683	235.7	3.0	143.3	-1.94	2286	NSD
Basic Logistic HM	2287	5	806	239.4	3.0	143.3	-3.45	2286	*
Basic Logistic AM	2287	5	806	239.4	3.0	143.3	8.06	2286	*
Max Range HM	2287	5	673	257.6	3.0	144.8	28.21	2286	*
VR2	2287	3	1210	345.0	3.9	188.3			

Table 2.6. Rankings by lowest positioning error for harmonic (H) and arithmetic (A) mean positioning estimators retroactively applied to various range test detection time series.

Tag Code	Test	N	VR2*	Simpfendorfer et al. (2002)		Max Range Weighted		'Basic' Logistic Weighted		'Reduced' Logistic Weighted		'Full' Logistic Weighted	
				H	A	H	A	H	A	H	A	H	A
767	9	24935	7	1	2	3	4	5	6	5	6	5	6
766	9	186	6	3	2	4	5	1	1	1	1	1	1
765	9	634	8	5	6	7	4	1	2	1	2	1	2
4093	9	719	6	3	2	5	4	1	1	1	1	1	1
4093	8	375	5	4	3	4	3	1	2	1	2	1	2
4091	5	2538	8	3	3	3	3	4	5	1	2	3	3
Mean Rank			6.7	3.2	3	4.3	3.8	2.2	2.8	1.7	2.3	2	2.5
Standard Deviation			1.2	1.3	1.5	1.5	0.8	1.8	2.1	1.6	1.9	1.7	1.9
Total #1 Rankings			0	1	0	0	0	4	2	5	2	4	2

NOTE: N denotes number of detections occurring within batching intervals featuring detections from more than one receiver.

* assumes tag is located at coordinates of receiver registering detection

Figure 2.1. Bathymetric chart of northwestern quadrant of Dry Tortugas National Park (DTNP) Research Natural Area (RNA) illustrating: **(A)** ‘Tortugas I’ (black labeled circles) receiver placements; paths for Test #4 (white asterisks) and Test #5 (*3H*, white line; *4H*, thin black line); and, **(B)** ‘Tortugas II’ (white labeled circles) receiver placements; drop sites for Tests #2 and #3 (black asterisks); path for Test #6 (thick black line); and drop sites for Test #7 (white triangles), Test #8 (white circles), and Test #9 (black squares). Bathymetries computed using NASA LIDAR data and USGS multi-beam data. Note intersection of three management zones: DTNP, Florida Keys National Marine Sanctuary (FKNMS) open zones and Tortugas North Ecological Reserve (TNER). Note insets in A) illustrate position of DTNP within Gulf of Mexico, and intersection of management zones in region.

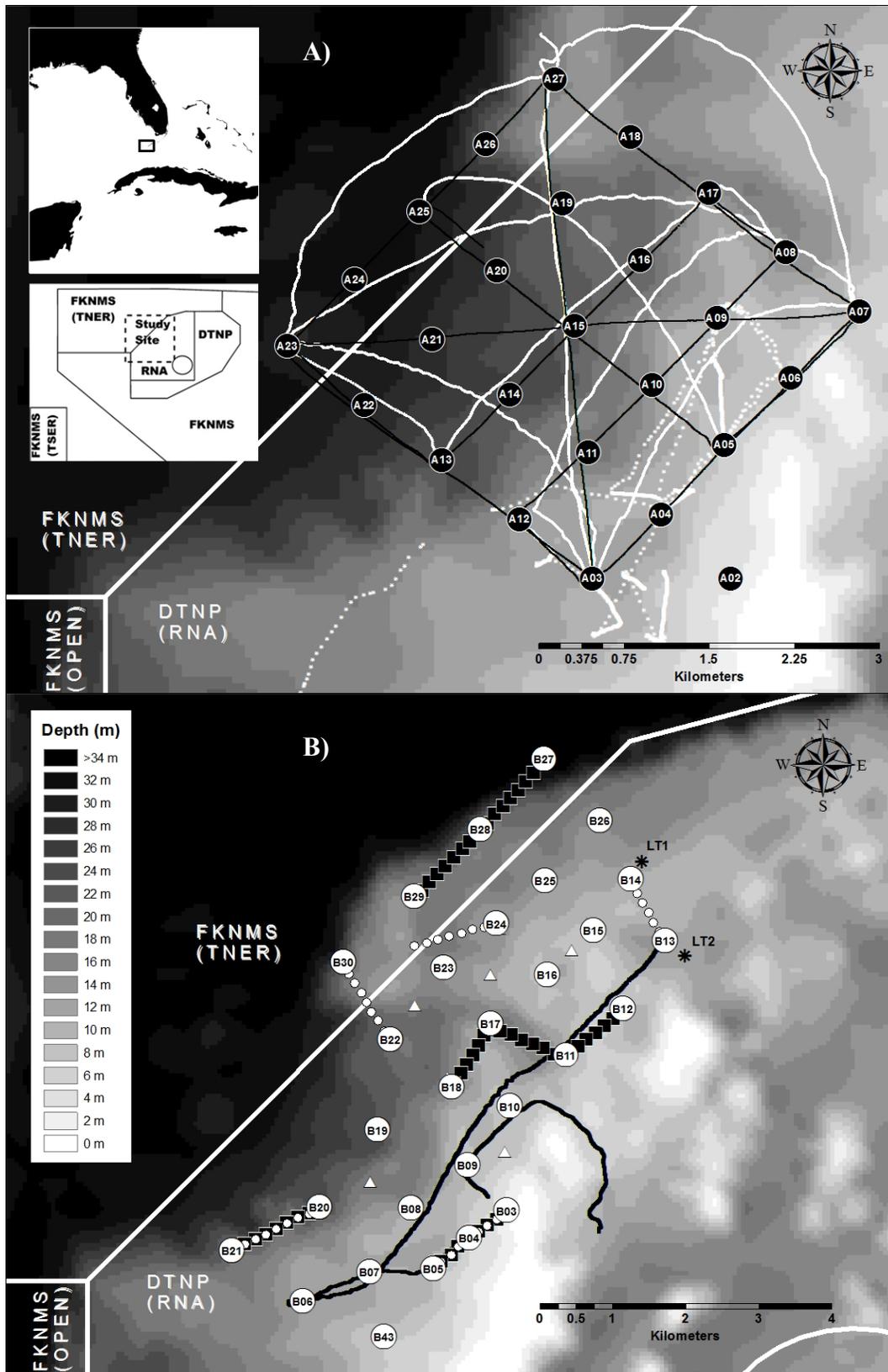


Figure 2.1

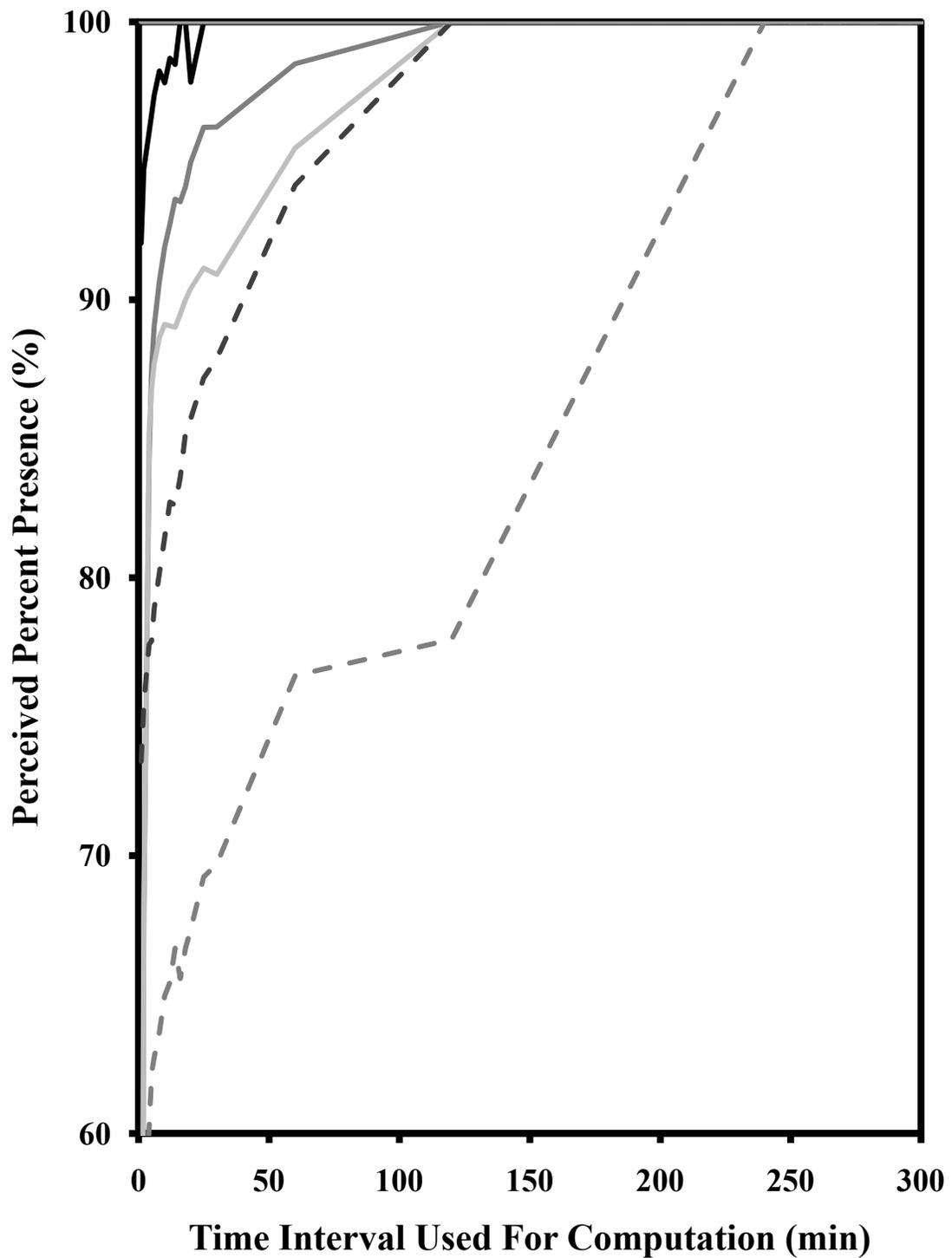


Figure 2.2. Percent intervals with at least one detection (e.g. ‘perceived presence’) for 5 tags anchored at 300 m from various receivers relative to time interval used for computation: Perceived Percent Presence = (Number of Intervals with Detections / Total Intervals).

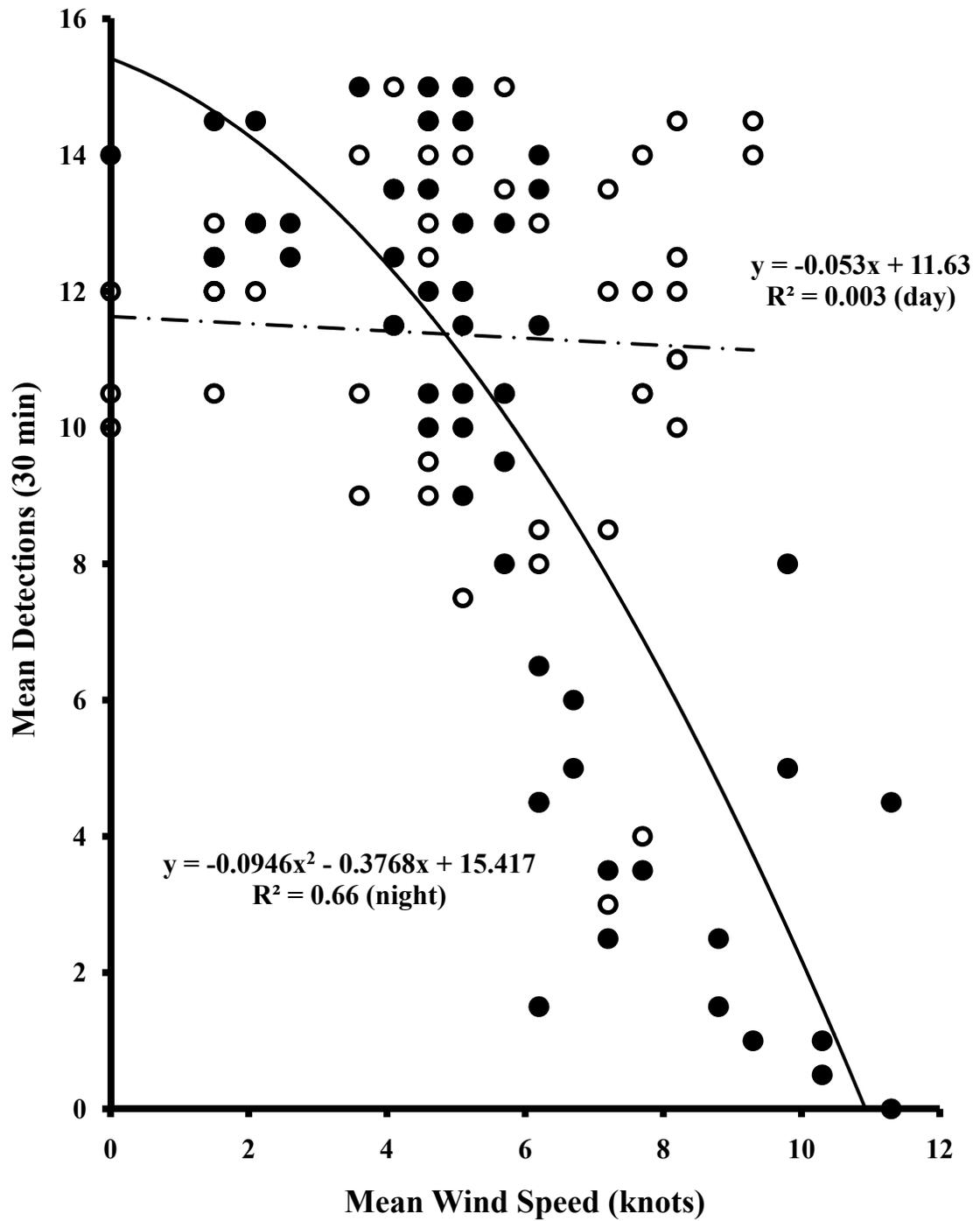


Figure 2.3. Mean number of detections vs. mean wind speed (knots) per 30 min interval for two tags located 300 m from a receiver in Dry Tortugas National Park, FL. Differences between day (open circles, n = 51) and night (closed circles, n = 61) detection patterns are illustrated, suggesting additional ambient noise factor at night contributing to reduced detection rates at high wind speeds.

Figure 2.4. Predictive range of A) linear, B) ‘reduced’ logistic, and C) ‘full’ logistic regression models for probability of tag signal detection at distance overlaid on data from Test #9. Logistic fits illustrate predictive range of multivariate models using maximum and minimum data values from observed data.

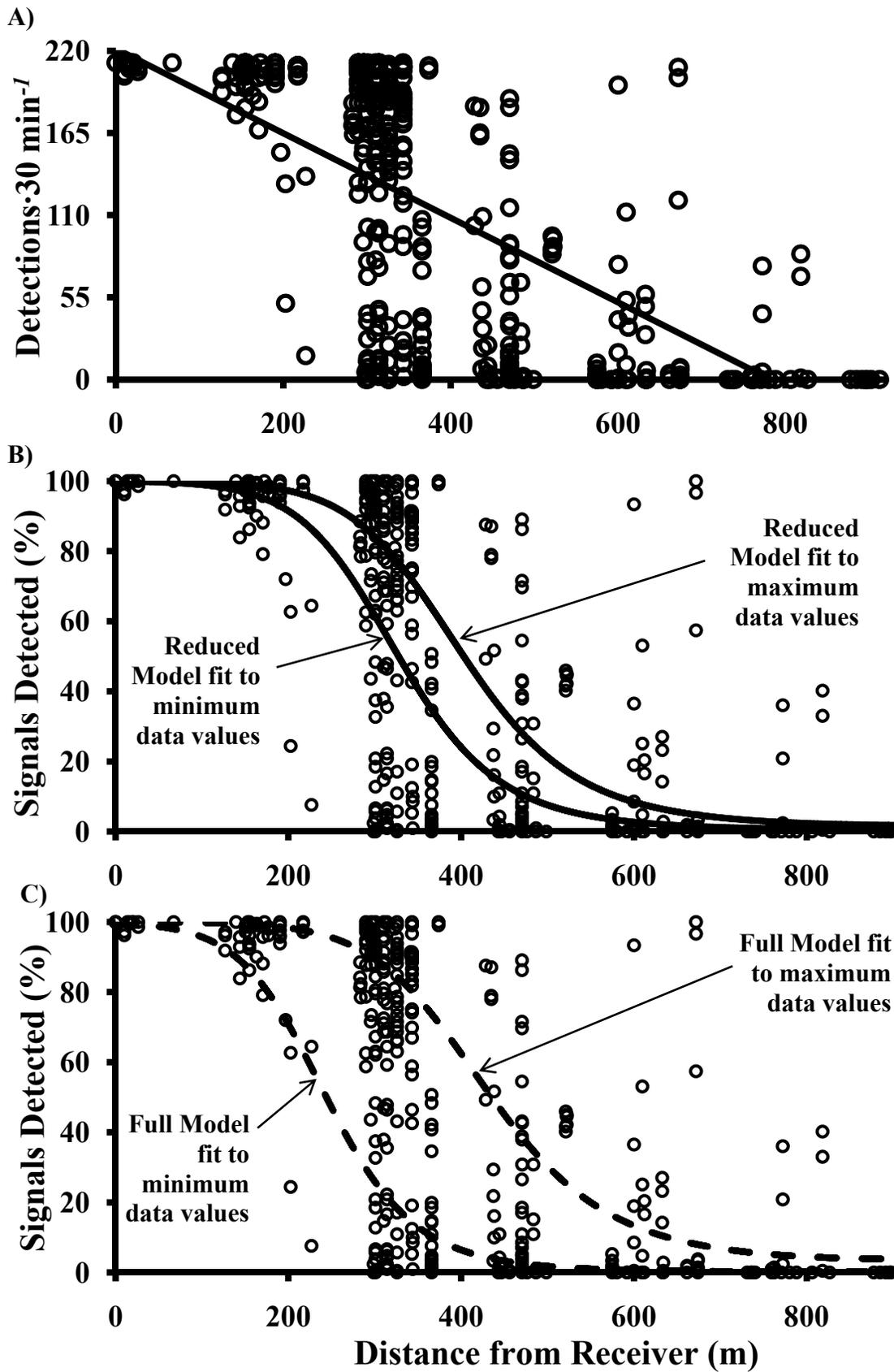


Figure 2.4.

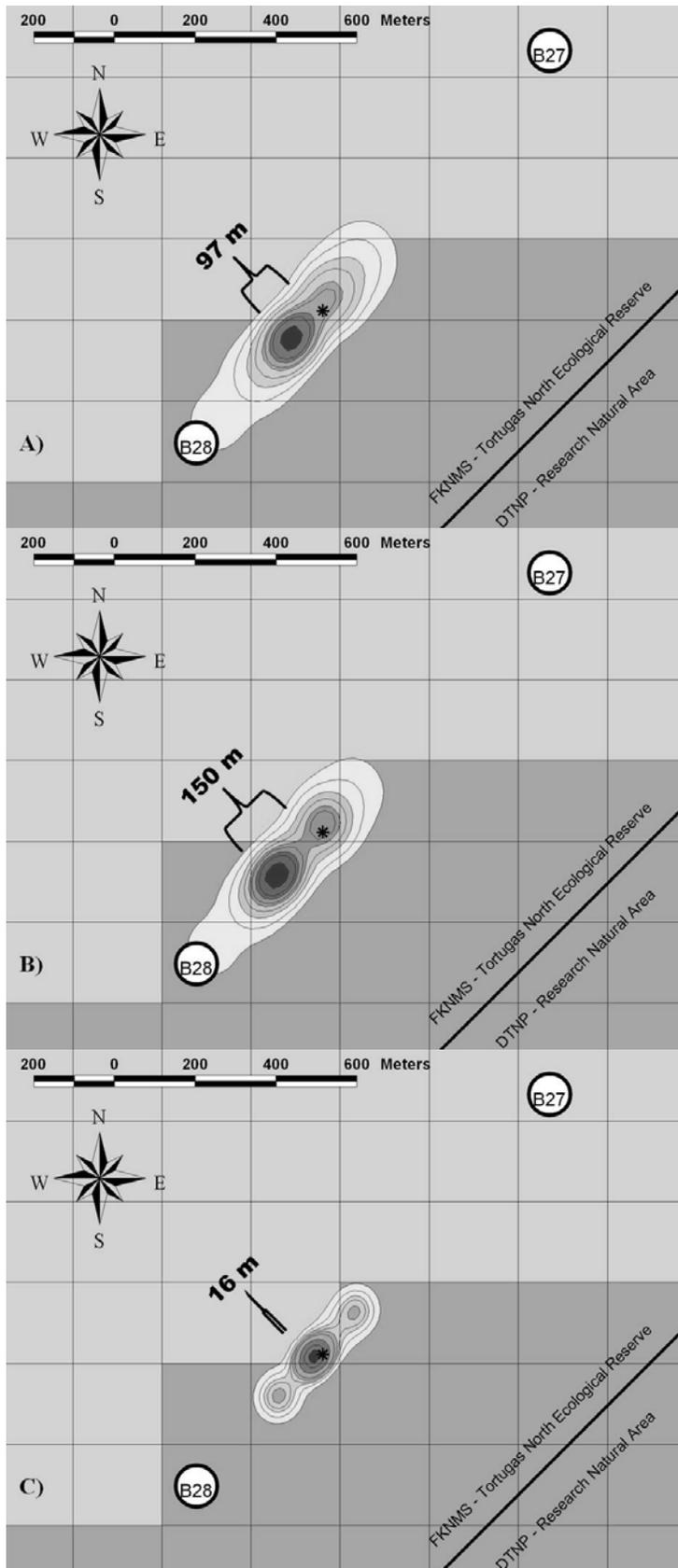


Figure 2.5. Estimated tag positions for 5 min batching intervals using A) Simpfendorfer et al. (2002) arithmetic mean, B) Simpfendorfer et al. (2002) harmonic mean, and C) ‘Reduced’ logistic weighted probability of detection harmonic mean estimator from this paper relative to actual tag positions from Test #9 (black asterisks). Receiver anchorages are shown as white circles with labels. Habitat types depicted are contiguous low-relief hardbottom (dark gray) and unknown (light gray). This separation corresponds roughly to the 20 m bathymetric contour. Kernel density contours ($h = 0.480750$) are plotted around each estimated location at 10% increments to illustrate spatial distribution of positioning estimates (see Worton 1989).

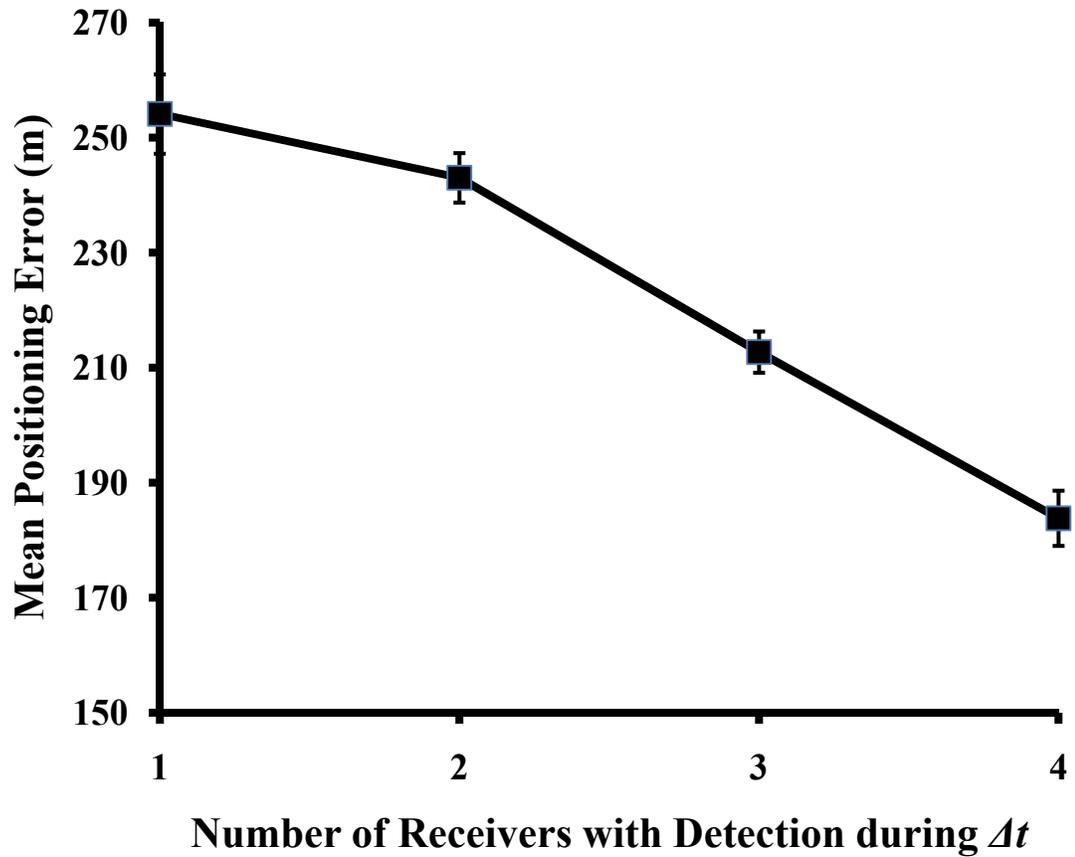


Figure 2.6. Illustration of mean positioning error associated with ‘Reduced’ logistic weighted harmonic mean positioning estimator relative to number of receivers recording detection of tag during 5-minute batching interval (Δt), computed through retroactive application of ‘Reduced’ logistic harmonic estimator to full dataset for Test #9.

Chapter 3

Movements and space use of groupers and snappers in the marine reserves of Dry Tortugas, Florida.

Summary

Movement patterns, home range size, and use of space by adult fishes are critical in determining the effectiveness of marine reserves in conserving adult fish biomass and/or providing biomass to adjacent fisheries through ‘spillover’. Home range, activity patterns, site fidelity and habitat preferences were examined for acoustically-tagged adult black grouper (*Mycteroperca bonaci*), red grouper (*Epinephelus morio*), mutton snapper (*Lutjanus analis*), gray snapper (*Lutjanus griseus*), and yellowtail snapper (*Ocyurus chrysurus*) using an array of omnidirectional hydroacoustic receivers deployed in the diverse coral reef environments of no-take marine reserves (NTMRs) in the Dry Tortugas, Florida. Grouper movements were small and infrequent, whereas mutton snapper and yellowtail snapper moved more frequently, and the gray snapper made long-distance diel migrations. Average home range sizes were $1.13 \pm 0.86 \text{ km}^2$ (\pm SE) for black grouper ($n = 2$, 57 – 75 cm total length, TL), $1.95 \pm 0.33 \text{ km}^2$ for red grouper ($n = 33$, 45 – 66 cm TL), 3.19 km^2 for gray snapper ($n = 1$, 54 cm TL), 7.64 km^2 for mutton snapper ($n = 1$, 70 cm TL), and $2.51 \pm 0.17 \text{ km}^2$ ($n = 4$, 48 – 55 cm TL) for yellowtail snapper. Exploited-phase groupers and snappers occasionally crossed reserve boundaries, and were more likely to do so where boundaries overlay contiguous reef, and when home range centers were close to reserve boundaries. Nevertheless, home range sizes estimated for red grouper, black grouper, and yellowtail snapper were small relative to the size of the NTMRs, suggesting that the NTMRs of the Dry Tortugas, Florida, afford significant protection for these species within the size ranges observed.

Background

The reef fish community of the Florida Keys and Dry Tortugas coral reef ecosystems supports a multibillion dollar industry for tourism and fishing (Ault et al. 2005a). A retrospective multispecies assessment of coral reef fish stocks has shown that the snapper-grouper complex has been serially overfished since the late 1970s, with many of these stocks below federal standards for sustainability (Ault et al. 1998, 2005b). In January 2007, a 158 km² no-take ‘Research Natural Area’ (RNA) was implemented in Dry Tortugas National Park (DTNP) as a shallow-water complement to the 391 km² Tortugas Ecological Reserve (TER), established in 2001 by the Florida Keys National Marine Sanctuary (FKNMS). These no-take marine reserves (NTMRs) are designed to protect valuable coral reefs and to ensure sustainability of intensely exploited regional fisheries resources (e.g., snapper-grouper complex).

Movement patterns, home range size, and use of space by adult fishes are critical in determining the effectiveness of marine reserves in conserving adult fish biomass and/or providing biomass to adjacent fisheries through ‘spillover’ (Russ & Alcala 1996, Zeller 1997b, Kramer & Chapman 1999, Lembo et al. 1999, Palumbi 2001, O’Dor et al. 2004). Unfortunately, for most exploited fish species, empirical data quantifying long-term movement patterns and space requirements are extremely limited (Roberts & Polunin 1991, Kramer & Chapman 1999, Sladek-Nowlis & Roberts 1999, Chapman & Kramer 2000, Meyer & Holland 2005, Meyer et al. 2007). As such, most reserves have been implemented on an *ad hoc* basis, which may generate over-confidence about resource protection (Eristhee & Oxenford 2001). Improperly configured reserves that fail to account for the scale of animal movements or the locations of core habitats may lead to

high levels of spillover that prevent the reserve from effectively functioning as a buffer against fishing effort (Eklund et al. 2000, Eristhee & Oxenford 2001).

There is a broad scientific and management interest in developing a better understanding of how the NTMRs of the Tortugas region will function as tools for rebuilding fisheries and conserving marine biodiversity throughout South Florida. In 2006, a broad-scale passive acoustic monitoring study was initiated to estimate home range size and quantify flux rates across reserve boundaries for key exploited reef fish species. This paper describes spatial and habitat requirements for black grouper (*Mycteroperca bonaci*), red grouper (*Epinephelus morio*), mutton snapper (*Lutjanus analis*), gray snapper (*Lutjanus griseus*), and yellowtail snapper (*Ocyurus chrysurus*) ascertained from acoustic telemetry. These findings highlight important considerations in reserve design (i.e. sites, shapes, sizes) and permit a qualitative assessment of the capacity of currently implemented reserves to promote sustainable fisheries.

Methods

The Dry Tortugas are a set of seven islands located approximately 112 km west of Key West, Florida, USA. The Tortugas region is nationally renowned for its productive coral reef ecosystem, diverse natural resources, broad recreational fishing opportunities, and spectacular scenic beauty. It is one of the best studied areas in the Florida Keys in terms of its benthic habitats and biological communities, bathymetry, and ocean physics (Ault et al. 2001, Franklin et al. 2004), and contains some of the broadest expanses of contiguous coral reef in the United States. Located upstream of the Florida Keys where the Florida Current merges into the Gulf Stream, the Tortugas region is believed to have

supported overexploited regional fisheries for greater than two decades through export of larvae and density dependent emigration of adult biomass (Ault et al. 2003b).

In March 2006, an array of 25 VEMCO VR2 (VEMCO Ltd., Nova Scotia, Canada; www.vemco.com) hydrophone-receivers were deployed in a representative suite of depths and benthic reef habitats in the northwestern quadrant of the DTNP RNA along the border of the North TER (Ault et al. 2007a; Fig. 3.1 & 3.2; black circles). In January 2007, this array was expanded and reconfigured to provide broader coverage of reef habitats (Fig. 3.1 & 3.2; white circles). Depths and benthic habitats were classified using by multibeam side-scan sonar, RVC ground-truthing, LIDAR, and aerial photography. Each omnidirectional VR2 hydrophone functions as a submersed passive acoustic listening station capable of detecting and archiving a unique ID code, date and time for acoustically tagged fish that pass within range. The 2006 receiver array provided partial acoustic coverage across approximately 16 km² (6.2 mi²), and the 2007 array covered approximately 30 km² (11.6 mi²), with an average receiver spacing of 832 m (0.52 miles). Spatially and temporally unique receiver detection ranges were rigorously calibrated using a variety of techniques described in Chapter 2.

External Tagging

Fish captured at locations in and nearby the acoustic array over a range of sizes using hook-and-line gears and trapping were tagged externally to provide information regarding long-distance movements. In 2006, streamer tags were anchored between the dorsal pterygiophores using a Mark II pistol grip gun with Floy FD-94 t-bar tags (www.floytag.com). In 2007, tags were inserted using a Floy 'jab stick' mounted with

Floy FIM-96 double-barb anchor tags (www.floytag.com). All streamer tags were marked with an ID number; instructions to record the fish length, date, time, and GPS position at time of capture; and a toll-free tag reporting number and email address.

Acoustic Telemetry Tagging

Selected fish exceeding 45 cm total length (TL) in good condition upon capture by hook and line underwent a surgical procedure in which an acoustic transmitter was placed in their abdomen. In 2006 (Fig. 3.2, yellow labels), VEMCO V16-3H coded tags operating on 69 kHz frequency with 158 dB (1 μ Pa @ 1 m) power output were used. Of the 33 tags used, 10 (e.g. ID Codes 862 – 872) were preprogrammed with 20 to 69 s random delays between coded transmissions (expected life ~ 56 d), and 23 (ID Codes 170 – 194) were preprogrammed with 30 to 79 s random delays (expected life ~ 62 d). In 2007 (Fig. 3.2, blue labels), VEMCO V16-3H coded tags (ID Codes 32 – 59) configured to ping randomly every 60 to 180 sec with 158 dB power output (expected life ~ 130 d) and VEMCO V16-4H coded tags (ID Codes 873 – 884) configured to ping every 20 to 69 sec with 153 dB power output (1 μ Pa @ 1 m; expected life ~ 570 d) were used. All tags were 58 mm long and 16 mm in diameter. Randomization of transmission times reduces the likelihood of tag signal collisions with multiple tagged individuals within the array (Pincock & Voegeli 2002). The relatively short delay times increase the probability of tag transmission when in range of a receiver (Lokkeberg et al. 2002). For all fish, the weight of the tag in water did not exceed 1.4% of the body weight.

The surgical tagging procedure was modified from Bolden (2001). Fish were brought to the surface as slowly as possible, to minimize swim-bladder expansion. As

fish were held in a recovery net over the side of the boat, a 192 quart cooler was filled with fresh seawater from the site of capture. An aerator or saltwater pump was used to continually cycle fresh oxygen through the cooler. When an aerator was used, 5 gallons of seawater were filtered out and replaced by a fresh bucket once during each 5 minute surgery. Fish were placed in the cooler and the hook was carefully removed. Length measurements were taken using a ruler on the side of the cooler, and weight measurements were taken using a calibrated jaw-locking weighing tool (BogaGrip, Eastaboga Tackle, Eastaboga, AL, USA). Surgical instruments were sterilized in 70% isopropyl alcohol and all surgical personnel wore clean latex gloves. Fish with slightly distended swim-bladders were vented using a venting tool applied at the junction of the fully extended pectoral fin and abdominal cavity. Gentle manual massage underwater was used to rapidly expel bubbles. All fish undergoing this procedure returned immediately to a normal swimming posture.

Healthy, oriented fish were then placed in a soft mesh sling that allowed them to be held on their backs while remaining fully immersed in the aerated seawater bath. A small para-medial incision (~1.5 cm) was made with a disposable scalpel midway between the pelvic fin origin and the cloaca. This incision was made in two steps: a preliminary cut through the integument and muscle, and a secondary cut through the parietal peritoneum into the coelom. Acoustic transmitters were inserted through the incision into the coelom of the fish to a position anterior to the anus and at least 9 cm behind the pelvic fin to reduce tension on the incision. Vicryl undyed 27" curved needles with 2-0 Chromic gut were used in conjunction with a hemostat to close the incision with 3-5 individual stitches. Powder-form antibiotic Oxytetracyclin was applied to the closed

incision to ward off infection. The fish was then released from the sling and assessed for overall health and swimming orientation. Fish next received an external “anchor” tag following the procedure described above (see ‘External Tagging’). A small amount of Oxytetracyclin was applied to this puncture. Fish were given approximately 2-3 minutes of recovery time in the cooler, and were then released and monitored to ensure they successfully reached the bottom.

Data Analysis

Unless otherwise specified, all operations below were performed on datasets for individual fish, and then pooled by species for analyses. Prior to data analysis, all VR2 receiver data were corrected for temporal drift using a correction formula assuming a linear degrade or prograde in recorded time based upon the time of initialization, recorded time of download, and actual time of download (D.M. Webber, VEMCO Ltd., pers. comm.). Next, data were adjusted for daylight savings time and filtered for spurious detections; considered to be any detection single transmitter code detection occurring alone in a 24 hr period. This reduced the influence of ‘false detections’ on the interpretation of tracking data (Heupel et al. 2006). Additionally, detections of each tag within the first 24 hrs after its deployment were excluded from analyses to reduce the impacts of ‘unnatural’ post-surgical behavior upon interpreted movements.

Tracking data were further filtered by applying a weighted harmonic mean estimator to archived tracks batched over 5 min and 2 hr intervals (see Chapter 2). This approach creates a series of short term ‘centers of activity,’ calculated as the means of receiver locations weighted by the estimated distance of the tag from the receiver during

each batching interval. Batching data into short time intervals reduces autocorrelation in position fixes and helps data meet assumptions of many statistical home range models. Use of a weighted arithmetic mean estimator reduces positioning error by accounting for the impacts of spatial differences in the depth of each receiver and the rugosity of its surrounding environment, and temporal differences in current flow and wind-generated noise upon the likelihood of a tag transmission being detected (see Chapter 2). In addition to generating a sequence of short term activity centers, an overall center of activity (e.g. ‘centroid’) was computed.

Distances Moved

Mobility was characterized both by distances moved and frequency of movement. Distances between consecutive position estimates were computed using custom software written in Java 6.10 (Sun Microsystems, Inc., Santa Clara, CA) and the Animal Movement Analysis Extension (AMAE) for ArcView (Hooge & Eichenlaub 1997). Relative frequency of movement was determined as percentage of consecutive intervals with a detected change in position (e.g. percent non-zero movements). Distances moved between detections were compared among species using a Kruskal-Wallis H test, with post-hoc pairwise comparisons conducted using Mann-Whitney U tests.

Boundary Crossings

A fish was considered to have crossed the Research Natural Area (RNA) boundary if a 5-min mean activity center was located outside of the RNA. A fish was considered to have remained outside the RNA until a subsequent mean activity center

was located within the RNA. One-way analysis of variance (ANOVA) was used to evaluate differences in time spent outside of the RNA across species using ‘Time Outside RNA’ as the response variable and ‘Species’ as the factor.

Percent Time in Array

As calibration work within the acoustic array suggested at least 2 hrs was necessary to determine the presence of a stationary tag at 300 m from a receiver (see Chapter 2), we expressed percent time in the array as the number of ratio of 2 hr intervals with detections to the total number of 2 hr intervals between the first and last detection of the fish. Use of 2 hr intervals also reduced the probability of extreme ambient noise (e.g. high wind speed, boat passage, rainfall, etc.) or tag signal interference (AMIRIX 2007) leading to false conclusions of tag absence.

Lunar Movement Patterns

Each 2 hr interval was assigned a lunar phase. To meet assumptions of homogeneity of variance and simplify interpretation, lunar phase was broken into quartiles, and one-way ANOVA was used to compare the percentage of expected detections obtained within 2 hr intervals for each species relative to the phase of the lunar cycle (Sokal & Rohlf 1995). Post-hoc comparisons were made using Dunnett’s C assuming unequal variances to identify whether detections were highest during the phase 0 (new to quarter full), 1 (quarter to half full), 2 (half full to three-quarters full), or 3 (three-quarters full to full) moon. Note this categorization makes no distinction between

‘waxing’ and ‘waning,’ instead expressing lunar phase as a function of nocturnal luminosity.

Diel and Seasonal Movement Patterns

To test the effects of the diel solar cycle on fish detection patterns, we coded each detection as occurring either within 1 hr of sunrise (‘Dawn’), within 1 hr of sunset (‘Dusk’), 1 hr after sunrise and 1 hr before sunset (‘Day’), or ‘Night’. We used independent t-tests assuming unequal variances to investigate differences in percent expected transmissions detected per 2 hr interval within species using ‘Day’ and ‘Night’ as factors. We then standardized the data for each diel interval by dividing the number of detections obtained during that interval by the total number of hours available during that interval for that day and the ping rate of the tag, resulting in an estimate of the percentage of expected transmissions actually detected. Data was pooled by species. One-way ANOVA was used to compare the percentage of expected detections relative to the diel category, with post-hoc comparisons using Dunnett’s C assuming unequal variances used to identify differences between diel categories. Non-parametric Friedman tests for related samples were used to test for differences in number of detections and number of receivers recording detections within diel intervals. To identify differences in distances moved, one-way ANOVA was used to compare distances between successive 5-min mean positioning estimates relative to diel category, with post-hoc comparisons using Dunnett’s C assuming unequal variances.

Home Range Utilization

To determine utilization of a home range, minimum convex polygon (MCP) home range estimates were generated for each day for each fish's tracking dataset using the AMAE (Hooge & Eichenlaub 1997), and were plotted as area-observation curves. If the area-observation curves achieved a visually-recognizable asymptote, the home range estimates were considered reliable for that fish (Laundré & Keller 1984). MCP home ranges were used to describe the overall shape and size of the area covered by each fish (MacDonald 1980, Meyer et al. 2000). For fish with linear home ranges (e.g. detections at multiple receivers in a straight line), home range size was estimated by multiplying the maximal detection area per receiver [$\pi (915 \text{ m})^2$] by the number of receivers in the line. Preliminary analyses suggested that fish with home ranges in the center of the array had detections registered in at least 10% of their 5-min batching intervals, so to reduce bias, fish detected at receivers along the periphery of the array were excluded from subsequent home range analyses if less than 10% of their 5-min batching intervals contained at least one detection.

To examine stability of home range size through time, single-factor ANOVA was used to evaluate differences between monthly MCP home ranges for each fish. Paired t-tests were used to compare daily MCP home range sizes between day and night for each fish. Linear regression was used to examine relationships between fish length and weight and home range size by species. Percent MCP home range overlap between conspecifics was computed using Hawth's Tools 'Polygon in Polygon Analysis' extension for ArcGIS (Beyer 2004). Linear regression was used to evaluate differences in percent home range overlap relative to size differences between individual conspecifics caught in the same

location. Independent t-tests were used to examine variation in mean percent overlap relative to dominant habitat type and level of structural relief. Identical tests were performed using linear distance between overall mean positions as the response variable.

Habitat Utilization

Differences in habitat utilization were computed by creating a habitat selection index (HSI) for each fish with a home range. Reef habitats were characterized by coverage: contiguous (C); isolated (I); and spur-and-groove (SG), and level of relief: low (L), medium (M), and high (H). HSI was computed as the ratio between the number of 5- min activity centers in a habitat relative to the availability of that habitat within the area defined by the fish's MCP home range. Number of activity centers within each habitat category was computed for each fish using the Hawth's Tools 'Count Points within Polygons' extension for ArcGIS (Beyer 2004). Multiple regression was used to examine whether home range size was partially explained by percentage of habitat type utilized. For this regression analysis, habitat was categorized as continuous, isolated, or spur-and-groove. A second analysis was conducted using habitat categorized as low- or high-profile relief. Natural boundaries to movement were identified by examining dominant habitat types around receivers recording no detections.

Results

Fish Tagged

Between Mar 2006 and Nov 2007, we tagged 161 fish representing 15 species with external streamer tags. Of these, 65 fish representing 11 species were also fitted

with acoustic transmitters. Through Nov 2008, we obtained nearly 2.5 million detections from these fish (Table 3.1), which include red grouper (*Epinephelus morio*), black grouper (*Mycteroperca bonaci*), gray snapper (*Lutjanus griseus*), yellowtail snapper (*Ocyurus chrysurus*), mutton snapper (*Lutjanus analis*), tiger shark (*Galeocerdo cuvier*), Caribbean reef shark (*Carcharhinus perezii*), greater amberjack (*Seriola dumerili*), jolthead porgy (*Calamus bajonado*), and horse-eye jack (*Caranx latus*). In addition, several nurse sharks (*Ginglymostoma cirratum*) acoustically tagged by Mote Marine Laboratory of Summerland Key, Florida were also detected within our array. Red grouper comprised 69% of the acoustically tagged fish; however, larger sizes were slightly underrepresented (Fig. 3.3) relative to population size structure as estimated by visual census methods (Ault et al. 2007a). Tracking periods across species ranged from 2 to 280 d, with an average of 102 ± 7.6 d (mean \pm SE).

In 2006, six (7%) of the 83 tagged fish were recaptured and of these, three were re-released in good condition (two by the author and another by a recreational charter guide). The three re-releases occurred within 25 days of initial capture. The three other recaptures occurred between 42 and 142 days after initial capture and external t-bar tags were absent, but internal tags were discovered during gutting of the fish. All recaptures in 2006 occurred within 2 km of the original capture location, with the majority (67%) occurring within 100 m of the original capture site. All fish were reported healthy and actively feeding, although those fish with silk sutures had developed an abscess around the surgical scar. No recaptures were reported following implementation of the RNA in January 2007.

Movement Patterns and Distances Moved

Movement patterns exhibited by fish were diverse. Percent of the total number of detections varied widely between receivers (Fig. 3.2). Most red and black groupers appeared to remain within a core habitat encompassed by the detection radii of one or two hydrophones across the expected life span of their acoustic tags, although rare to occasional detections at other locations did occur. For groupers and snappers, similar receiver detection patterns were almost invariably observed for individuals that had been tagged at the same location (e.g. Fig. 3.4).

A few red grouper did not demonstrate utilization of a core habitat. Fish 172, 179, and 870 were all detected at a high number of unique receivers and were only present in the array for a short while (2, 23, and 25 d) as compared to the mean in 2006 of 75 d. Fish 172 and 179 were the only two red grouper detected leaving the array in 2006, and fish 870 had only 8 days of consistent detections, oscillating between Sites A7 and A8 with sporadic detections at adjacent sites, then essentially disappeared, with only 4 additional detections over the next 17 days. In 2007, fish 36 and 47 both displayed broad-ranging movement patterns and were only present in the array a short while (17 and 10 d) as compared to the mean in 2007 for their tag type of 102 d. These two fish were the only fish with complications during their surgeries; as such, the movements exhibited by these fish may be “unnatural”. There was no significant trend in terms of total size associated with these movement strategies as compared to the fish demonstrating high site fidelity.

Relative frequency of detected movement varied between species (Fig. 3.5). Movement frequency for black grouper ($N = 2$), red grouper ($N = 45$), and gray snapper

($N = 1$) was less than 1%. Movement frequency for mutton snapper ($N = 2$) and yellowtail snapper ($N = 5$) was less than 6%.

When movements were detected, the distances moved varied significantly between species ($F_{4,23842} = 565.3$, $p < 0.001$, Fig. 3.6). Post-hoc testing with Dunnett's C found significant differences for all interspecies comparisons ($p < 0.001$) save red grouper and mutton snapper. The majority of yellowtail snapper (*mean*: 137.5 ± 0.11 m) movements were less than 400 m in distance. The majority of movements by black grouper (*mean*: 210.71 ± 0.35 m), red grouper (*mean*: 400.63 ± 0.02 m), and mutton snapper (*mean*: 363.42 ± 0.14 m) were less than 600 m in distance. All movements by gray snapper (*mean*: 1215.16 ± 0.13 m) exceeded 1000 m.

Boundary Crossings

Detected flux rates across reserve boundaries varied by species and by year. In 2006, only 2 of 31 (6%) grouper were detected moving across RNA boundaries. During 2007, 4 of 14 (29%) acoustically tagged red grouper were detected moving across RNA boundaries periodically into TNER. Fish 36 crossed the RNA boundary 118 times and spent 34% of its time in the TNER. Fish 47 and Fish 875 both crossed the boundary 4 times, but the amount of time they spent outside the reserve was less than 1% of their total time in the array. Fish 884, Fish 179, and Fish 172 all crossed the boundary 2 times, but spent less than 2% of their total time in the TNER.

No black grouper were detected moving across reserve boundaries in either year. Only 1 of 5 (20%) of tagged yellowtail snapper moved across the reserve boundary; Fish 57 crossed the boundary 62 times but spent less than 2% of its total time in TNER. The

gray snapper crossed the boundary 10 times, spending 3.4% of its time in TNER. Only 1 of 2 (50%) mutton snapper moved across reserve boundaries, but it did so 702 times, spending 9% of its time in TNER. Linear regression analysis revealed that log-transformed distance of home range center from RNA boundaries was a significant predictor of time spent outside of the RNA for red grouper ($\beta = -0.638$, $F_{1,43} = 29.51$, $p < 0.001$), accounting for 40% of the variance in time spent outside the reserve.

Percent Time in Array

Percent time fish were detected in the acoustic array varied by species. No significant differences in percentage of full 5-min batches were detected between any snapper or grouper species (Fig. 3.7). Fish that were always detected within the center of the acoustic array (e.g. no edge effects) had a recorded detection in at least 10% of their 5 min batching intervals.

Lunar Effects

A significant association between percentage of transmissions detected and lunar phase was found for yellowtail snapper ($F_{3,4982} = 5.70$, $p < 0.01$), with more detections during the half full to full moon than during the new to half full moon. Mutton snapper ($F_{3,2156} = 4.64$, $p < 0.01$) showed the opposite pattern, with significantly higher detections during the new moon than the full moon. This is due in part to two long absences by Fish 53 prior to the full moon, which may correspond to spawning migrations (Fig. 3.8). Red grouper ($F_{3,60321} = 69.32$, $p < 0.001$) had the most detections during the half to three-quarters full moon and lowest at the new moon. No significant associations between

percentage of transmissions detected and lunar phase were found for black grouper ($F_{3,3234} = 2.31, p = 0.075$).

Diel Movement Patterns

The percentage of expected transmissions detected varied by species and by time of day (Fig. 3.9; BG: $F_{3,1068} = 27.59; p < 0.001$, GS: $F_{3,464} = 64.02; p < 0.001$, RG: $F_{3,18564} = 87.35, p < 0.001$, YTS: $F_{3,1536} = 8.06, p < 0.001$). Post-hoc comparisons revealed black grouper and the gray snapper were detected most frequently during the day, and more frequently at dawn than at dusk, and more frequently at dusk than at night. Red grouper were detected most frequently during the day, and more frequently at dawn and dusk than at night. Yellowtail snapper were detected most frequently during the day.

Despite ‘crepuscular’ time periods representing less than half the total time allotted to the ‘day’ and ‘night’ time periods, respectively, the majority of species tracked were detected at more receivers during these ‘crepuscular’ time periods than any other. Black grouper, red grouper, mutton snapper, and yellowtail snapper were detected at more receivers during crepuscular time periods than during the day (BG: $\chi^2_{268,1} = 157.3, p < 0.001$; RG: $\chi^2_{4642,1} = 2160.6, p < 0.001$; MS: $\chi^2_{150,1} = 14.4, p < 0.001$; YTS: $\chi^2_{385,1} = 27.9, p < 0.001$), and at more receivers during the day than at night (BG: $\chi^2_{268,1} = 62.1, p < 0.001$; RG: $\chi^2_{4642,1} = 305.7, p < 0.001$; MS: $\chi^2_{150,1} = 31.3, p < 0.001$; YTS: $\chi^2_{385,1} = 32.0, p < 0.001$). The gray snapper was detected at more receivers during crepuscular time periods than during the night ($\chi^2_{117,1} = 13.6, p < 0.001$) or the day ($\chi^2_{117,1} = 71.2, p < 0.001$).

Distances moved varied by species and by time of day. Black grouper moved farther during the day than any other time ($F_{3,84103} = 56.90$; $p < 0.001$). Red grouper moved farther during the day than at night ($F_{3,2103423} = 95.37$; $p < 0.001$). The gray snapper moved much farther at night than any other time, and farther at dawn than at dusk or during the day ($F_{3,25454} = 256.23$; $p < 0.001$). Mutton snapper moved farther during the day and at dusk than any other time, and farther at night than at dawn ($F_{3,22001} = 62.63$; $p < 0.001$). Yellowtail snapper moved farthest at night and at dawn ($F_{3,88760} = 10.51$; $p < 0.001$).

Home Range Utilization

Most groupers and snappers exhibited movements consistent with use of a home range contained within the bounds of the acoustic array (Table 3.2). Mutton snapper MCP home range was 16.10 km²; however, elimination of sites visited only in transit during presumed spawning migrations reduced this estimate to 7.64 km² (Fig. 3.8). No significant differences were found in home range sizes between species (Fig. 3.11). No significant relationships were found between red grouper total length ($F_{1,31} = 0.05$, $p > 0.05$) or weight ($F_{1,31} = 0.14$, $p > 0.05$) and MCP home range size.

No significant differences in MCP area between months were detected for black grouper ($F_{4,2} = 0.82$, $p > 0.05$), red grouper ($F_{5,60} = 0.74$, $p > 0.05$), or yellowtail snapper ($F_{4,4} = 0.67$, $p > 0.05$). Insufficient data were available to test other species. No significant differences between day and night activity spaces were found for any species. Due to limitations on sample size, percent MCP home range overlap could only be computed for red grouper and yellowtail snapper. On average, red grouper ($n = 160$

comparisons) home ranges overlapped $0.243 \pm 0.03 \text{ km}^2$ ($21.93 \pm 2.61\%$), and yellowtail snapper ($n = 3$ comparisons) home ranges overlapped $0.818 \pm 0.570 \text{ km}^2$ ($27.05 \pm 20.15\%$). Restricting this analysis to comparisons between fish captured at the same location increases estimates of overlap for red grouper ($n = 25$) to $0.537 \pm 0.125 \text{ km}^2$ ($43.01 \pm 7.12\%$) and 1.96 km^2 (67.31%) for yellowtail snapper ($n = 1$). Linear regression analysis revealed that percent overlap between fish MCP home ranges increased significantly with increasing fish total length ($\beta = 2.88$, $F_{1,48} = 5.40$, $\text{adj. } r^2 = 0.08$, $p < 0.05$) and weight ($\beta = 23.41$, $F_{1,48} = 10.21$, $\text{adj. } r^2 = 0.16$, $p < 0.05$). Red grouper in continuous habitat ($n = 31$) had significantly lower mean percent MCP home range overlap ($38.01 \pm 5.42\%$) than red grouper in isolated habitat ($n = 7$; $\text{mean} = 90.12 \pm 5.68\%$; $t = -4.42$, $df = 36$, $p < 0.001$) and spur-and-groove habitat ($n = 2$; $\text{mean} = 97.41 \pm 2.59\%$; $t = -2.74$, $df = 31$, $p < 0.05$). Red grouper in high relief habitats ($n = 6$) had significantly higher mean percent MCP home range overlap ($87.34 \pm 6.45\%$) than red grouper in low-relief habitats ($n = 34$; $\text{mean} = 43.53 \pm 5.81\%$; $t = 3.09$, $df = 38$, $p < 0.01$). Similar analyses with distance between home range centroids failed to reveal any significant relationships with total length, weight, dominant habitat type, or dominant level of relief. Mean distance between home range centers for red grouper ($n = 25$) caught at the same time and location was $611.36 \pm 179.53 \text{ m}$.

Habitat Utilization

Habitat utilization varied among species. Black grouper ($n = 2$) were associated with two identified habitat types, showing the highest percent utilization for ILR ($49.94 \pm 49.87\%$), followed by CLR ($0.42 \pm 0.34\%$). Mutton snapper ($N = 2$) were associated with

CLR (86.85 ± 12.34). Red grouper ($n = 45$) were associated with six identified habitats, showing the highest percent utilization of ILR ($31.95 \pm 6.17\%$), followed by CLR ($26.65 \pm 5.90\%$), CHR ($7.81 \pm 3.53\%$), CMR ($4.00 \pm 2.56\%$), and SGHR ($2.67 \pm 1.82\%$).

Yellowtail snapper ($n = 5$) were associated with six identified habitats, showing the highest percent utilization of CLR ($92.62 \pm 2.42\%$), followed by IHR ($1.06 \pm 1.06\%$), CHR ($0.14 \pm 0.10\%$), ILR ($0.13 \pm 0.12\%$), SGHR ($0.04 \pm 0.04\%$), and IMR ($0.02 \pm 0.02\%$).

Habitat selection varied among species (Fig. 3.12). In general, black grouper, gray snapper, and red grouper underutilized CLR relative to its abundance within their home range; whereas mutton snapper and yellowtail snapper appeared to select it. Red grouper appeared to avoid isolated reef structures in favor of contiguous structures. Yellowtail snapper appeared to avoid isolated and high relief habitats. There was no significant relationship between red grouper home range size and percentage of continuous, isolated, or spur-and-groove habitat utilized ($r^2 = 0.02$, $p < 0.89$); nor percentage of low- or high-profile habitat utilized ($r^2 = 0.007$, $p < 0.91$).

Broad, deep, continuous expanses of sand appeared to be a natural boundary to movement for reef fish. In 2006, receivers at sites A23, A24, and A25 were located in sand habitats off the reef shelf. No detections of groupers or snappers occurred in sand habitats. These three receivers were the only receivers in either phase of the study never to register reef fish detections.

Discussion

This study provided a comprehensive description of red grouper movement patterns and spatial requirements, and also provided some information regarding the movements and spatial requirements of a variety of other grouper and snapper species within the newly-established no-take Research Natural Area. Assuming the fish tracked by this study were representative of the species, the wide regional distributions of these species suggest broad applicability of our findings within the size ranges observed.

Groupers

In general, red groupers and black groupers spent the majority of their time (>95%) within the detection radius of one receiver for periods of several months to a year. During their time in the array, individuals of both species were detected with extremely high consistency. In most cases, failure to detect these individuals during any given 2-hr block is more likely due to movement into a shelter blocking the acoustic signal, rather than movement out of the acoustic array (see Chapter 2). The majority of grouper tracks exceeded the estimated life of the transmitter; as such, cessation of tag detections for the majority of individuals was probably due to acoustic tag battery expiration, rather than movement out of the array. The majority of recaptured red grouper were collected within 100 m of their initial capture site. All of these observations suggest small home ranges with limited ranging behavior for red and black grouper. Similar home ranging behavior has previously been documented for a variety of fish species, including Nassau grouper (*Epinephelus striatus*) on Bahamian patch reefs (Bolden 2001), juvenile dusky groupers (*Epinephelus marginatus* Lowe) in a marine

reserve (Lembo et al. 2002), juvenile pinfish (*Lagodon rhomboids*) in salt marsh creeks (Potthoff & Allen 2003), blacktip sharks (*Carcharhinus limbatus*) in a shallow coastal bay (Simpfendorfer et al. 2002), and adult kelp bass (*Paralabrax clathratus*) in a temperate no-take marine reserve (Lowe et al. 2003). Beaumariage & Bullock (1976) conducted a conventional tagging study on black grouper and found strong home-reef specificity, commenting that “even a hurricane failed to disrupt their residence” (quoted in Jory & Iversen 1989). Home range specificity likely develops as individuals capable of spatial learning return to areas in which they have had positive experiences (Lind 1990, Warburton 1990, Vannini & Cannicci 1995). This process is likely to be advantageous for any animal wandering in a spatially heterogenous, temporally stable environment such as a coral reef (Stamps & Krishnan 1999).

For the individual, the decision to move has consequences in terms of bioenergetics (Forseth et al. 1999), susceptibility to predation (Gilliam & Fraser 2001), and mortality (Elliot 1994). 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). Black grouper are also opportunistic feeders, although they are more piscivorous and are less associated with the bottom (Randall 1967). Like most groupers, these two species are ambush predators who lurk near structures then dart out and engulf their prey whole. This feeding strategy, as well as their strong affiliation

with dens and cleaning stations (Smith 1961), probably explains their localized clusters of detections and infrequent, short distance movements.

As with many other organisms, fish populations appear to be comprised of both mobile and sedentary fractions (Funk 1957), although it is unclear whether individuals only exhibit one strategy or switch-off occasionally throughout their lives (Smithson & Johnston 1999). Studies of stream fish have found that although most spend the majority of their lives in a home pool, at least some proportion of the population makes regular exploratory trips (Funk 1957, Stott 1967, Bruylants et al. 1986, Heggenes et al. 1991, Freeman 1995, Smithson & Johnston 1999). Repopulation of depleted areas may occur through the exploratory movements of individuals (Peterson & Bayley 1993) and during seasonal migrations such as spawning runs (Larimore et al. 1959). A small percentage of highly mobile individuals within a generally sedentary population may serve an important function as a buffer against extinction (Schaefer 2001). In addition, mobile individuals may be able to recolonize disturbed areas, such as areas depleted by fishing, and find higher quality or less competitive habitats (Hanski 1982, 1985; Fahrig & Merriam 1985; Burkey 1989, review in Saunders & Hobbs 1991). A small percentage of our tagged red grouper were highly mobile as compared to the majority of red grouper observed. Although several studies have suggested that smaller, less competitive individuals (e.g. juveniles) are more likely to make these movements (Young 1963; Kramer & Chapman 1999; Bell & Kramer 2000), we found no significant size-related trends in movement distance or frequency in this study. There may be other, unidentified factors influencing movement rates, as several acoustic tracking studies have failed to

find a relationship between size and movement rate (Zeller & Russ 1998; Lowe et al. 2003).

Our failure to identify a relationship between size and movement rate for red grouper may also be attributable to our somewhat restricted size range (45 – 66 cm TL) and sample size (45 fish). Although our maximum size tagged is close to the L_{inf} of Moe (1969) of 67.0 cm SL, a recent fishery-independent survey found that red grouper greater than 70 cm TL comprise approximately 4% of the observed population within the RNA and 18% of the observed population in the Tortugas North Ecological Reserve (Ault et al. 2007a). As such, juvenile (< 45 cm TL) and sexually-mature male (> 66 cm TL) red grouper may be underrepresented or absent in this study. It is well known that juvenile red grouper (< 40 – 45 cm) are most commonly found in shallow water (3 – 18 m deep), and undergo an ontogenetic migration to deeper waters (> 36 m) as they reach larger sizes (Moe 1969, Dahlgren & Eggleston 2000).

Offshore movements of red grouper may correspond to the onset of sexual maturity (Moe 1969; Pollock 1982). It is important to note that there are no waters deeper than 36 m within our study site, so our observed movements may only be representative of grouper within the RNA and not in deeper waters or unprotected areas. It is also unclear whether our tagged red grouper were sexually mature. No red grouper tagged were observed ‘running ripe,’ and there is substantial debate as to the length at sexual maturity for red grouper (Moe 1969, Brule et al. 1999, Burgos 2001, Collins et al. 2002, Fitzhugh et al. 2006). Based on histological interpretations of ‘definitely’ mature and immature females, Fitzhugh et al. (2006) place size ($L50$) and age ($T50$) at 50% maturity for red grouper at 28.0 cm TL and 2 yrs. Using effective maturity determined

from active females during the spawning season, they obtain increased estimates of size and age, at 38.0 cm TL and 3.5 yrs (Fitzhugh et al. 2006). Fitzhugh et al. (2006)'s estimates are significantly smaller than previous estimates by Moe (1969; Length at maturity = 48.5 cm FL), Brule et al. (1999; L50 = 50.9 cm FL), and Burgos et al. (2001; L50 = 48.7 cm TL, T50 = 2.4 yrs). Thus, the red grouper tagged in this study were probably either at or on the cusp of reaching sexual maturity. Red grouper are protogynous hermaphrodites, and the proportion of males increases with age (Collins et al. 2002). Fitzhugh et al. (2006) estimate size at 50% transition ($L50_{\text{transition}}$) at 74.0 cm TL. Collins et al. (2002) estimated $L50_{\text{transition}}$ between 80.0 – 90.0 cm TL. Burgos et al. (2001) and Brule et al. (1999) estimate $L50_{\text{transition}}$ at 69.0 cm TL and 59.7 cm FL, respectively. Therefore, it seems unlikely, but possible, that some of the larger red grouper in our study may have been males; however, we did not collect any data on sex. The black grouper in our sample ranged from 57 – 75 cm, and L50 for this species is estimated at 82.6 cm (Ault et al. 2007b). It appears likely that none of our black grouper were at maturity – we observed no spawning migrations for our tagged black grouper, although these migrations are known to occur for mature individuals (Eklund et al. 2000). Future studies should attempt to expand the sample sizes and size ranges of tagged individuals for both of these species.

Previous calibration work within these acoustic arrays (see Chapter 2) suggested that acoustic transmitters located higher in the water column tended to have a higher probability of detection and a greater maximal detection range, and that the placement of tags near or in reef would reduce the probability of detection. We used these findings to help interpret diel movement data, making the assumption that an increased probability of

detection might correspond to the animal spending less time in shelter, more time up in the water column, or both. Our findings suggested that red grouper and black grouper spend less time in shelter during the day than at night, and move the most during the day (as indicated by distances moved) and at dawn and dusk (as indicated by number of receivers registering detections). These findings agreed with Randall (1967), who found that grouper feed most actively at dawn and dusk. Increased activity after dawn and before dusk allows fish to take advantage of the moderate light levels and transitional nature of the crepuscular period to more efficiently capture prey (Helfman 1993). Crepuscular feeding behavior is common in visual predators (Hobson 1965, Major 1977, Potts 1980, Hobson et al. 1981, Løkkeborg et al. 2000), including black grouper (Eggleston et al. 1998). It should be noted; however, that we caught both red and black grouper at all hours of the day and night during our tagging efforts.

Many vertebrates use a particular area for their daily movements (Seton 1909, Burt 1943, Sale 1978, Schoener & Schoener 1982, Mace et al. 1983). The area that an animal stays in for the majority of its activities during certain portions of the year or certain stages of its life cycle is commonly referred to as a home range (see Harris et al. 1990 for a review). Familiarity with the location of important features in a habitat, knowledge of safe and efficient connecting routes and pathways between these features, and improvements in the safety, speed, and accuracy of movements within the area owing to this knowledge are all reasons why animals might establish a home range within a spatially heterogeneous, temporally stable habitat (Aronson 1951, 1971; Gallistel 1990; Shulter & Weatherhead 1992; O'Neill 1992; Stamps 1992; Poucet 1993). Furthermore, numerous studies have suggested that an animal's ability to evade predators or predator-

surrogates (e.g. models or humans) increases with their level of familiarity with the space (Aronson 1951, 1971; Metzgar 1967; Ambrose 1972; Synder et al. 1976). Foraging efficiency also improves with increased familiarity with a habitat; spatial learning has been shown to improve feeding rates (Healy & Hurly 1995, Douglas 1996), residents have higher feeding rates than newcomers feeding in the same area (Davies & Houston 1981), and newcomer foraging rates improve over time in previously novel territories (Tobias 1997).

Numerous studies have documented home range use in fish (Goeden 1978; van Rooij et al. 1996; Shapiro et al. 1994; Zeller 1997a, b; Kramer & Chapman 1999; Bell & Kramer 2000; Eristhee & Oxenford 2001; Bolden 2001; Lembo et al. 2002; Baras et al. 2002). Home range size may be a function of resource distribution (Gill & Wolf 1975; Carpenter & MacMillen 1976, 1980; Gass et al. 1976; Ewald & Carpenter 1978; Kodric-Brown & Brown 1978; Gass 1979; Frost & Frost 1980; Carpenter 1987; Armstrong 1991; Grant 1997; Maher & Lott 2000), predation risk (Aronson 1951, 1971; Metzgar 1967; Ambrose 1972; Synder et al. 1976; Clarke et al. 1993), body size and bioenergetic requirements (Harestad & Bunnell 1979, Harvey & Clutton-Brock 1981, Mace et al. 1983, Swihart et al. 1988, Kelt & Van Vuren 1999, review in McLoughlin & Ferguson 2000), intraspecific interactions and territoriality (Burt 1943, Madison 1980, Norman & Jones 1984, Grant et al. 1992, Ribble & Stanley 1998), reproductive dynamics (Hixon 1987, Ostfeld 1990, McCarthy & Lindenmayer 1998), and other factors. Understanding home range size is recognized as a critical question when evaluating the effectiveness of spatial management tools such as marine reserves (Kenchington 1990, Kramer & Chapman 1999, Sale et al. 2005).

The majority of red grouper and black grouper in our study exhibited movements consistent with the utilization of a home range. MCP home range estimates for red grouper ($\overline{MCP}_{rg} = 1.94 \text{ km}^2$) and black grouper ($\overline{MCP}_{bg} = 1.13 \text{ km}^2$) are significantly higher than previously estimated by Bolden (2001) for Nassau grouper ($\overline{MCP}_{ng} = 0.02 \text{ km}^2$), which may reflect differences between species or be a consequence of the environment available to the fish. Bolden (2001) conducted her study on two isolated patch reefs, whereas our study zone featured large areas (tens of square kilometers) of contiguous reef track. Bolden (2001) did note larger home ranges on the larger patch reef. Although we failed to detect significant differences in overall home range size by habitat, we did find significantly greater overlap in red grouper home ranges in isolated (90%) as compared to contiguous (38%) habitats. The ‘resource dispersion hypothesis’ (Macdonald 1983) argues that resource (especially food) dispersion is the main structuring factor for home range and group size in carnivore populations, with home range determined by the dispersal of food in space, and group size determined by the quantity and size of the food patches. Differences in home range and group size between different populations (MacDonald 1983) and within populations (Carr & Macdonald 1986) of the same species appear to occur quite often, and are typically attributable to different ecological conditions (Macdonald 1983, Buskirk & McDonald 1989, Stander 1991, Payer 1999) and different life stages (Devillard et al. 2008). The spatial arrangement of resources within fragmented landscapes has significant structuring effects upon mammalian space use and behavior (Atwood & Weeks 2003). As isolated reefs represent compressed habitats, it is not surprising that red grouper home range overlap would be higher due to spatial limitations. Fishery-independent surveys of the Tortugas

region suggest that red grouper population densities are higher in contiguous as compared to isolated habitats (Chapter 5).

The majority of red grouper tagged at the same time and location utilized the same core habitat (e.g. 95% of their detections occurred at the same receiver), similar to patterns observed for Bermuda chub (*Kyphosus sectatrix* L.) by Eristhee & Oxenford (2001). We also found a relatively high level of overlap in MCP home ranges of fish tagged at the same location (43%), with some home ranges overlapping 100%. As home range overlap may be viewed as a proxy for territoriality (Nemtzov 1997), these observations suggest that if red grouper are territorial fish (Colin et al. 1997, Weaver 1996), demonstrating a behavioral intolerance of conspecific intrusion into a nuclear range (Schenkel 1966; cited in Owen-Smith 1977), their nuclear ranges must be smaller than the area covered by a single receiver in this study (approximately 2.6 km²).

There are a variety of evolutionary advantages to maintaining a defended core home range including improved foraging efficiency through exclusive access to known resources (Schoener 1971, Healy & Hurly 1995, Douglas 1996) and reduced predation risk through familiarity with locations of shelters (Aronson 1951, 1971; Metzgar 1967; Ambrose 1972; Synder et al. 1976; Clarke et al. 1993; Wilkinson et al. 1998). It is important to note that although the defended home range of these fish may be relatively small, undefended home range size may be much larger (Burt 1943, Grant et al. 1992, Grant 1997). In a review of terrestrial mammalian home ranges, Grant et al. (1992) found that undefended home ranges for carnivores and male ungulates were 5.4 and 15.2 times larger than defended home ranges, respectively. These are critical parameters to understand for marine reserve design because density-dependent territoriality, increased

intraspecific competition, and declines in resource availability are all proximal motivators for the spillover of adult fish biomass from reserves into fished areas (Russ 2002, Gell & Roberts 2003, Sobel & Dahlgren 2004, Sale et al. 2005, Abesamis & Russ 2005).

We also found increased overlap in red grouper home ranges in high relief habitats (87%) relative to low relief habitats (43%). Food value theory (Stenger 1958, Wilson 1975) and theoretical and empirical cost-benefit analyses (Brown 1964) have suggested that resource availability plays a major role in determining animal home range overlap (e.g. Gill & Wolf 1975; Carpenter & MacMillen 1976, 1980; Gass et al. 1976; Ewald & Carpenter 1978; Kodric-Brown & Brown 1978; Gass 1979; Frost & Frost 1980; Carpenter 1987; Armstrong 1991; Maher & Lott 2000). A model of brown bear (*Ursus arctos*) home range use by McLoughlin et al. (2000) predicts that in areas of high habitat quality, populations will be characterized by small home ranges and high percentages of home range overlap, and in areas of moderate habitat quality, home ranges will be larger with decreased overlap. High relief habitats provide higher prey densities for red grouper (Ault et al. 2007a), and presumably contain more locations for shelter. Areas with high habitat quality are expected to contain enough food to allow animals to maximize energy intake in a small space, with or without territorial defense (Carpenter & MacMillen 1976). In moderate quality habitat, large ranges are needed to collect enough food; yet enough food is present to make it energetically feasible to defend an area (Carpenter & MacMillen 1976). Measurements of resource availability (visual estimates of benthic habitat, density and size of potential prey, and rugosity measurements of substrate complexity) suggested that availability and size of refuge holes was important in determining the home range size of Nassau grouper (Bolden 2001). Our habitat selection

analysis suggested that red grouper underutilize low relief and isolated habitats relative to their availability.

Although we did not observe a significant relationship between home range size and body length for any species tagged, we did find significantly higher levels of home range overlap for red grouper with increasing body size. This result seems counter-intuitive, as a larger fish would be expected to require a greater range to service its metabolic requirements (McNab 1963) and might be better equipped to defend a territory from conspecific intrusion. It may be that the specific resources being defended (e.g. shelters, cleaning stations) are separated spatially or temporally at a scale we were unable to observe, or that larger fish are more tolerant of conspecifics. Red grouper spawn up to 26 times during the peak spawning months of Mar – May (Collins et al. 2002), and unlike most grouper and snappers, do not appear to make spawning migrations. As such, tolerance of conspecifics in larger (e.g. possibly mature) fish may have reproductive advantages by increasing access to potential mates.

Snappers

A mark-recapture study of mutton and yellowtail snapper by Beaumarriage (1969) found minimal displacement 262 d post-release. The observed for yellowtail snapper appear to confirm observations by Moe (1972) that they are semi-pelagic wanderers over the reef habitat; although they showed a high level of short-term (3-4 month) home range specificity. In this study, yellowtail snapper made frequent, small-scale movements. Detections were often concentrated at 1 – 2 receivers with periodic detections at several adjacent receivers. We observed no major transitions in space use over the life of the tag,

although Fish 182 was only tracked for 26 d in 2006 before disappearing. This fish may have moved out of the array or been captured and not reported. Fish 57 may have undergone a compression in habitat use, as it was detected at 7 receivers between July and Sept, and then from Sept to Oct was only detected at its primary site (B23). Fish 58 was tracked for 68 d, but was undetected between June 9 and June 23, 2007, and was undetected after July 1. Fish 59 was tracked for 77 d in the same area, but disappeared on July 10. It appears likely that Fish 58 and 59 may have left the array or been eaten by a predator. Fish 58 and 59 were 48 and 52 cm TL, respectively; well above the estimated size at 50% maturity of 20.9 cm (Muller et al. 2003). As peak spawning for yellowtail snapper occurs at Riley's Hump in the Tortugas South Ecological Reserve during May – July (Lindeman et al. 2000), it is possible that their departures corresponded to a spawning migration. It is worth noting that a larger (55 cm TL) fish (Fish 55) which was tagged at the same time as Fish 58 and 59 and showed similar patterns of space use, was detected every day for 153 d, exceeding the expected life of the tag.

Yellowtail snapper occur in a variety of depths and forage throughout the water column (pers. obs.). We detected yellowtail snapper more frequently near the full moon than at other stages of the lunar cycle. This finding suggests increased foraging activity, possibly taking advantage of the increased light afforded by the full moon. Yellowtail snapper were detected at the most receivers during crepuscular time periods, and their greatest movements were observed at dawn and night. These observations seem to confirm that yellowtail snapper are mostly nocturnal predators (Muller et al. 2003). They are known to eat fish, crustaceans, and mollusks (Randall 1967; Piedra 1969); in addition, they eat a wide variety of holoplankton such as larval stages, pelagic mollusks and

polychaetes, and gelatinous invertebrates (Schroeder 1980, Parrish 1987). We found that yellowtail appear to underutilize isolated and high relief habitats in favor of contiguous, low-relief habitats. Muller et al. (2003) note that adult yellowtail snapper typically inhabit sandy areas near offshore reefs. The majority of contiguous, low-relief habitats in our study are located near unidentified deeper habitats that are most likely sand (see Fig. 3.2). It should be noted that our sample size for yellowtail snapper was small ($n = 5$), and the size range was constricted (48 – 55 cm TL). It is possible that juveniles and larger adults might exhibit different movement patterns.

Mutton snapper also made frequent, small-scale movements. They are known to associate with a wide variety of habitats, including reef, sand, seagrass, and coral rubble (Randall 1967). One of the two tagged mutton snapper showed a high level of site fidelity: Fish 53 (70 cm TL) was tracked for 168 d, exceeding the expected life of the tag. This fish had two extended absences from the array (16 d and 8 d) with departures that roughly corresponded to the full moon. These absences were bookended by sequential detections at a unique suite of receivers that were never revisited at any other time. Given that Fish 53 was well above the most conservative estimate for size at sexual maturity for mutton snapper (52.0 cm TL; Claro 1981), the direction of travel implied by receiver detection patterns, and the presence of a well-known spawning aggregation of mutton snapper over Riley's Hump in the Tortugas South Ecological Reserve during the full moon in May, June, and July (Burton et al. 2006), we believe that these two extended absences correspond to two spawning migrations. The departure of this fish twice near the full moon also explains our finding of significantly higher detections of mutton snapper during the new moon.

Randall (1967) reports that mutton snapper are both nocturnal and diurnal predators; however, Mueller et al. (2005) report that they feed diurnally, and Watanabe (2001) reports that the mutton feeds during all times of the day. In this study, mutton snapper were detected at a greater number of receivers during crepuscular time periods, and had the largest movements at dusk and during the day. These observations suggest reduced activity for mutton snappers at night. It should be noted that our sample size for mutton snapper was small ($n = 2$), but the size range was broad (43 – 70 cm TL). Fish 50, a 43 cm TL mutton snapper, was tagged on Oct 9, 2007 to the southeast of our acoustic array, and was detected for 3 days at receivers managed by Mote Marine Laboratory of Summerland Key, Florida located in sand habitats around Garden Key, approximately 6 km east of its capture location, before disappearing. As this fish was below the size at sexual maturity, these observations suggest that juvenile mutton snapper may be more broadly roaming than reef-associated adults.

Unlike the yellowtail snapper and the mutton snapper, the gray snapper made large, infrequent movements. Moe (1972) described adult gray snapper as nocturnal predators that forage away from their day reef habitats, where they feed primarily on fish (especially grunts), shrimp, and crabs (Harrigan et al. 1989; Hettler 1989). Our observations supported this claim, as the gray snapper was detected at the most receivers at dusk and dawn, presumably during migrations to and from nocturnal feeding grounds. It was detected most frequently in the array during the day, suggesting higher daytime use of the reef habitat, and its greatest movements were recorded at night. The low frequency of detections and movement observed for gray snapper is likely due to undetected (e.g. outside the array) movements. The gray snapper was primarily detected

at site B19 during the daytime (0600 – 2000), whereas nocturnal detections were far less frequent and occurred primarily at site B18, with periodic detections at B08, B29, and B30. Patterns of movement suggest periodic utilization of a nocturnal foraging habitat west of the acoustic array.

We found the gray snapper underutilized low relief habitat relative to its availability. The gray snapper was detected more frequently during the full moon, suggesting increased utilization of the reef habitats within the array at night with increased light. It is unknown whether any of these movements correspond to spawning events. Starck (1971) speculated that gray snapper spawn at dusk as part of a daily activity cycle with peaks following the full moon. Domeier et al. (1996) used a gonadosomatic index (GSI) to determine that gray snapper spawning peaked with the new and full moon, but Allman & Grimes (2002) found no significant trends. Anecdotally, we observed ‘running ripe’ gray snapper much smaller than Fish 882 in approximately 22 m of water south of the Marquesas (midway between DTNP and Key West) two days after the full moon in July 2008. Allman & Grimes (2002) back-calculated fertilization dates and identified mid-July in southwest Florida as a spawning peak for gray snapper.

Marine Reserve Effectiveness

Barrett (1995) recommended that a reserve’s diameter be, at minimum, an order of magnitude larger than the daily movements of the targeted organisms. Estimated home range size ranged considerably between individuals for red grouper (0.01 to 5.76 km²) and black grouper (0.27 to 1.99 km²), but was relatively consistent for yellowtail

snapper (2.17 to 2.91 km²). Mean home range sizes for red grouper, black grouper, and yellowtail snapper were small (1 – 2%) relative to the size of the reserve. In addition, only a few (6 of 45) red grouper and no black grouper or yellowtail snapper were detected moving out of the RNA. If these tracked individuals are representative of other adults within the RNA, then these data indicate that the RNA affords significant protection for these species within the size ranges observed.

Our home range estimates for groupers and snappers were significantly higher than those estimated by other researchers for similar species (Table 3.3). It is important to note that the perception of mobility is dependent upon the scale of time and space over which movement is monitored (Steingrímsson & Grant 2003). Many active tracking and diver observation studies of fish movement are constrained in the duration and periodicity of observations, often representing less than one month of animal movements with inconsistent monitoring that might miss important diel transitions. Our long term monitoring indicated that tracks of black grouper, red grouper, and yellowtail snapper all required longer than one month to achieve asymptotic home range size estimates.

Many previous passive acoustic monitoring studies have been constrained in their spatial scale due to financial limitations on the number of receivers in the array. Movements out of an acoustic array might result in severe underestimation of fish home range size. The larger size of our acoustic array and increased monitoring duration may partially explain our higher home range estimates. It should be noted that due to the high concentration of detections at single receivers and the repeated position estimates at duplicate spatial locations (e.g. receiver coordinates), we were unable to compute 95% KUD home range estimates for most fish in the study (following Worton 1989). If home

range estimates from the tracking studies described above are indeed representative of the spatial requirements for a broad suite of benthic coral reef fish species, it appears that a reserve designed to encompass the larger movements of red grouper, black grouper, and yellowtail snapper would afford substantial protection to many smaller coral reef species.

In this study, the hydroacoustic array covered less than 20% of the habitat contained within the new RNA, and important reef habitat types such as high-relief spur and groove were underrepresented. The high site fidelity exhibited by groupers, snappers, and more mobile species (N. Farmer, unpublished data) suggests that the RNA provides significant protection for many species on a daily basis. No-take marine protected areas such as the RNA provide numerous benefits in addition to increasing biomass of exploited species, including protection of coral reef habitats, restoration of natural community dynamics, and reduced bycatch of important prey species for large, highly migratory predators (see review in Bohnsack et al. 2004). As such, the area within the RNA may increase in value as a habitat and foraging ground for even highly mobile species after several years of protection. Coupled with the substantial protection afforded by the Tortugas North Ecological Reserve (312 km²) and the Tortugas South Ecological Reserve (206 km²), the marine reserve network of the Dry Tortugas probably provides an important refuge from fishing pressure for a variety of organisms.

A major concern voiced by fishermen impacted by RNA establishment was that the reserve might function as a biological sink (e.g. Tremain et al. 2004), enhancing biomass within its boundaries with no correspondent density-dependent movements of adults into fishable waters. In this study, no detections were made by receivers placed in the 2 – 6 km wide sand channel (depth > 40 m) located between the contiguous reef of

the study area and the nearest known reef habitat on Tortugas Bank. All detected movements out of the RNA occurred along contiguous reef. We observed a higher rate of spillover in 2007 than in 2006, presumably due to the reconfiguration of the acoustic array to provide better coverage of contiguous reef habitats overlaying reserve boundaries. Observed detection rates suggested that groupers and snappers remain within the RNA for the majority of their diel activities, whereas more mobile organisms such as sharks and pelagic might cross reserve boundaries more frequently or permanently emigrate from the reserve. Nevertheless, our observations clearly demonstrated that exploited-phase red grouper and a variety of other species are capable of, and occasionally do, cross RNA boundaries, and are more likely to do so where boundaries overlay contiguous reef. In this study, all grouper and snapper movements observed out of the RNA were into another no-take marine reserve (TNER); however, it seems likely that some movement of adult fish into zones open to fishing might occur along other boundaries of the RNA featuring contiguous reef. Future studies should focus on expanding the temporal and spatial scales of monitoring and the numbers and size ranges of individuals tagged and tracked.

Table 3.1. Data for fish fitted with acoustic transmitters.

Tag	Code	Date	Common Name	Species Name	Length (cm)	Weight (kg)
3H	174	03/07/06	Black Grouper	<i>Mycteroperca bonaci</i>	50.0	2.5
3H	170	03/07/06	Red Grouper	<i>Epinephelus morio</i>	61.0	4.1
3H	172	03/07/06	Red Grouper	<i>Epinephelus morio</i>	49.0	1.8
3H	171	03/07/06	Red Grouper	<i>Epinephelus morio</i>	60.0	3.0
3H	173	03/07/06	Red Grouper	<i>Epinephelus morio</i>	49.0	1.8
3H	175	03/07/06	Red Grouper	<i>Epinephelus morio</i>	53.0	2.7
3H	176	03/07/06	Red Grouper	<i>Epinephelus morio</i>	55.0	3.0
3H	177	03/07/06	Red Grouper	<i>Epinephelus morio</i>	50.0	2.0
3H	178	03/07/06	Red Grouper	<i>Epinephelus morio</i>	65.0	4.5
3H	179	03/27/06	Red Grouper	<i>Epinephelus morio</i>	57.0	2.7
3H	180	03/27/06	Red Grouper	<i>Epinephelus morio</i>	55.0	2.7
3H	181	03/27/06	Red Grouper	<i>Epinephelus morio</i>	49.0	1.8
3H	183	03/28/06	Red Grouper	<i>Epinephelus morio</i>	48.0	2.0
3H	184	03/27/06	Red Grouper	<i>Epinephelus morio</i>	55.0	3.0
3H	185	03/27/06	Red Grouper	<i>Epinephelus morio</i>	55.0	2.3
3H	186	03/27/06	Red Grouper	<i>Epinephelus morio</i>	51.0	2.7
3H	187	03/27/06	Red Grouper	<i>Epinephelus morio</i>	50.0	2.0
3H	189	03/07/06	Red Grouper	<i>Epinephelus morio</i>	59.0	3.6
3H	190	03/06/06	Red Grouper	<i>Epinephelus morio</i>	62.0	4.1
3H	191	03/06/06	Red Grouper	<i>Epinephelus morio</i>	51.0	1.8
3H	194	03/06/06	Red Grouper	<i>Epinephelus morio</i>	54.0	3.0
3H	862	03/06/06	Red Grouper	<i>Epinephelus morio</i>	54.0	2.0
3H	863	03/05/06	Red Grouper	<i>Epinephelus morio</i>	51.0	3.0
3H	864	03/06/06	Red Grouper	<i>Epinephelus morio</i>	55.0	2.7
3H	865	03/05/06	Red Grouper	<i>Epinephelus morio</i>	56.0	3.6
3H	866	03/06/06	Red Grouper	<i>Epinephelus morio</i>	53.0	2.3
3H	867	03/05/06	Red Grouper	<i>Epinephelus morio</i>	55.0	2.5
3H	868	03/05/06	Red Grouper	<i>Epinephelus morio</i>	49.0	2.0
3H	869	03/06/06	Red Grouper	<i>Epinephelus morio</i>	60.0	X
3H	870	03/05/06	Red Grouper	<i>Epinephelus morio</i>	45.0	1.1
3H	871	03/05/06	Red Grouper	<i>Epinephelus morio</i>	57.0	3.6
3H	872	03/05/06	Red Grouper	<i>Epinephelus morio</i>	53.0	2.0
3H	182	03/28/06	Yellowtail Snapper	<i>Ocyurus chrysurus</i>	52.0	1.1
3H	43	01/07/07	Black Grouper	<i>Mycteroperca bonaci</i>	74.9	6.6
3H	35	10/09/07	Black Grouper	<i>Mycteroperca bonaci</i>	57.0	4.5
3H	54	04/24/07	Horse-Eye Jack	<i>Caranx latus</i>	71.0	3.6
3H	49	04/25/07	Jolthead Porgy	<i>Calamus bajonado</i>	50.0	1.8
3H	56	04/25/07	Jolthead Porgy	<i>Calamus bajonado</i>	48.0	1.8
3H	53	04/25/07	Mutton Snapper	<i>Lutjanus analis</i>	70.0	5.4
3H	40	10/09/07	Mutton Snapper	<i>Lutjanus analis</i>	53.0	4.5
3H	50	10/09/07	Mutton Snapper	<i>Lutjanus analis</i>	43.0	2.5
3H	36	01/07/07	Red Grouper	<i>Epinephelus morio</i>	63.5	3.6
3H	37	01/07/07	Red Grouper	<i>Epinephelus morio</i>	47.0	1.4
3H	41	01/07/07	Red Grouper	<i>Epinephelus morio</i>	47.0	1.1
3H	42	01/07/07	Red Grouper	<i>Epinephelus morio</i>	48.3	1.8
3H	47	01/07/07	Red Grouper	<i>Epinephelus morio</i>	48.3	1.8
3H	51	02/27/07	Red Grouper	<i>Epinephelus morio</i>	66.0	5.4
3H	48	02/28/07	Tiger shark	<i>Galeocerdo cuvier</i>	274.3	X
3H	55	04/24/07	Yellowtail Snapper	<i>Ocyurus chrysurus</i>	55.0	1.8
3H	58	04/24/07	Yellowtail Snapper	<i>Ocyurus chrysurus</i>	48.0	0.9
3H	59	04/24/07	Yellowtail Snapper	<i>Ocyurus chrysurus</i>	52.0	0.9
3H	57	07/11/07	Yellowtail snapper	<i>Ocyurus chrysurus</i>	52.0	1.4
3H	52	10/09/07	Yellowtail Snapper	<i>Ocyurus chrysurus</i>	49.0	2.0
4H	876	07/11/07	Caribbean Reef Shark	<i>Carcharhinus perezii</i>	98.0	6.4
4H	882	07/10/07	Gray snapper	<i>Lutjanus griseus</i>	54.0	2.7
4H	879	02/27/07	Greater Amberjack	<i>Seriola dumerili</i>	124.5	26.3
4H	883	02/27/07	Greater Amberjack	<i>Seriola dumerili</i>	75.0	5.4
4H	873	01/04/07	Red Grouper	<i>Epinephelus morio</i>	48.3	1.8
4H	875	01/04/07	Red Grouper	<i>Epinephelus morio</i>	52.1	2.0
4H	877	01/04/07	Red Grouper	<i>Epinephelus morio</i>	57.2	2.7
4H	878	01/04/07	Red Grouper	<i>Epinephelus morio</i>	48.3	1.8
4H	880	01/04/07	Red Grouper	<i>Epinephelus morio</i>	48.9	1.8
4H	881	01/04/07	Red Grouper	<i>Epinephelus morio</i>	49.5	1.8
4H	884	01/04/07	Red Grouper	<i>Epinephelus morio</i>	53.3	2.0
4H	874	01/05/07	Red Grouper	<i>Epinephelus morio</i>	59.7	2.9

----Denotes fish tracked by 2006 (above) and 2007 receiver configurations (below).

Table 3.2. Minimum convex polygon (MCP) home range estimates for acoustically-tagged fish in Dry Tortugas, Florida, and time required to obtain asymptotic MCP home range estimate (mean \pm SE).

Common name	Species	n	Time to Asymptote (d)	MCP Home Range (km ²)
Black grouper	<i>Mycteroperca bonaci</i>	2 of 3 (66%)	46.5 \pm 0.5	1.13 \pm 0.86
Red grouper	<i>Epinephelus morio</i>	33 of 45 (73%)	38.5 \pm 6.4	1.94 \pm 0.33
Gray snapper	<i>Lutjanus griseus</i>	1 of 1 (100%)	9	3.19
Mutton Snapper	<i>Lutjanus analis</i>	1 of 2 (50%)	72	7.64
Yellowtail Snapper	<i>Ocyurus chrysurus</i>	4 of 5 (80%)	46.2 \pm 29.2	2.51 \pm 0.17

Note: n denotes number of acoustically tagged fish meeting assumptions of home range contained within acoustic array.

Table 3.3. Summary of published fish home range estimates along with method, duration, and periodicity of tracking.

Common Name	Species Name	Age	n	MCP Home Range (m ²)	Method of Tracking	Length of Tracking (days)	P	Study Area (m ²)	Habitat	Region	Author
Blue Tang	<i>Acanthurus coeruleus</i>	Juvenile	35	0.07 - 15.65 (mean = 2.18)	Markers (diver)	14	N	n/a	Reef	Barbados, West Indies	Bell & Kramer (2000)
Red hind	<i>Epinephelus guttatus</i>	Adult	22	112 - 5,636 (mean = 867)	Visual (diver)	152	N	10,000	Reef	Puerto Rico	Shapiro et al. (1994)
Stoplight parrotfish	<i>Sparisoma viride</i>	Juveniles & Adults	88	240 - 820	Visual (diver)	<1 to >365	N	10,940	Fringing Reef	Bonaire	van Rooij et al. (1996)
Bluespine unicornfish	<i>Naso unicornis</i>	Adult?	5	325 - 7,650 (mean = 3,717)	Active	14 - 21	N	n/a	Reef	Hawaii, USA	Meyer & Holland (2005)
Graysby	<i>Cephalopholis cruentata</i>	Adult	10	1,200 - 4,000 (mean = 2,120)	Active	<7	N	n/a	Reef	St. Lucia, West Indies	Popple & Hunte (2005)
Kelp bass	<i>Paralabrax clathratus</i>	Adult	12	3,349 - 3,328*	Active	30	N	n/a	Kelp, Rock Reef, Sand	Santa Catalina Island, USA	Lowe et al. (2003)
Coral trout	<i>Plectropomus leopardus</i>	Juveniles & Adults	39	10,458 ± 962 fringing reef, 18,797 ± 3189 patch reef	Active	30 - 90	N	n/a	Fringing & Patch Reef	Lizard Island, Australia	Zeller (1997)
Nassau grouper	<i>Epinephelus striatus</i>	Adult	22	18,305 ± 5,806	3 radio-linked buoys	21 per reef	C	~100,000	2 Isolated Patch Reefs	Bahamas	Bolden (2001)
Bermuda chub	<i>Kyphosus sectatrix</i>	Adult	11	30,514 - 39,114	Active	5 - 51 (mean 21.5)	N	n/a	Reef	St. Lucia, West Indies	Eristhee & Oxenford (2001)
Blacktip shark	<i>Carcharhinus limbatus</i>	Juvenile	74	700,000 - 1,200,000**	Acoustic Array	1 - 167	C	~70 million	Coastal Bay	Florida, USA	Heupel et al. (2004)

Note: n denotes number of fish observed or tagged; P denotes periodicity of tracking, with C denoting continuous, and N denoting noncontinuous.

*95% Kernel Utilization Distribution home range (MCP not provided)

**Daily MCP

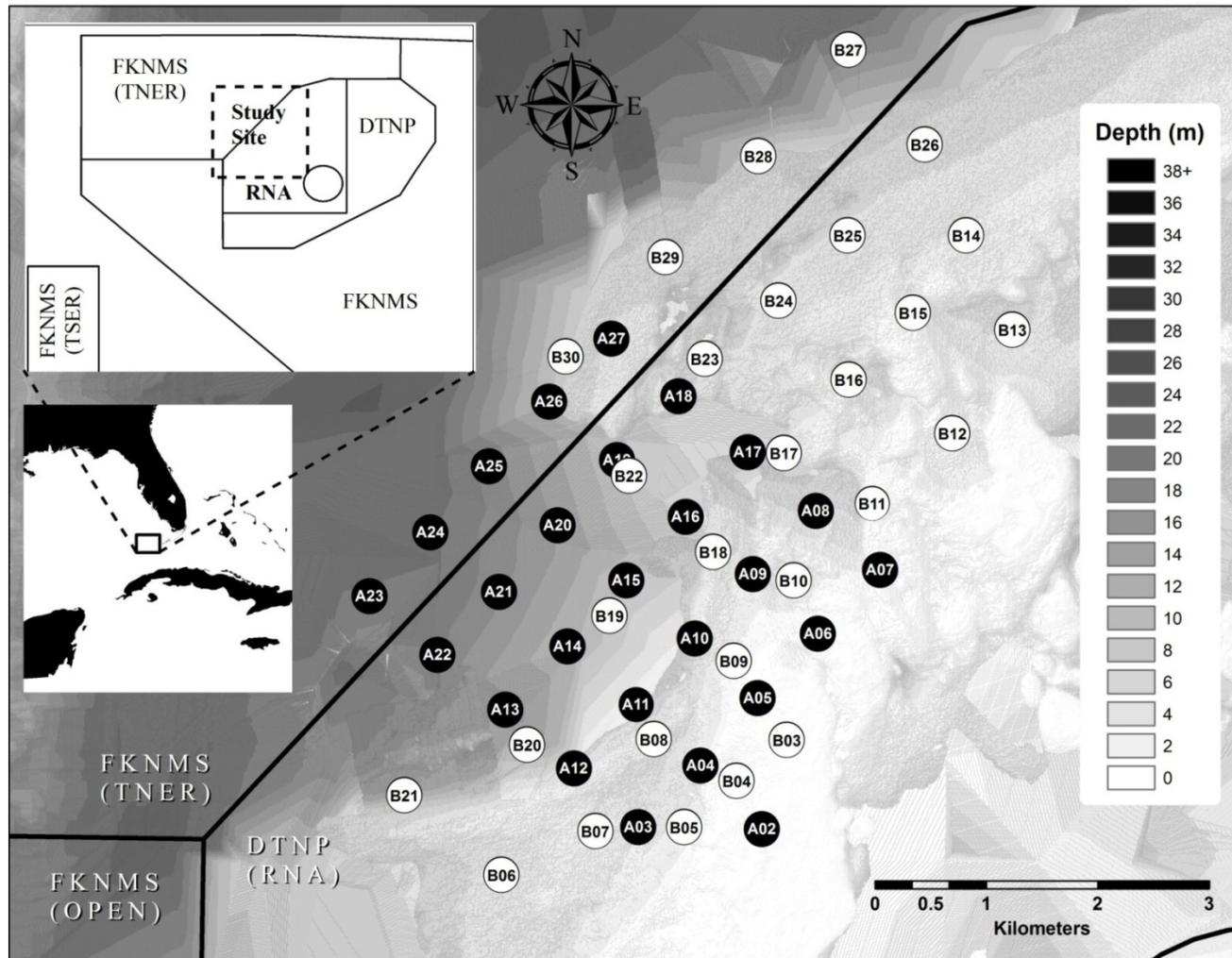


Figure 3.1. Map of hydroacoustic receiver placements for 2006 (black circles) and 2007 (white circles) relative to bathymetry in Dry Tortugas National Park’s (DTNP) Research Natural Area (RNA). Insets indicate location of Dry Tortugas, approximately 70 miles west of Key West in the Straits of Florida, and of study site relative to multiple management zones including fishable (“open”) waters of DTNP and Florida Keys National Marine Sanctuary (FKNMS), the no-take RNA, and the no-take Tortugas North Ecological Reserve (TNER) and South Ecological Reserve (TSER).

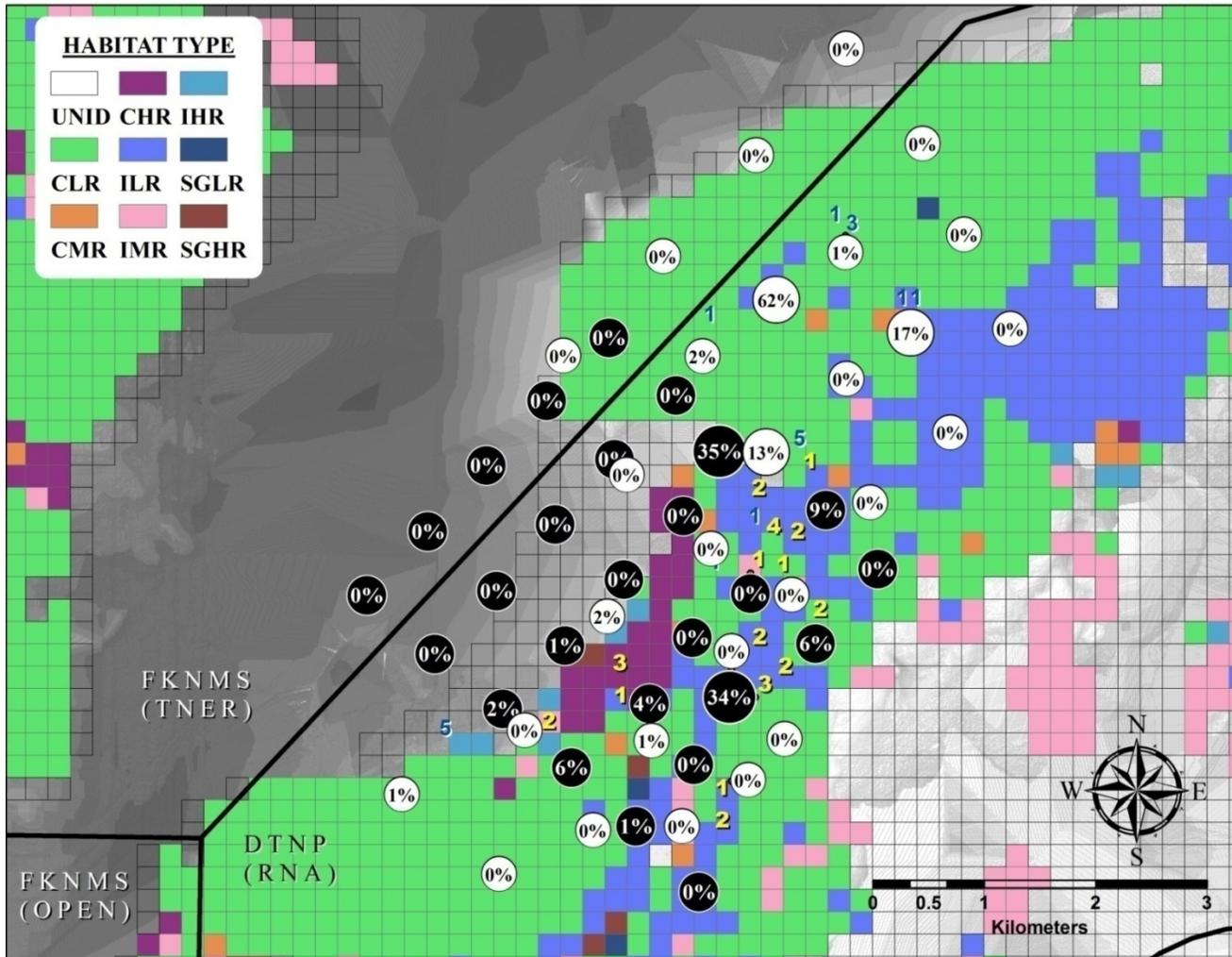


Figure 3.2. Map of percent detections by receiver for 2006 (black circles) and 2007 (white circles) relative to benthic habitats (see Legend; C = continuous, I = isolated, SG = spur and groove, HR = high relief, MR = medium relief, LR = low relief; UNID = unidentified) in DTNP RNA and FKNMS TNER. Note habitat map is overlaid on bathymetric map; lighter colors denote shallower waters. Number of internally tagged fish released at each capture location are listed for 2006 (yellow) and 2007 (blue).

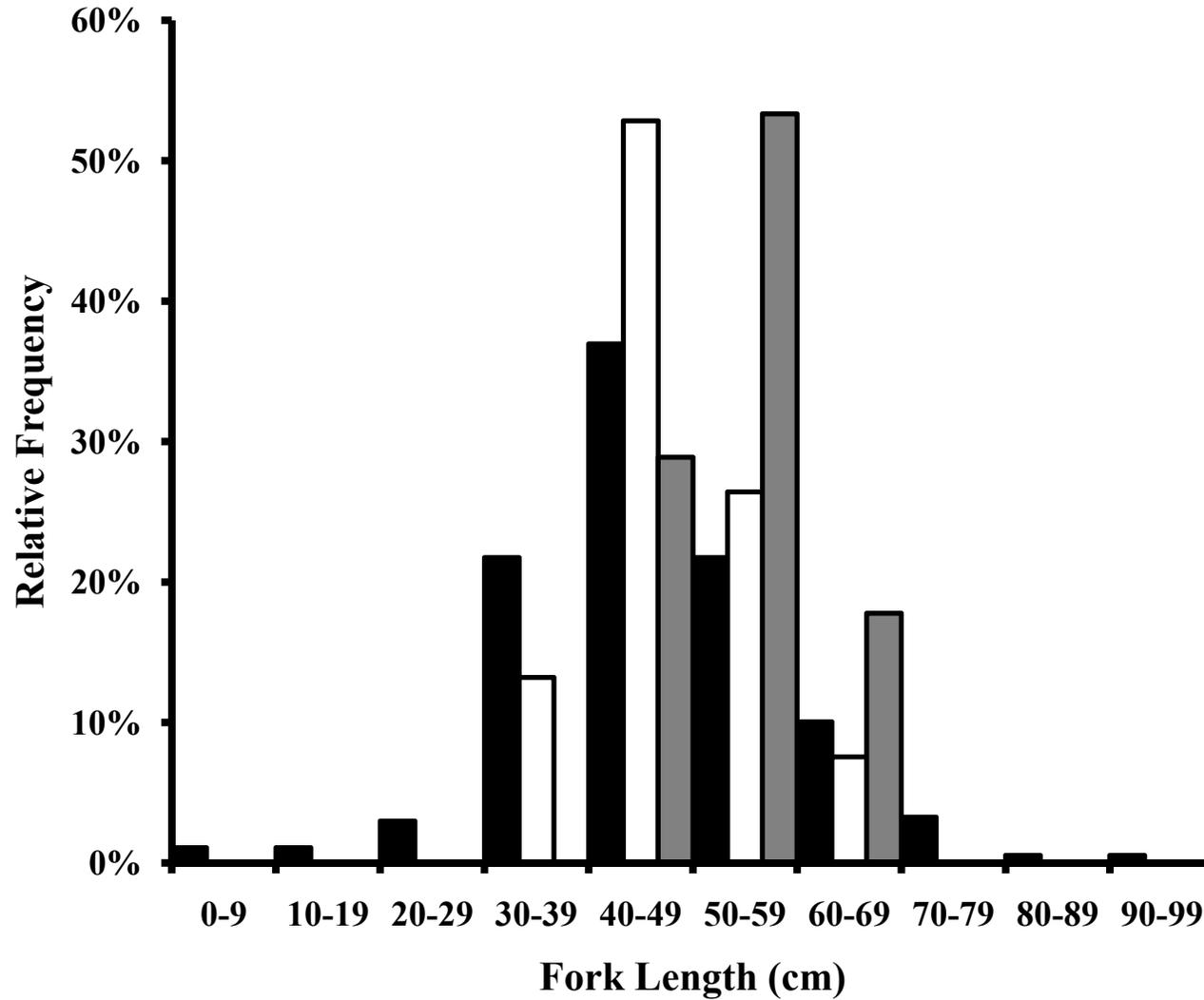


Figure 3.3. Length frequency histogram for red grouper (*Epinephelus morio*) in Dry Tortugas National Park (DTNP). Black bars denote fisheries-independent reef visual census (RVC) observations within DTNP from 2006 ($N = 184$). Gray bars denote fish tagged both internally and externally for this study ($N = 45$); white bars denote fish tagged externally only ($N = 53$). RVC data courtesy Ault et al. (2007a).

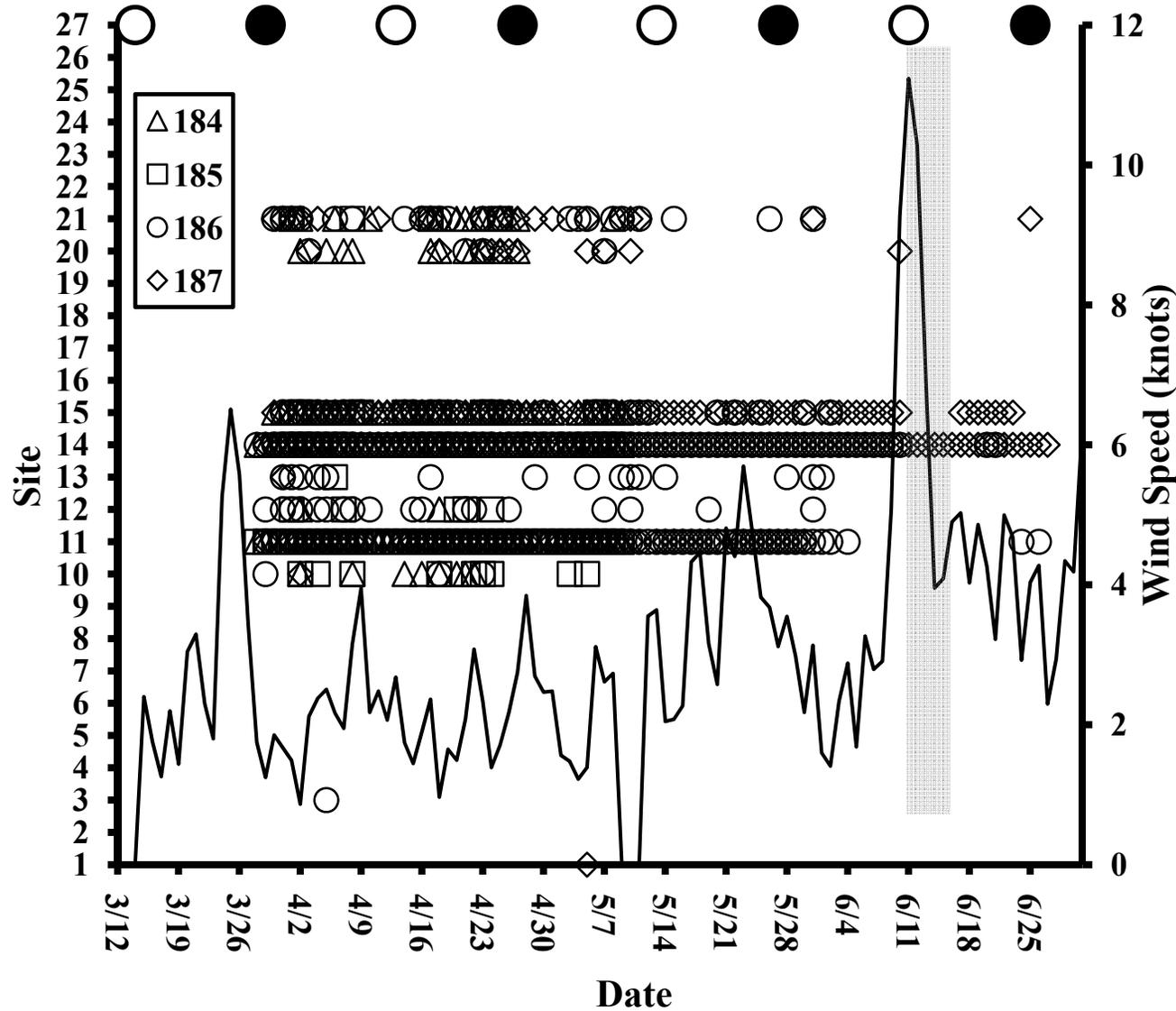


Figure 3.4. Detections by site for four red grouper tagged at the same location on the morning of March 27, 2006. Note the overlap in detections between individuals, suggesting similar space use and movement patterns. Wind speed and lunar cycle are co-plotted, with open circles denoting full moons. The passage of Tropical Storm Alberto is denoted in shaded gray, and appears to correspond with a brief lack of detections for fish 186. Fish 184 and 185 were both captured and killed on 5/9/2006 by a charter boat captain.

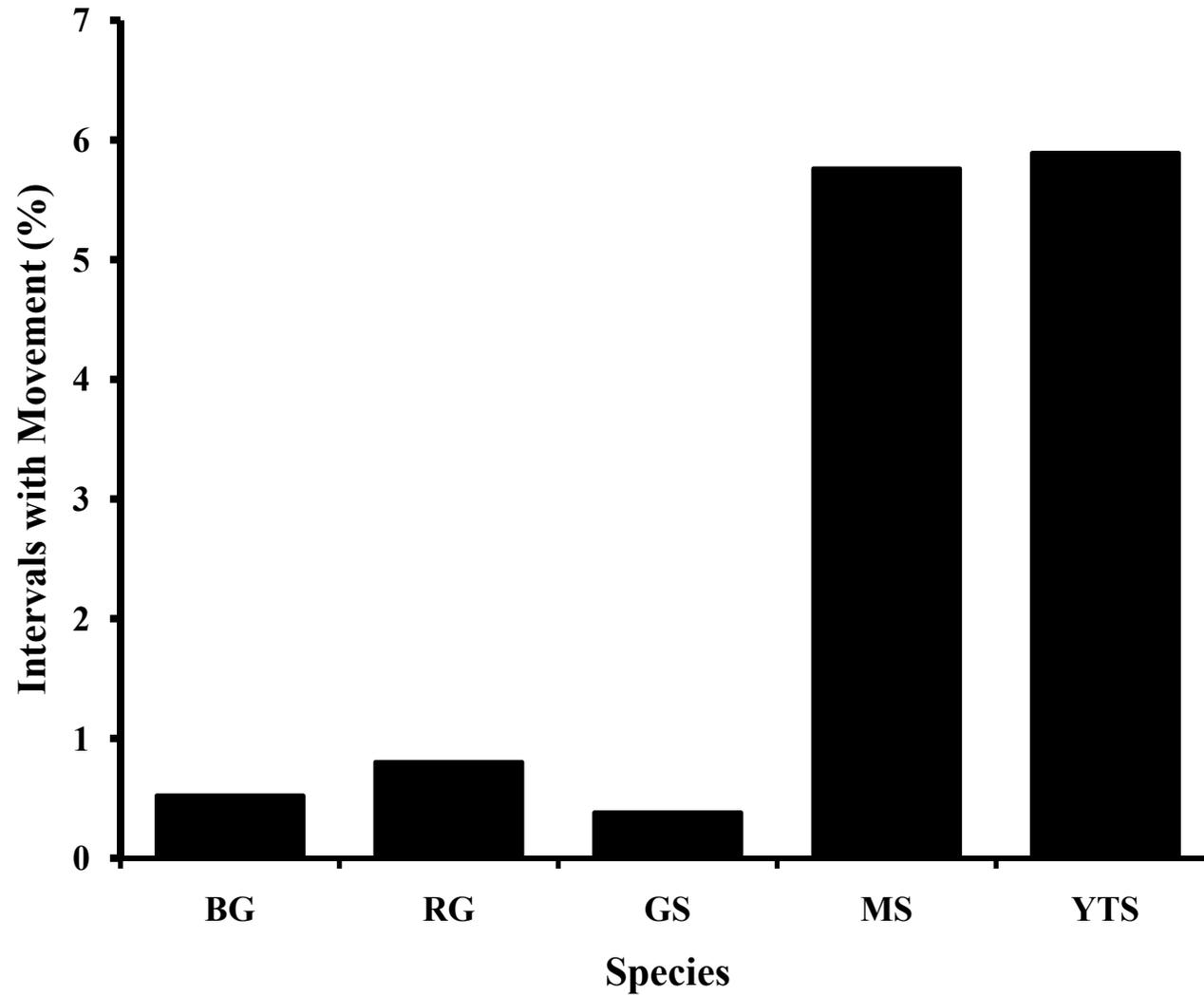


Figure 3.5. Relative frequency of movement as determined by percentage of non-overlapping consecutive position estimates for BG: black grouper, RG: red grouper, GS: gray snapper, MS: mutton snapper, and YTS: yellowtail snapper.

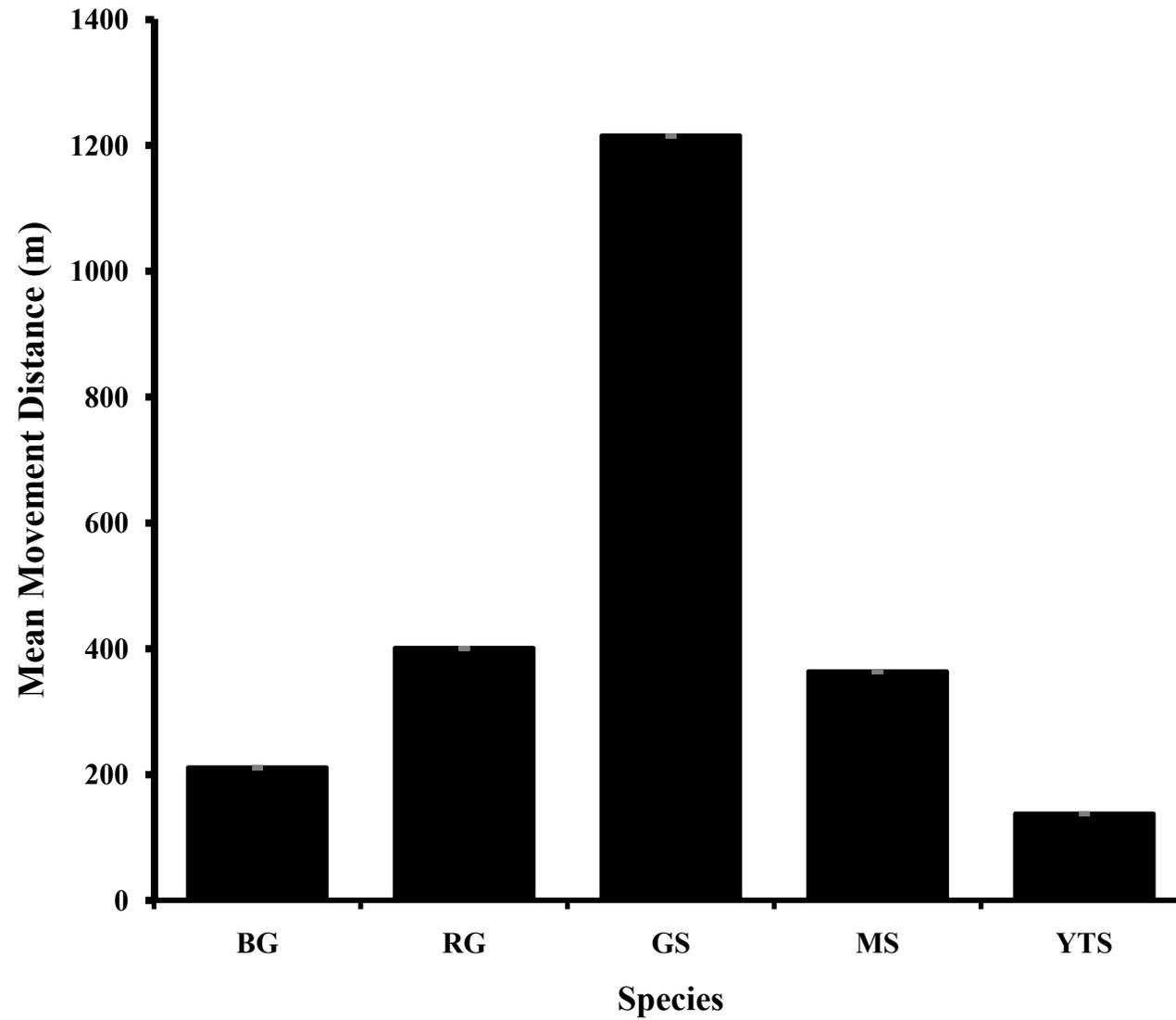


Figure 3.6. Mean recorded non-zero movement distances between consecutive 5-min positioning intervals for acoustically tracked groupers and snappers (BG: black grouper; RG: red grouper; GS: gray snapper; MS: mutton snapper; and, YTS: yellowtail snapper).

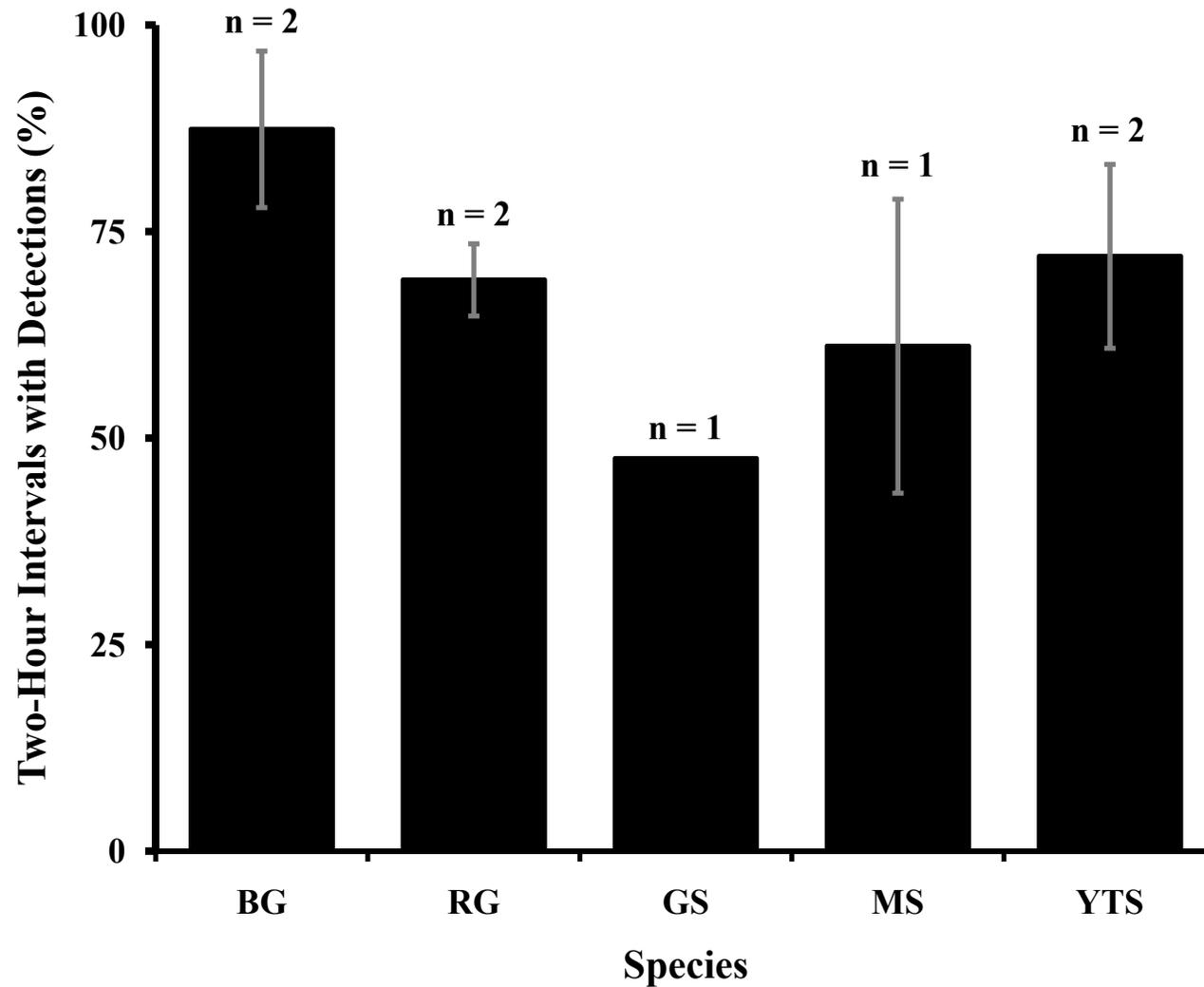


Figure 3.7. Mean percentage of 2-hr batching intervals with detections pooled within species ('BG' = black grouper; 'RG' = red grouper; 'GS' = gray snapper; 'MS' = mutton snapper; 'YTS' = yellowtail snapper). Error bars denote standard error.

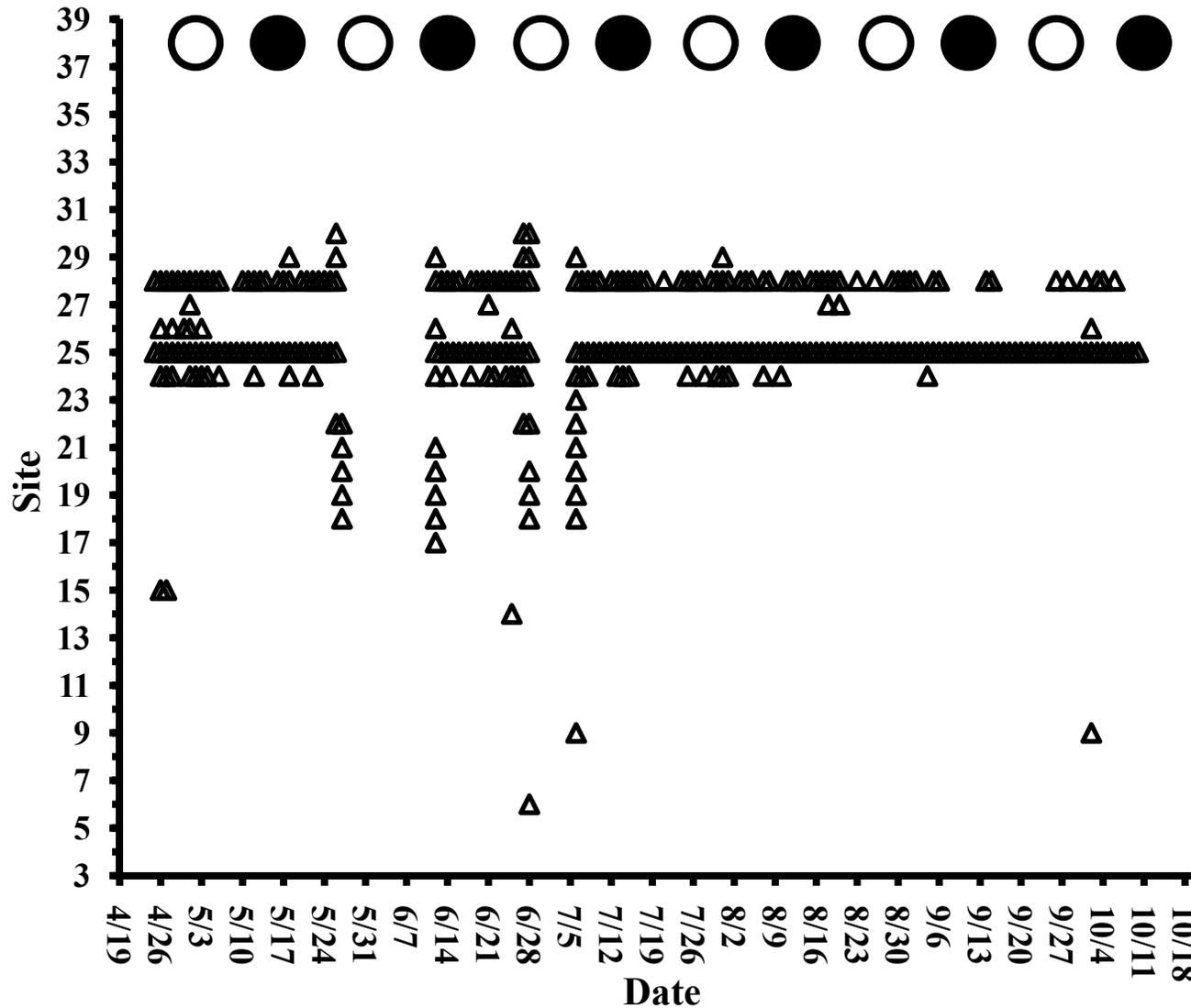


Figure 3.8. Detections by site for Fish 53, a 70 cm, 5.4 kg mutton snapper (*Lutjanus analis*) tagged April 25, 2007. Note absences between May 27 – June 13 and June 28 – July 6, which appear to correspond with full moon. Note also extreme amounts of movement prior to and immediately following these potential spawning migrations relative to other dates in the 168-day track.

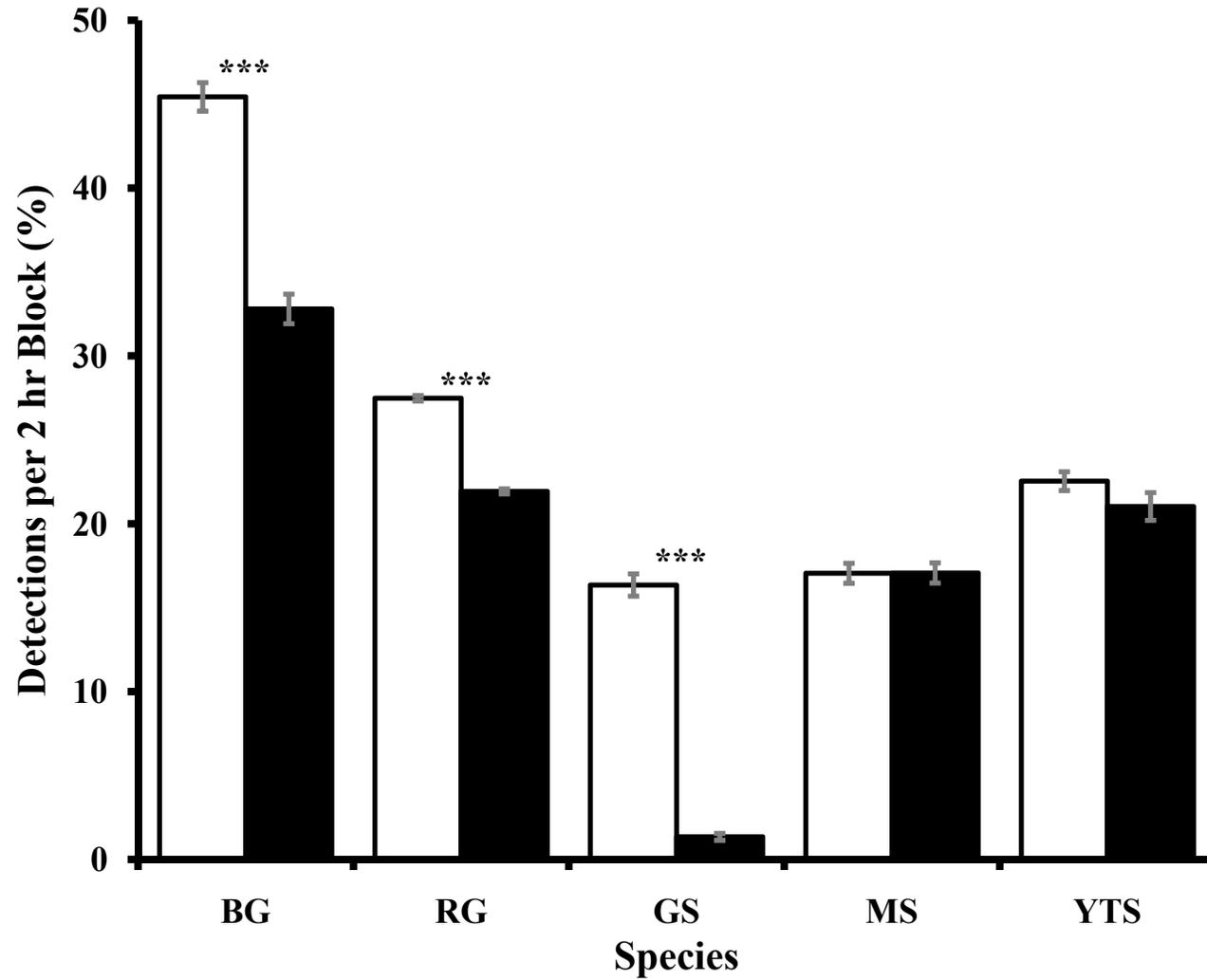


Figure 3.9. Mean percentage of 2-hr batching intervals with detections at night (black bars) and during the day (white bars), pooled within species ('BG' = black grouper; 'RG' = red grouper; 'GS' = gray snapper; 'MS' = mutton snapper; 'YTS' = yellowtail snapper). Asterisks denote significant differences at $p < 0.001$. Error bars denote standard error.

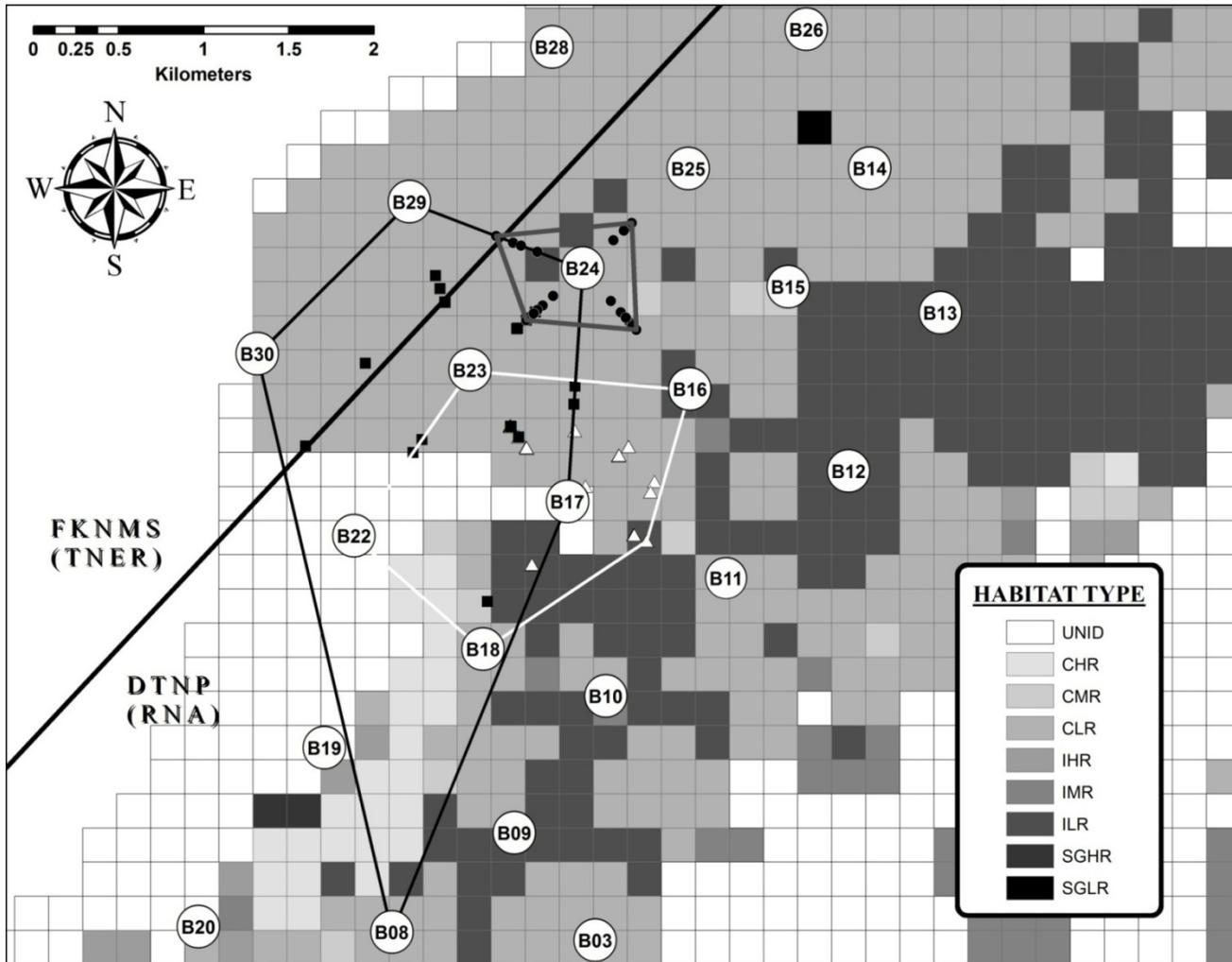


Figure 3.10. Example minimum convex polygon (MCP) home range areas based on 5 min harmonic mean positioning estimates for a yellowtail snapper (Fish 57; black line and squares), red grouper (Fish 884; gray line and black circles), and black grouper (Fish 43; white line and triangles) in Dry Tortugas National Park (DTNP) Research Natural Area (RNA). MCPs are depicted relative to habitat type (UNID = unidentified, C = continuous, I = isolated, SG = spur-and-groove, HR = high relief, MR = medium relief, LR = low relief) and 2007 receiver positions (labeled white circles). Note that >95% of detections for each individual occurred at one central receiver (B23 for Fish 57, B24 for Fish 884, and B17 for Fish 43).

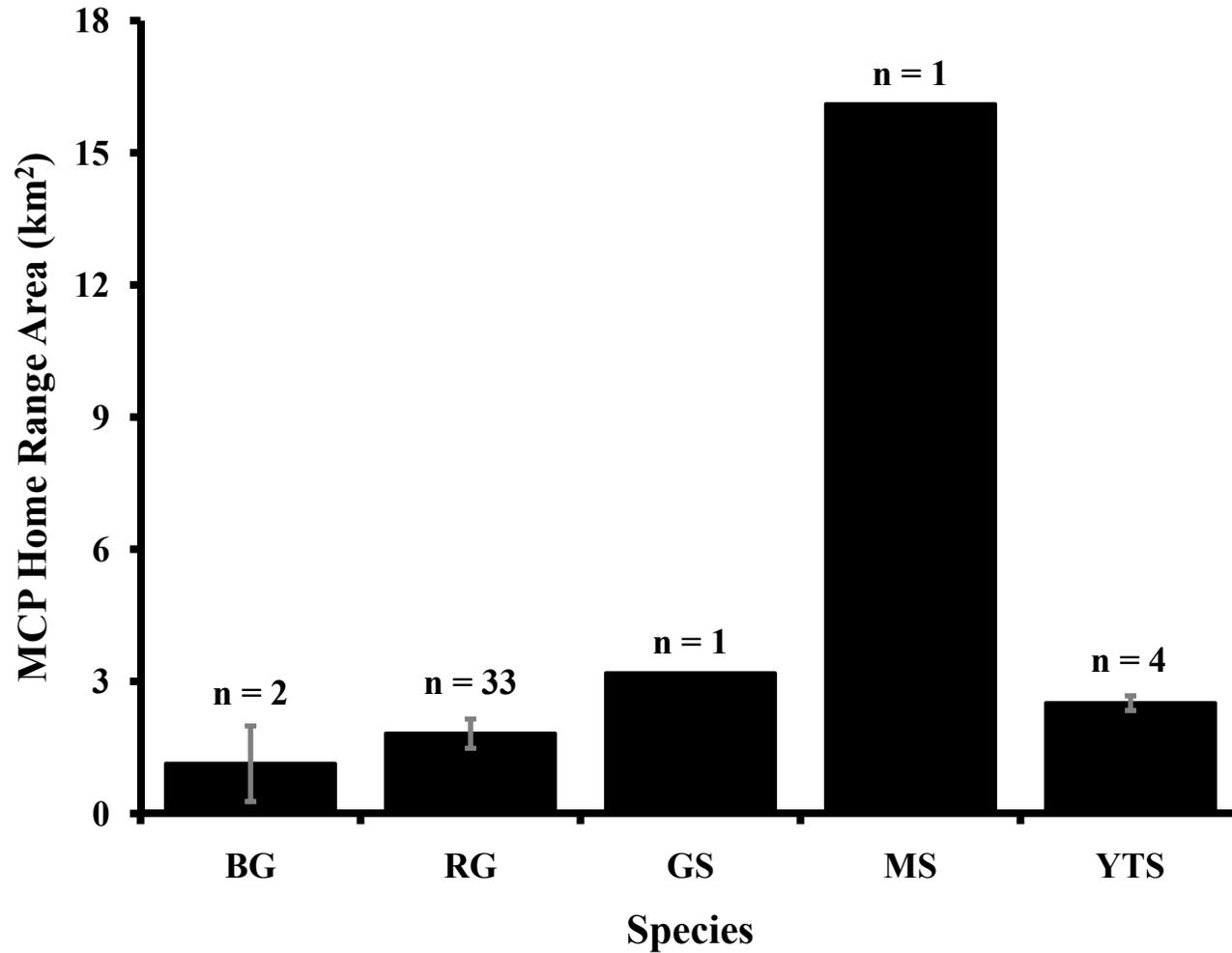


Figure 3.11. Mean minimum convex polygon (MCP) home range areas (\pm SE) by species (BG: black grouper, GS: gray snapper, MS: mutton snapper, RG: red grouper, and YTS: yellowtail snapper) for fish meeting assumptions of MCP home range contained within the boundaries of the acoustic array. Error bars denote standard error.

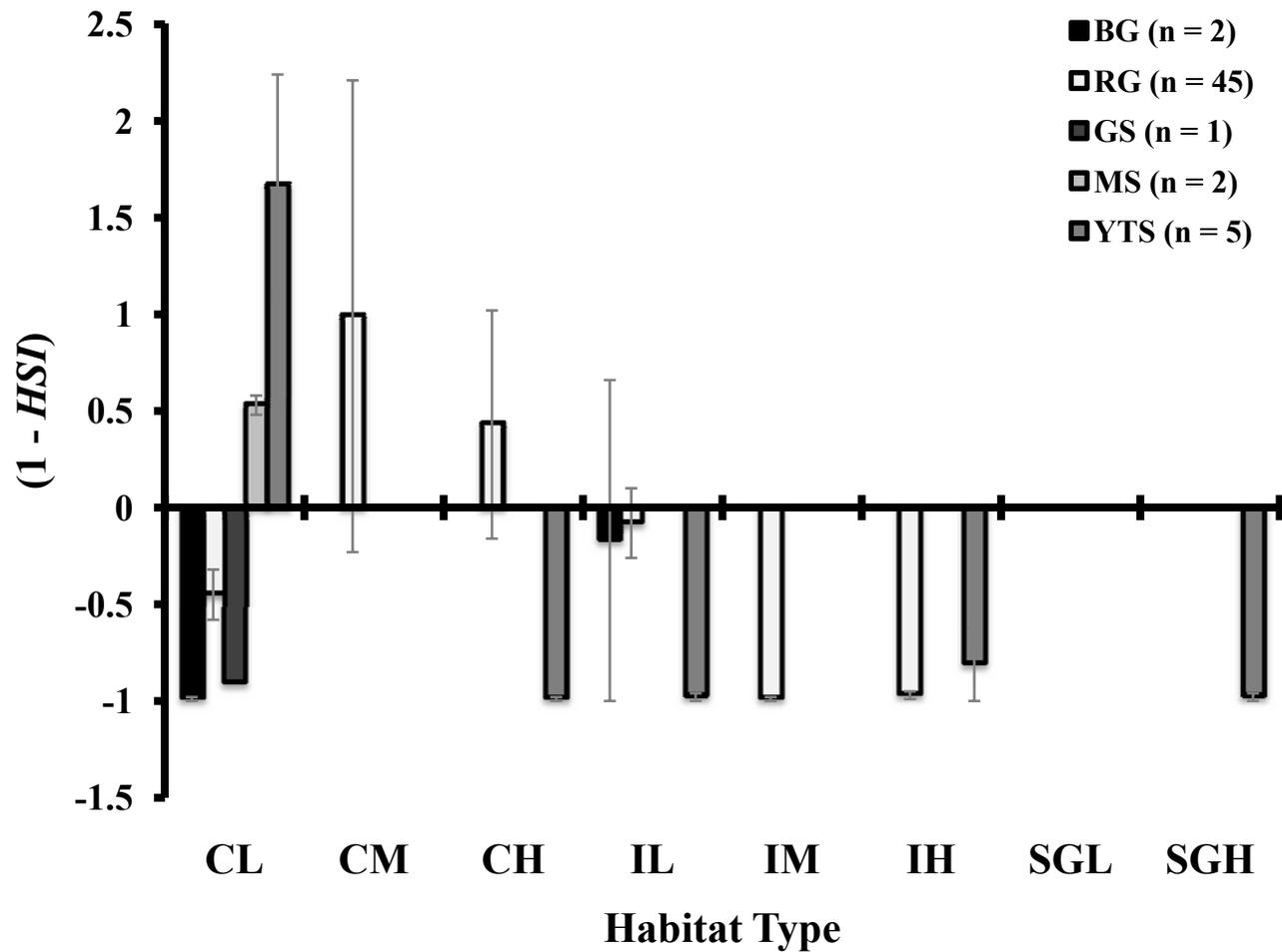


Figure 3.12. Mean habitat selection index (HSI) values (\pm SE) by species, depicted as deviation from 1. Positive values indicate habitats utilized greater than their percent availability within the MCP home range and negative values indicate habitats utilized less than their percent availability within the MCP home range for BG: black grouper, GS: gray snapper, MS: mutton snapper, RG: red grouper, and YTS: yellowtail snapper. Habitat types are categorized by coverage: contiguous (C); isolated (I); and spur-and-groove (SG), and profile: low (L), medium (M), and high (H).

Chapter 4

An individual-based localizing tendency home range model of reef fish movements in Dry Tortugas, Florida

Summary

An individual-based localizing tendency model of reef fish movement within a home range was developed to efficiently utilize fine-scale movement information from telemetry data. In the model, motion is characterized as a sequence of movements at different speeds, orientations, and turning frequencies. The model was parameterized for red grouper (*Epinephelus morio*), black grouper (*Mycteroperca bonaci*), and mutton snapper (*Lutjanus analis*) using fine-scale acoustic tracking data from the Dry Tortugas, Florida. Simulated movement sequences were generated by randomly selecting distances moved and turning angles relative to a home range center from distributions fit to empirical acoustic telemetry data for each species. A spatially-explicit simulation environment was developed in which fish movements were monitored by a simulated array of acoustic receivers. Results of this simulation were used to validate model performance and identify potential errors in statistical home range analysis methods. Overall, the pattern of simulated relocations relative to home range center showed a good fit to empirical observations. Analyses suggested that the limitations of the MCP method as applied to telemetry data may lead to underestimation of mean home range size. Additionally, analyses of spatially-explicit simulated movements suggested the spatial and temporal scale of the acoustic monitoring methodology, as well as the configuration of the acoustic array relative to animal home range centers, may all have a profound influence upon the accuracy of resultant empirical home range estimates.

Background

Many vertebrates use a particular area for their daily movements (Seton 1909, Burt 1943, Sale 1978, Schoener & Schoener 1982, Mace et al. 1983). The area that an animal stays in for the majority of its activities during certain time periods or life stages is commonly referred to as a home range (see Harris et al. 1990 for a review). Literature in terrestrial ecology is replete with home range theory and examples. Although numerous studies have documented home range use in fish (Goeden 1978; van Rooij et al. 1996; Shapiro et al. 1994; Zeller 1997a, b; Kramer & Chapman 1999; Bell & Kramer 2000; Eristhee & Oxenford 2001; Bolden 2001; Lembo et al. 2002; Baras et al. 2002), few have precisely quantified use of space or examined it in the context of resource protection (but see Zeller & Russ 1998, Eristhee & Oxenford 2001). Information about reef fish movement patterns and home range sizes is critical for the effective implementation and performance evaluation of no-take marine reserves designed to protect overexploited stocks and generate sustainable fisheries (e.g., Roberts 1997a, Lembo et al. 1999, Palumbi 2001, O'Dor et al. 2004).

A number of statistical home range models have been developed to convert spatial distributions of telemetry relocations into estimates of range size. These include the minimum convex polygon (MCP) method (Odum & Kuenzler 1955) and density estimation models such as the bivariate normal (Jennrich & Turner 1969), harmonic mean (Dixon & Chapman 1980), and kernel models (Worton 1989). These models are capable of generating significantly different estimates of home range size and overlap when applied to the same dataset (Schoener 1981, Samuel et al. 1985). The treatment of outliers in the MCP method may have a significant impact on the result size and

configuration of the home range, and unused territory may be included within its boundaries. The bivariate normal distribution generates home ranges that are inappropriately peaked with tails that are unrealistically long. Negative values and low numbers of fixes cause problems for harmonic mean estimates (Harris et al. 1990). Selection of an appropriate smoothing parameter is problematic for kernel methods, and parametric kernel methods fail to capture hard boundaries common to many natural systems (Getz et al. 2007). While these models provide useful aggregate measures of home range size and home range overlap, their descriptive nature means they lack theoretical or predictive value. By aggregating data, they ignore fine-scale information on the precise spatial and temporal sequence of movements available from most telemetry studies, and the relationships of these movement decisions relative to habitat or the presence of conspecifics (Moorcroft & Lewis 2006).

To efficiently utilize fine-scale movement information, telemetry data may be mathematically analyzed in the context of a correlated random walk (CRW), in which motion is characterized as a sequence of movements at different speeds, orientations, and turning frequencies (Skellam 1973, Okubo 1980, Okubo & Levin 2001). These CRW models are referred to as mechanistic because the organism's space use is simulated through explicit mathematical scaling of the underlying rules of movement, which may incorporate responses to both local and non-local orientation cues (Okubo 1980, Levin & Pacala 1996). Thus, they capture the biological reality that the spatial distribution of relocations in a telemetry dataset is the product of numerous movement decisions made in response to a variety of environmental and social factors (Moorcroft & Lewis 2006).

This chapter describes the development of a mechanistic home range model for reef fish, using data generated by the University of Miami Reef Fish Tracking Project (see Chapter 3). The model’s utility as a simulation tool is evaluated through the comparison of simulated movements to empirically observed fine-scale, high-frequency relocation data. In the subsequent chapter, this predictive model of grouper space use will be used to evaluate the impacts of spatial fisheries management tools.

Methods

Movement data for black grouper (*Mycteroperca bonaci*), red grouper (*Epinephelus morio*), and mutton snapper (*Lutjanus analis*) were collected and processed as described in Chapter 3. Use of 5-minute batching intervals for aggregating detections enhanced spatial positioning resolution (see Chapter 2) and reduced autocorrelation between position estimates. The majority of individuals tracked for each of these species met assumptions for use of home ranges contained within the acoustic array.

Mechanistic home range models were developed for each species following the simple “localizing tendency” (LT) model developed by Holgate (1971) and Okubo (1980). My description of this model closely follows Moorcroft & Lewis (2006). Individual movement decisions are expressed as a redistribution kernel, describing the probability of an individual moving from one location to another as a function of time and current spatial position. The localizing tendency of an animal with a home range may be expressed as a non-uniform distribution of movement directions:

$$K\left(\phi, \hat{\phi}\right),$$

where $K(\phi, \hat{\phi})d\phi$ represents the probability of moving in direction ϕ , and this probability is biased towards a particular location (e.g., the centroid of the home range), indicated by the angle $\hat{\phi}$. The functional form for K is expressed as a *von Mises* distribution, a unimodal distribution described by the probability density function

$$K(\phi, \hat{\phi}) = \frac{1}{2\pi I_0(\kappa)} \exp[\kappa \cos(\phi - \hat{\phi})],$$

and two parameters, $\hat{\phi}(-\pi \leq \hat{\phi} \leq \pi)$ and $\kappa(\kappa \geq 0)$. The angle $\hat{\phi}$ is the mode of the distribution and also the mean direction. $I_0(\kappa)$ is a modified Bessel function that normalizes K to integrate to 1. The parameter κ is the concentration parameter, governing the degree of uniformity in the distribution of movement directions. When $\kappa = 0$, the distribution is circular uniform, meaning there is no preferred direction of movement. Higher values of κ are indicative of greater home range affinity.

When aggregated over time (τ), reef fish movements may be expressed as the product of two distributions; one describing distances moved, and another describing angles of movement. Mathematically, the redistribution kernel:

$$k(\mathbf{x}, \mathbf{x}', \tau, t) = \frac{1}{\rho} f_{\tau}(\rho) \cdot K_{\tau}(\phi, \hat{\phi}),$$

describes the probability density of moving from location \mathbf{x}' to \mathbf{x} , where the kernel k has been translated from Cartesian (x, y) coordinates to polar (ρ, ϕ) coordinates (Moorcroft & Lewis 2006). Here $\rho = |\mathbf{x}' - \mathbf{x}|$, the distance between the starting point \mathbf{x}' and the finishing point \mathbf{x} , and $\phi = \tan^{-1}(y - y' / x - x')$, the angle between the starting point and the finishing point, where $\hat{\phi}$ is the direction of the individual's home range center from its

current position. The probability of moving in direction ϕ during the time interval τ is

described by $K\left(\phi, \hat{\phi}\right)d\phi$. The probability that an individual at point \mathbf{x}' will move to a

point \mathbf{x} that is between distance ρ and $\rho + d\rho$ from \mathbf{x}' is described by the quantity $f_{\tau}(\rho)d\rho$.

The $1/\rho$ translates the probability of moving a given distance and direction into a

probability of moving from one area to another. The localizing tendency is incorporated

through specification of the individual's distribution of movement directions (K_{τ}) given

by the von Mises density function with concentration parameter κ_{τ} , and $\hat{\phi}$ is the angle

between the individual's current position and the home range center (x_H, y_H) as given by

$$\hat{\phi} = \tan^{-1}(y - y_H / x - x_H).$$

Custom software was written in Java 6.10 (Sun Microsystems, Santa Clara, CA) to process time-sequenced reef fish position fixes and distance from previous point, ρ_{prev} ; distance from home range center, $\rho_{centroid}$; and turning angle ϕ relative to angle to home range centroid, $\hat{\phi}$. Data were pooled within species. Movement data from all individuals for each species were included, including individuals that failed to meet assumptions of a home range contained within the acoustic array (see Chapter 3: Home Range Utilization).

As a large proportion of 5-min time steps involved no discernable movement, distances moved were expressed as a two-step process: 1) a probability of moving during any given time step; and, 2) a distance moved (when movement occurred). Movement distances were modeled using the best fitting distribution for ρ_{prev} , fit using Input Analyzer for Arena (Rockwell Automation, Warrendale, PA). The 'von Mises Maximum Likelihood Estimator' in the 'circular' package for R (www.r-project.org) was used to fit

von Mises distributions to species-specific aggregated turning angles relative to home range center ($\phi - \hat{\phi}$).

To assess model performance, simulated polar coordinate plots of turning angle of movement and distance from home range center were qualitatively compared to polar coordinate plots of actual angle and distance from home range center. Data was plotted three-dimensionally using Surfer (Golden Software, Inc., Golden, Colorado) to facilitate interpretation.

In addition, simulated detection sequences were generated using a spatially-explicit model implemented in Java 6.10 using the Repast Agent Modeling Toolkit (North et al. 2006). This model parsed the Dry Tortugas, FL region described in Chapter 3 into 22,620 cells of 200 m X 200 m size. Each cell was assigned a unique identification code and depth. An array of simulated receivers was implemented in grid cells corresponding to the locations of receivers during the “Tortugas Phase II” project described in Chapters 2 and 3 (Fig. 4.1). For each simulation run, a fish was randomly instantiated at the spatial position of each receiver, and movements and receiver detection patterns were tracked for one year.

In the simulation, if a random number drawn from a uniform distribution between 0 and 1 was less than the probability of moving a discernable distance, a movement distance was randomly drawn from the distribution fit to ρ_{prev} . Maximum movement distance was bounded at 6000 m per move. Randomly drawn movement distance was converted from meters to simulation grid cell units. If the grid cell distance was greater than zero, the optimal movement was determined by randomly selecting a turning angle from a von Mises distribution generated with the concentration parameter (κ_{τ}) for the

species under examination. The simulation then evaluated all the spatial cells within the desired distance, and moved the fish to the cell in the direction of the selected turning angle. If more than one cell met criteria, the final selection was chosen randomly from among the matches. After each movement, for each fish, the number of detections registered by receivers within the array was recorded for the interval.

The number of detections registered by a receiver during a given batching interval was computed by dividing the length of the interval (5 min) by the ping rate of the simulated fish tag (120 sec), then multiplying by the probability (P) of detecting that fish (f) at that receiver (r) during that interval (τ). This probability was determined using an analytical solution of the reduced logistic model for probability of tag detection in a coral reef habitat described in Chapter 2:

$$P_{f,r,\tau} = \frac{e^{8.08844 - 0.025872(\rho) + 0.000013724(\rho^2) - 0.08663(w) + 0.10745(d)}}{(1 + e^{8.08844 - 0.025872(\rho) + 0.000013724(\rho^2) - 0.08663(w) + 0.10745(d)})}$$

where w is wind speed (knots) and d is depth of receiver (m). Wind speeds were determined by randomly drawing from normal distributions fit to monthly Tortugas regional wind speed data obtained from the National Data Buoy Center's Pulaski Shoal Light Data Buoy, located approximately 14 miles from the acoustic array. Receiver depths were determined using actual bathymetric soundings from the receiver site.

As in Chapter 2, the probability of detecting a tag beyond 915 m from a receiver was set to zero. Simulated relocation data was post-processed using the logistic weighted harmonic mean positioning estimator described in Chapter 2, which increases positioning resolution during intervals when detections are recorded at multiple receivers. The overall number of positioning intervals with one or more detections was compared to empirically observed detection rates. Finally, MCP home ranges for simulated fish

detection patterns were computed using Hawth's Tools (Beyer 2004) for ArcGIS (ESRI, Redlands, CA), and subsequently compared to empirically observed home ranges. As in Chapter 3, for fish with linear home ranges, home range size was estimated by multiplying the maximal detection area per receiver [$\pi (915 \text{ m})^2$] by the number of receivers in the line.

Results

Empirical observations of reef fish movements (see Chapter 3) found that black grouper exhibited detectable movement in only 473 of 84108 (0.56%) 5-min intervals, red grouper in only 16821/2103428 (0.80%) 5-min intervals, and mutton snapper in 1267 of 22006 (5.76%) 5-min intervals. For all three species, the exponential distribution provided satisfactory fits ($p < 0.005$) to the non-zero movement data (Fig. 4.2). The MLE best-fit von Mises distributions ($p < 0.01$) for turning angles are displayed in Fig. 4.3.

In general, mutton snapper moved most frequently and, on average, moved the farthest per move; as such, they might be considered the most 'mobile' species examined. Black grouper moved least frequently and, on average, moved the shortest distance per move; however, their affinity towards a home range center was less than one-third as intense as that for red grouper.

A comparison of spatial distribution of observations relative to home range center between observed and simulated movements showed satisfactory fits for all species (Fig. 4.4). Mean detection rates across 12 months of simulation were higher than observed

detection rates; however, minimum detection rates were lower for simulated fish (Table 4.1).

MCP home ranges estimated from 12 months of simulated detection patterns were significantly larger than home range estimates generated from empirical observations of reef fish movement; however, home range estimates from 3 months of simulation were very similar to empirical observations for black grouper and red grouper (Table 4.2A, B). Paired t-tests for means indicated MCP home range sizes were consistently underestimated by the simulated acoustic array relative to the actual space use (Table 4.2C) after 12 months of movement by simulated black grouper ($t = -2.43$, $df = 30$, $p < 0.05$) and mutton snapper ($t = -6.37$, $df = 30$, $p < 0.001$), but were not significantly underestimated for red grouper ($t = -1.24$, $df = 30$, $p > 0.05$).

MCP home range size estimated from simulated acoustic detection patterns (Fig. 4.5) showed an asymptotically (logarithmic) increasing trend through time for black grouper ($F_{1,369} = 134.9$, $p < 0.001$), red grouper ($F_{1,369} = 83.4$, $p < 0.001$), and mutton snapper ($F_{1,369} = 52.0$, $p < 0.001$). Estimated mean MCP home range size after 12 months of simulation was highly dependent upon location of the home range center with respect to the configuration of the acoustic array; one-tailed two sample t-tests assuming equal variances revealed significantly lower estimated home range sizes for black grouper ($t = -3.82$, $df = 29$, $p < 0.001$), red grouper ($t = -2.41$, $df = 29$, $p < 0.001$), and mutton snapper ($t = -1.96$, $df = 29$, $p < 0.05$) with home range centers along the edges of the acoustic array versus those with home range centers in the core of the array (Fig. 4.6).

Discussion

Evaluation of reef fish space utilization patterns may be objectively performed through examinations of distributions fit to empirical data for fish movement between fixed time intervals and turning angles relative to home range center. The mean of the exponential distribution for movement is a useful proxy for overall mobility, and the concentration parameter of the von Mises distribution for turning angles is a significant indicator of affinity to a home range center. Examination of distributions fit within this paper indicates that black grouper have lower mobility than red grouper or mutton snapper. Red grouper affinity to home range center was nearly three times as high as that for black grouper. This difference is not surprising, considering black grouper are more piscivorous than red grouper and are less associated with the bottom (Randall 1967). Both species are ambush predators who often lurk near structures then dart out and engulf their prey whole (Randall 1967). This feeding strategy, as well as their strong affiliation with dens and cleaning stations (Smith 1961), probably explains their relatively short distance movements and affinities towards a home range center. Mutton snapper exhibited the higher mobility than groupers but maintained a strong association with a home range, as evidence by their tendency to turn back towards their home range center. Little is known about the movements of mutton snapper, although a mark-recapture study of mutton and yellowtail snapper by Beaumarriage (1969) found minimal displacement 262 d post-release, suggesting utilization of a reasonably small home range.

The larger home ranges predicted by mechanistic simulations suggest potential underestimation of home ranges by fixed acoustic arrays (see Chapter 3) due to the limited spatial and temporal scale of empirical observations available (Steingrímsson &

Grant 2003). The mechanistic simulations described by this paper were conducted over one year; whereas the majority of empirical estimates of MCP home range size described in Chapter 3 were derived from approximately three months of tracking data. Home ranges derived from simulated acoustic detection patterns after three months were relatively consistent with empirical observations, but size of estimated home range increased logarithmically through time, suggesting length of acoustic tracking may have a profound influence upon the resultant estimate of home range size. The correlation with time in our simulations may also result from more long-range movements being drawn from the tails of the exponential movement distribution, although this distribution was bounded at 6000 m to reduce unrealistically large movements. Empirical observations suggest these species require between 1-2 months of monitoring before their space use reaches a visually recognizable asymptote (see Table 3.2).

The limited spatial scale of the simulated acoustic array resulted in significant underestimation of actual home range utilization by simulated fish. Significantly smaller home ranges were estimated for fish with home range centers along the boundaries of the acoustic array due to an increased frequency of undetected movements out of the array. This finding suggests that the location of capture and subsequent release of acoustically tagged fish exhibiting home range behavior should be near the core of a spatially-limited acoustic array to increase the accuracy of resultant estimates of space use.

The empirical estimates of MCP home range size presented in Table 4.2 were additionally constrained by the assumptions of the MCP method; namely, that MCP estimates needed to reach an asymptote when plotted over time as area-observation curves (Laundré & Keller 1984). This led to the exclusion of 1 of 3 black grouper (33%),

12 of 45 red grouper (27%), and 1 of 2 mutton snapper (50%) from consideration in empirical MCP home range size estimates. Most of these organisms were excluded because their movements exceeded the spatial scale of the acoustic array. Because mechanistic simulations incorporated movements and turning angles from all individuals tracked within each species, it is not surprising that simulated reef fish movements resulted in larger estimates of home range size. MCP home range sizes for simulated red grouper estimated from simulated acoustic detection patterns were not significantly smaller relative to ‘actual’ MCP home range sizes for simulated red grouper. This observation is probably explained by the reduced scale of movements for red grouper relative to mutton snapper as well as the increased sample size (in terms of numbers of fish tracked and length of tracking) for empirically-observed red grouper relative to black grouper and mutton snapper (see Chapter 3).

Finally, it is worth noting that although animal affinity to a home range center was incorporated as a ‘behavior’ in these simulations, numerous other behaviors surely important to reef fish movement patterns were omitted. For example, detection rates within the simulated acoustic array were significantly higher than empirically-observed detection rates because simulated reef fish never sought shelter (resulting in complete acoustic signal blockage) nor rested. These artificially enhanced detection rates might also have resulted in a higher probability of detection at distant locations. This omission also probably accounts for the ‘smoothing’ effect of the simulation upon the distribution of relocations (see Fig. 4.4).

This chapter demonstrates that empirically-observed movements of groupers and snappers can be coarsely-replicated using a simple localizing tendency mechanistic home

range model. Following a bottom-up modeling process, simple behavioral rules were developed that, when driven by distributions fit to empirical data, provided satisfactory replication of patterns observed in the field (Grimm et al. 2005). Analysis of model outputs identified potential bias in empirically-estimated home range sizes, and suggested the spatial and temporal scale of the acoustic monitoring methodology, as well as the configuration of the acoustic array relative to animal home range centers, may all have a profound influence upon the accuracy of resultant home range estimates. Perhaps more significantly, the mechanistic nature of this model means that it contains a temporal variable in its formulation, allowing for its application in individual-based, spatially-explicit simulation models. Such applications would be useful in considering the impacts of reef fish movement upon the effectiveness of spatial management regimes such as no-take marine protected areas. The simple formulation of the model also allows for easy manipulation of home range affinity and distances moved, allowing for easy extension to various movement strategies and extrapolation to new species as data becomes available.

Table 4.1. Percentage of five minute intervals with at least one detection for A) empirically observed and B) simulated reef fish after 12 months of simulation.

A)			
Full Batch Intervals (%)			
Species	<i>n</i>	<i>mean</i>	<i>min</i>
Black grouper	2	62.47	24.79
Red grouper	33	46.54	10.27
Mutton snapper	1	30.28	30.28

B)			
Full Batch Intervals (%)			
Species	<i>n</i>	<i>mean</i>	<i>min</i>
Black grouper	32	67.22	26.52
Red grouper	32	70.93	19.35
Mutton snapper	32	66.77	10.56

Table 4.2. Estimated minimum convex polygon (MCP) home range of A) empirically observed and B) simulated reef fish after 3 and 12 months of simulation, and actual MCP home range of C) simulated reef fish after 12 months of simulation.

A)					
Species	<i>n</i>	Estimated MCP Home Range (km ²)			
		<i>mean</i>	<i>se</i>	<i>min</i>	<i>max</i>
Black grouper*	2	1.13	0.86	0.27	1.99
Red grouper*	33	1.94	0.33	0.01	5.76
Mutton snapper*	1	16.10	16.10	16.10	16.10

B)									
Species	<i>n</i>	Estimated MCP Home Range (km ²)							
		3 Months				12 Months			
		<i>mean</i>	<i>se</i>	<i>min</i>	<i>max</i>	<i>mean</i>	<i>se</i>	<i>min</i>	<i>max</i>
Black grouper	32	1.22	0.18	0.00	3.52	3.40	0.25	0.00	6.94
Red grouper	32	1.58	0.21	0.00	3.68	4.55	0.29	0.00	10.82
Mutton snapper	32	4.79	0.52	0.28	11.06	7.14	0.35	0.28	15.36

C)					
Species	<i>n</i>	Actual MCP Home Range (km ²)			
		<i>mean</i>	<i>se</i>	<i>min</i>	<i>max</i>
Black grouper	32	4.14	0.17	2.33	6.43
Red grouper	32	4.85	0.28	0.97	7.89
Mutton snapper	32	12.95	0.61	4.82	18.61

*See Chapter Three for details

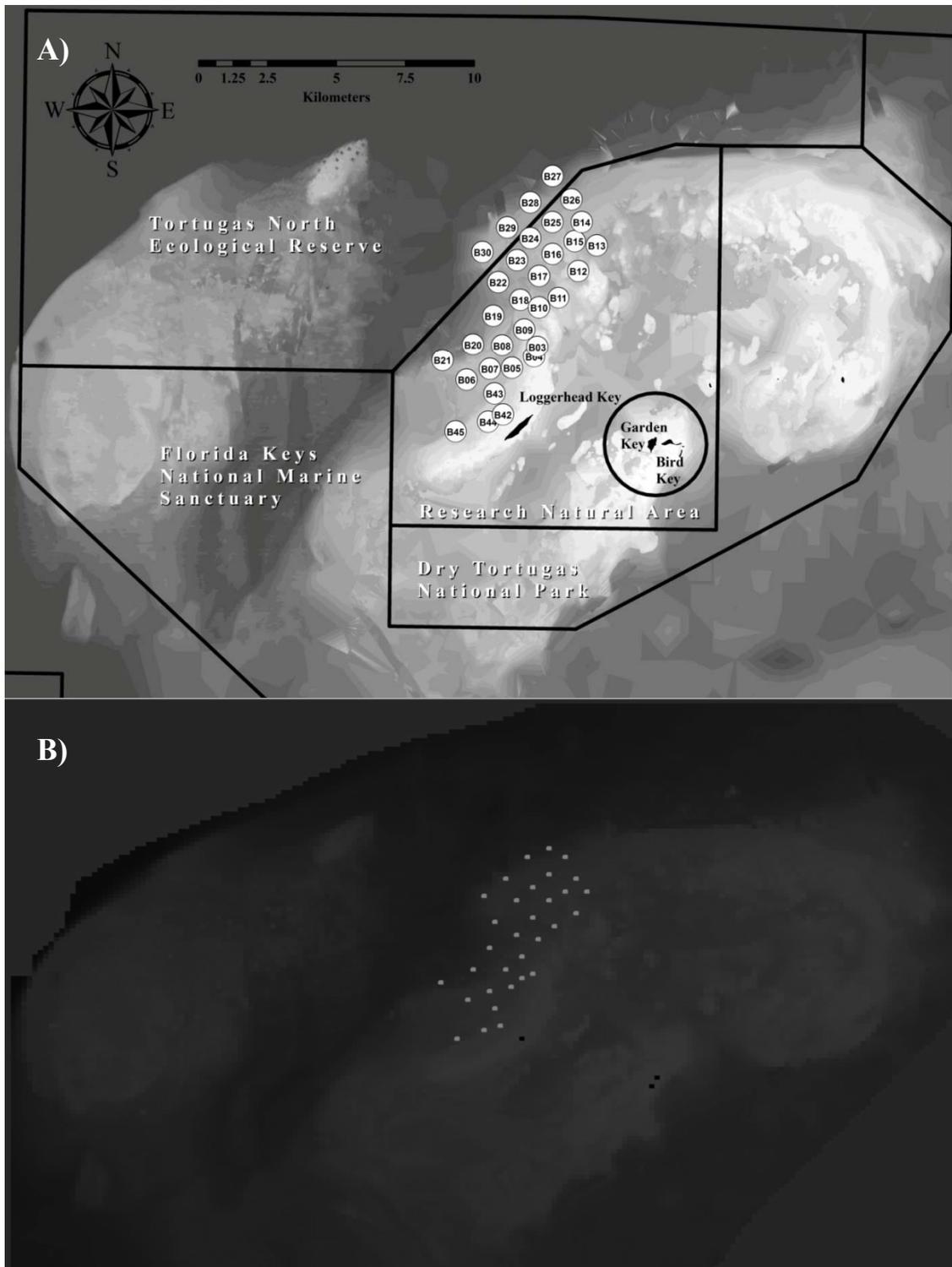


Figure 4.1. Actual (A) and Simulated (B) reef fish movement environments of Dry Tortugas, FL with associated bathymetries and hydroacoustic receiver placements in Dry Tortugas, Florida. Movement simulation model implemented in Repast Agent Modeling Toolkit (North et al. 2006).

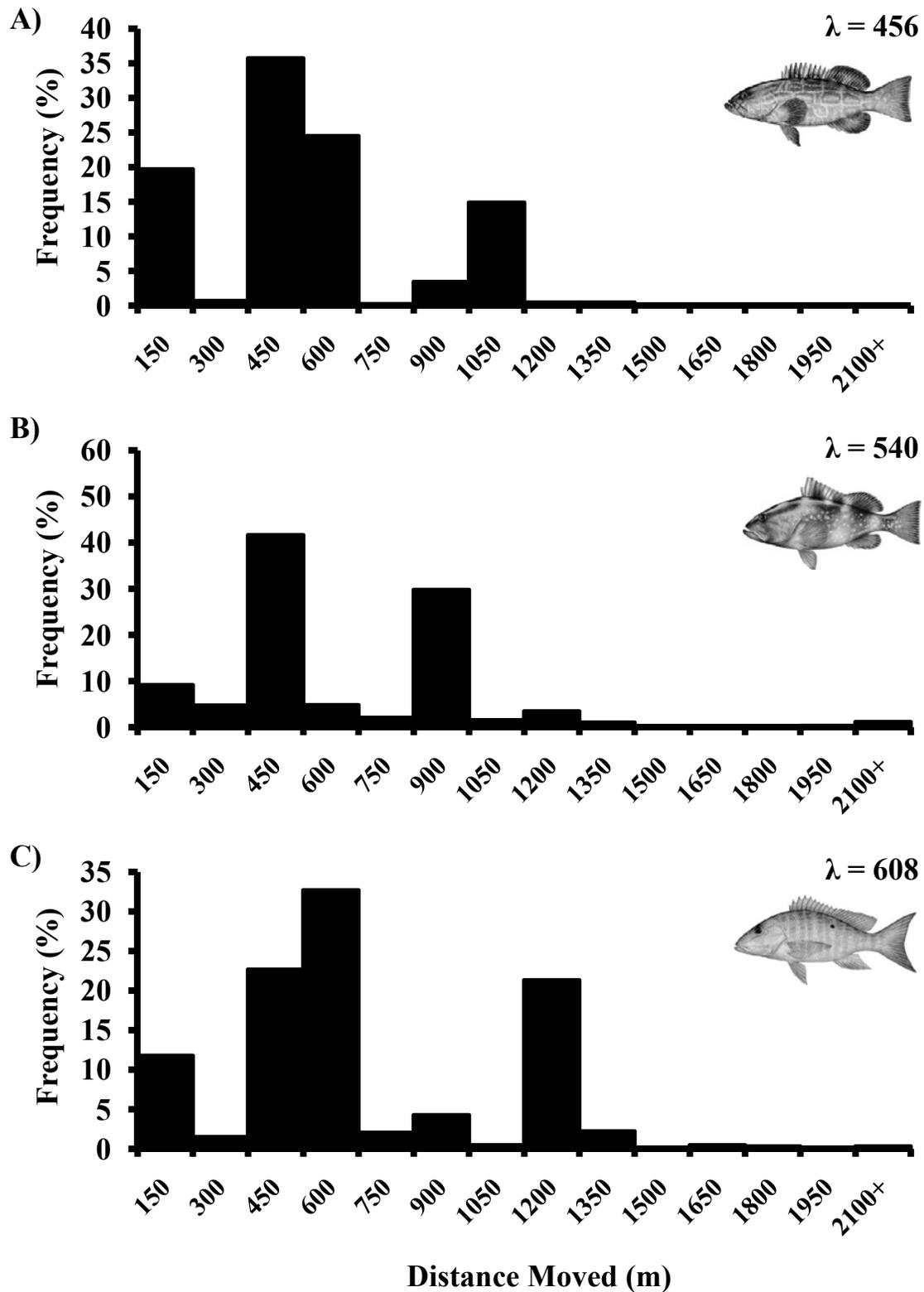


Figure 4.2. Relative frequency histograms of empirical observations of movement for A) black grouper (*Mycteroperca bonaci*), B) red grouper (*Epinephelus morio*), and C) mutton snapper (*Lutjanus analis*). Mean (λ) of best fit exponential distribution indicated.

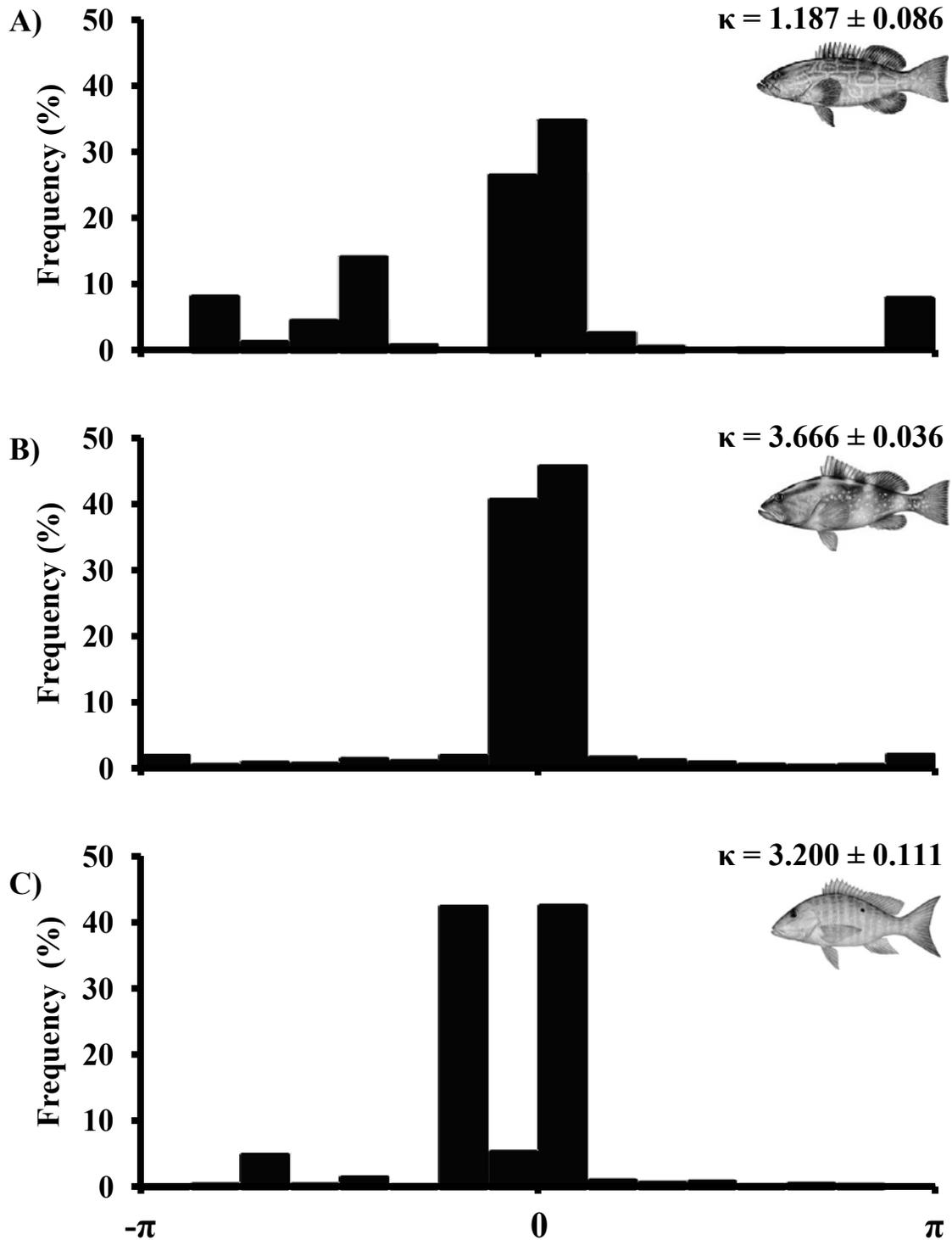


Figure 4.3. Relative frequency histograms of empirical observations of turning angles relative to home range center for A) black grouper (*Mycteroperca bonaci*), B) red grouper (*Epinephelus morio*), and C) mutton snapper (*Lutjanus analis*). Concentration parameter (κ) of best fit von Mises distribution indicated.

Figure 4.4. Distribution of spatial position fixes relative to home range center for (1) empirically-observed and (2) simulated movements of A) black grouper (*Mycteroperca bonaci*), B) red grouper (*Epinephelus morio*), and C) mutton snapper (*Lutjanus analis*).

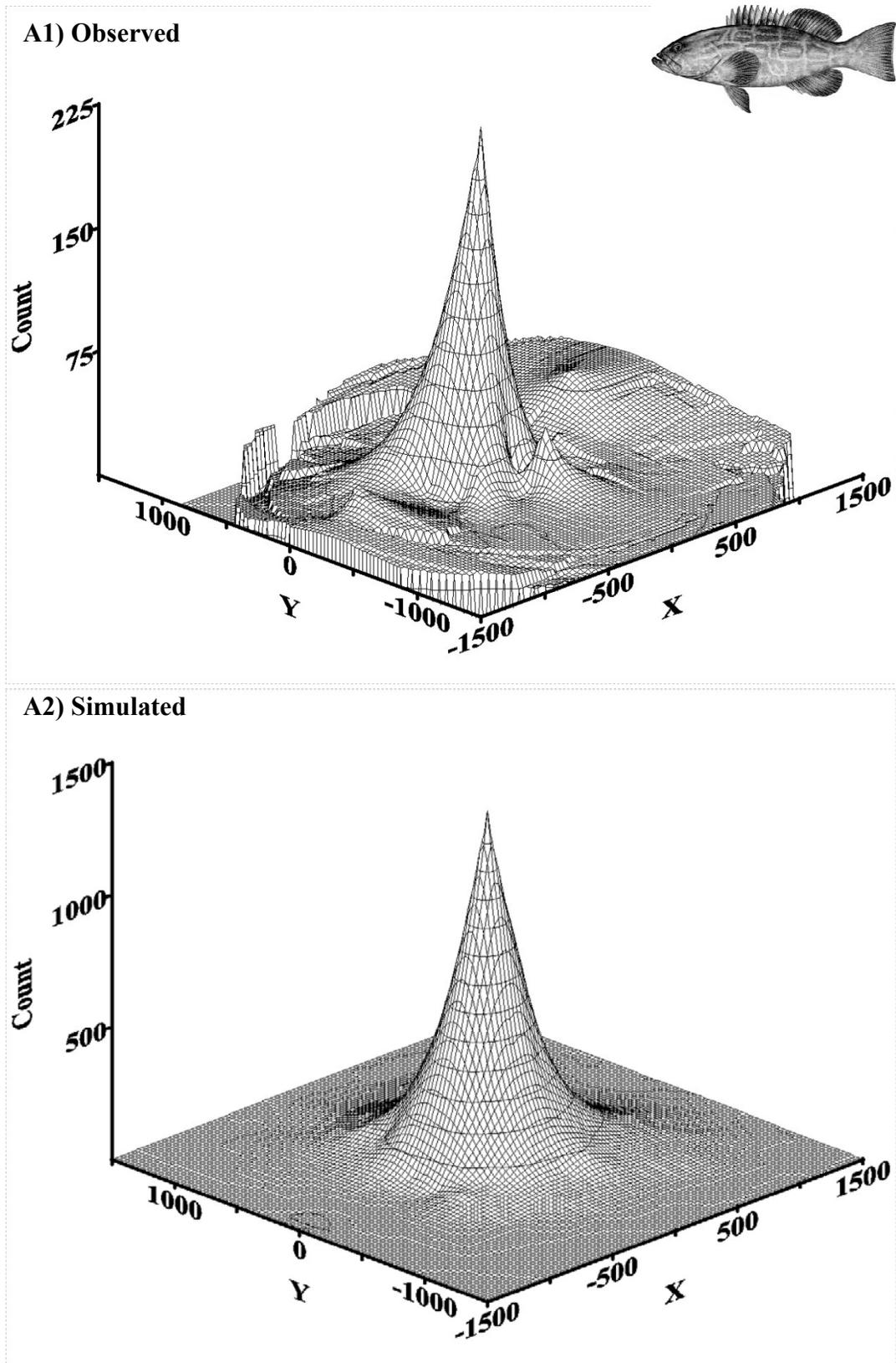


Figure 4.4A.

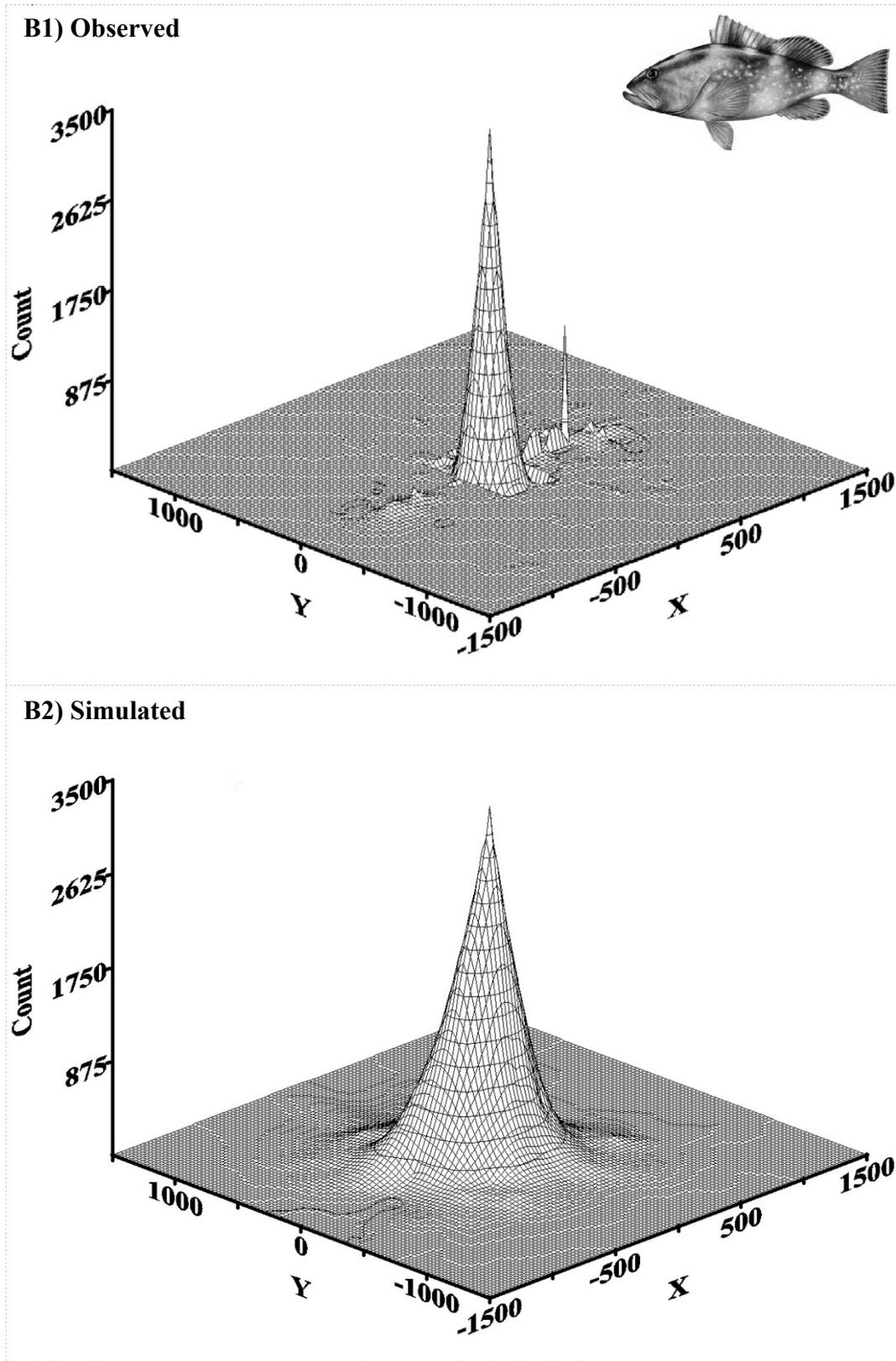


Figure 4.4B.

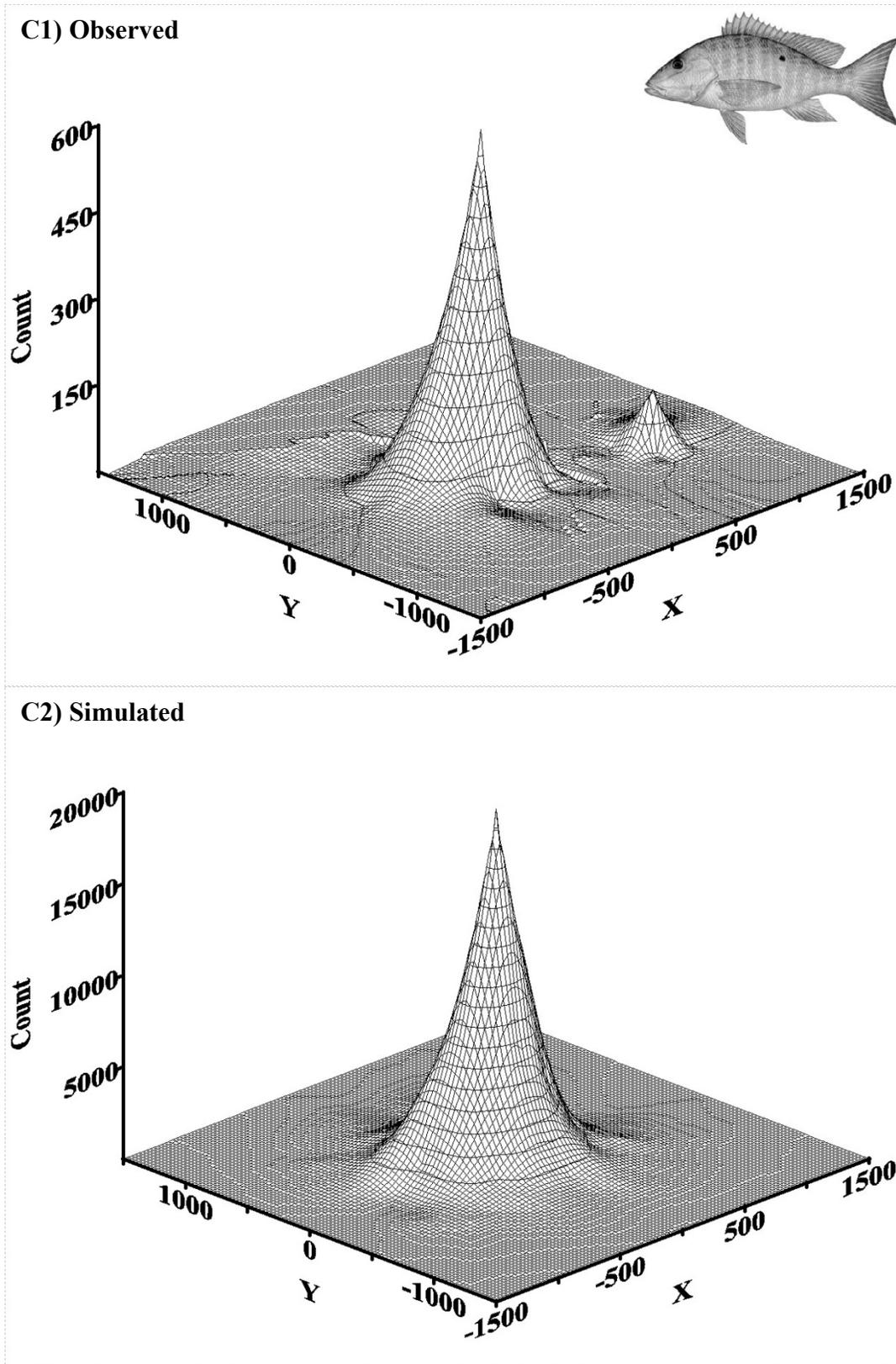


Figure 4.4C.

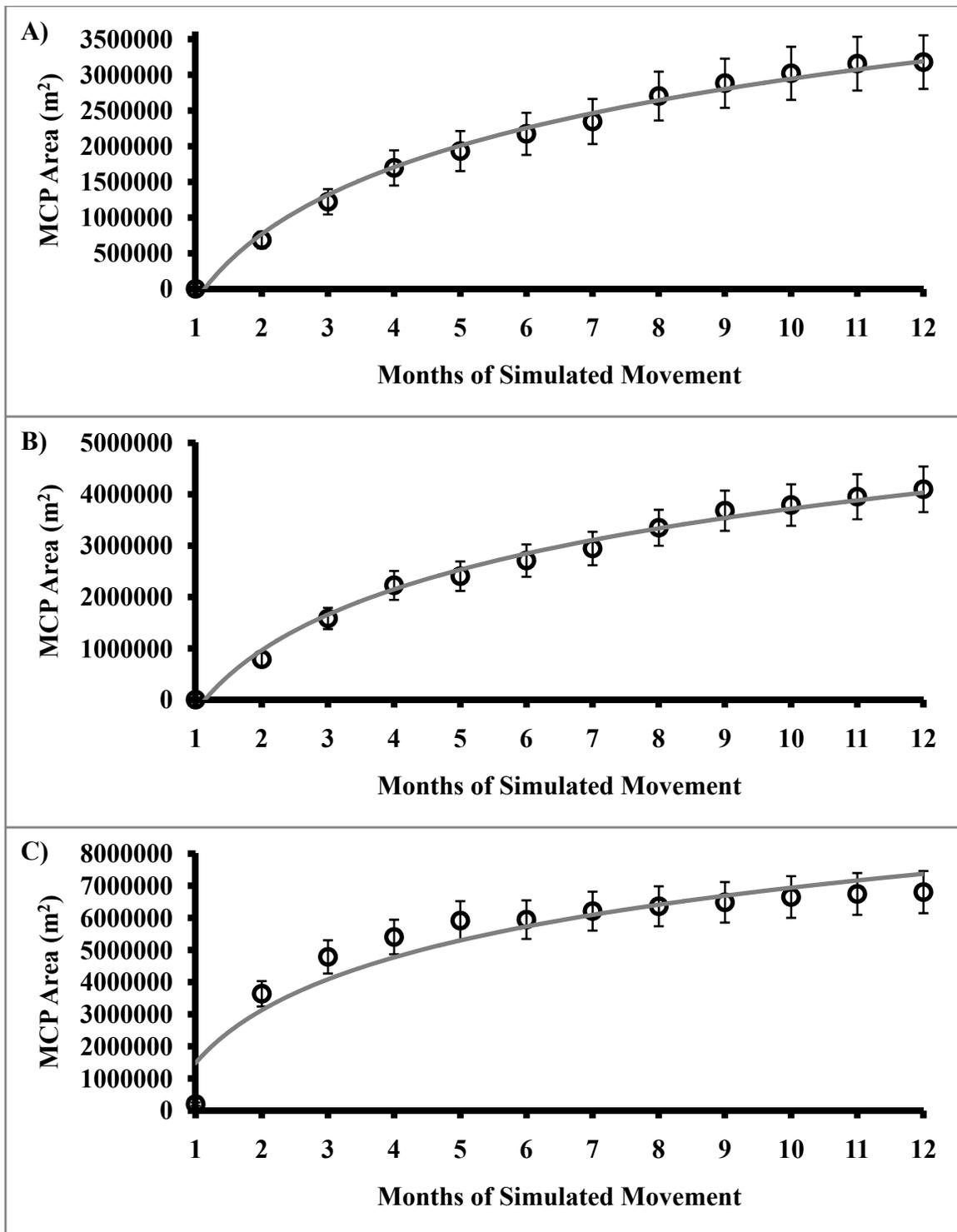


Figure 4.5. Estimated minimum convex polygon (MCP) home range area within a simulated acoustic array for 31 simulated A) black grouper, B) red grouper, and C) mutton snapper plotted against months of simulation, illustrating asymptotic increase in estimated home range size through time.

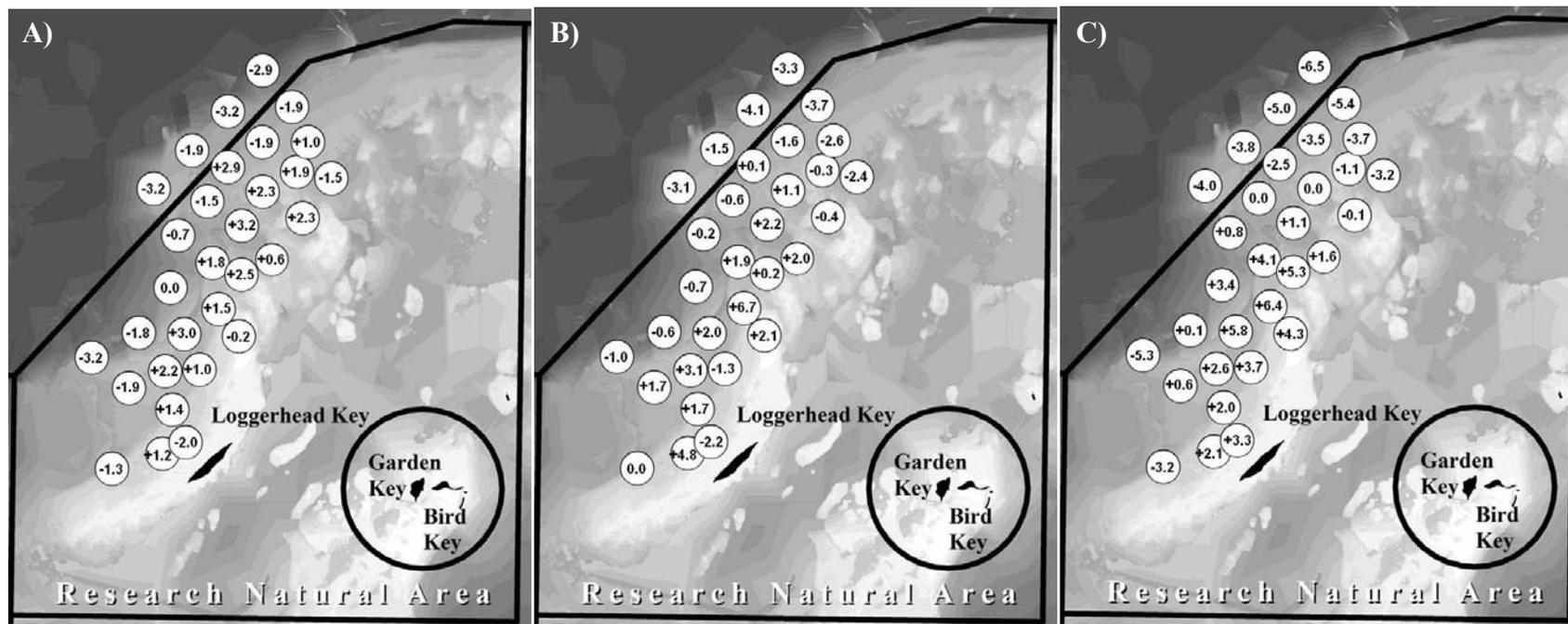


Figure 4.6. Spatially-explicit systematic bias in estimated home range size attributable to location of individual home range centers relative to configuration of acoustic array for simulated A) black grouper, B) red grouper, and C) mutton snapper. White circles indicate 31 simulated acoustic receiver locations; numbers within circles indicate deviation from mean estimated minimum convex polygon home range area (km²) for fish with home range center at location of circle.

Chapter 5

Impacts of reef fish movements and life histories upon marine reserve performance

Summary

An individually-based, spatially-explicit reef fish population dynamic simulation model was developed to evaluate the impacts of no-take marine reserves (NTMRs) in the Dry Tortugas, Florida upon three overfished stocks in the lucrative snapper-grouper fishery: red grouper (*Epinephelus morio*), black grouper (*Mycteroperca bonaci*), and mutton snapper (*Lutjanus analis*). These species have different life histories, movement patterns and speeds, and respond differently to spatial protection. Simulated movements were parameterized from empirical data. NTMR impacts were evaluated using metrics of long-term stock sustainability, as measured by annual changes in spawning potential ratio (SPR), and long-term stock productivity, as measured by annual changes in fisheries yield-in-weight per recruit (Y_w/R). Under assumptions of constant regional fishing pressure and constant recruitment, simulations from initial conditions in 2000 suggested that by 2014, the Tortugas NTMR network should function to restore red grouper populations to 30% SPR, a Federal management benchmark for sustainability. Due to their high mobility, mutton snapper are not predicted to attain this target by 2021 without additional protections. Black grouper are currently fished at over 9 times sustainable levels. Coupling an increase in minimum size at capture of 20 – 25 cm with NTMR implementation is predicted to result in substantial short term losses in yield, but would restore both black grouper and mutton snapper populations to 30% SPR by 2021 and lead to increased long-term yields.

Background

Continued overexploitation has led to significant declines, and in some cases total collapses, of many marine resources (Pauly et al. 1998; NRC 1999; Ault et al. 1998, 2005a). Overexploitation has been attributed to flaws in traditional management models, political breakdowns in the management process, and lack of community support (McManus et al. 1988, Ludwig et al. 1993, Sharp 1995, Ault et al. 1998). Fish stock spatial dynamics—including preferential habitat utilization, movements and migratory behaviors—play a critical role in determining how fishing pressure will impact the stock, and result in fish stocks being heterogeneously distributed throughout the oceans (Rothschild 1986, Longhurst & Pauly 1987, MacCall 1990, Mann & Lazier 1991, Bakun 1996, Humston et al. 2000). The majority of traditional fisheries models neglect the complex spatial dynamics of fish stocks and the anthropogenic stressors impacting them (Pollnac et al. 2000, Meester et al. 2001).

Spatial closures, such as no-take marine reserves (NTMRs), have been endorsed as fisheries management tools that, when used in conjunction with traditional management, may help ensure sustainability of intensely exploited regional fisheries resources (Bohnsack et al. 2004). Theory suggests that buildup of fish biomass, density, and average size in an NTMR due to reduced exploitation (e.g., Ault et al. 2006, 2007a; Bartholomew et al. 2008) will result in density-dependent emigration of adult fish across reserve boundaries (Crowder et al. 2000). Additionally, larval production should be amplified by the larger, older population within the reserve due to its increased spawning stock biomass (Botsford et al. 2001, Lubchenco et al. 2003). The advection of these eggs

and larvae by ocean currents may enhance recruitment in fishable areas (Crowder et al. 2000).

The diverse reef fish community of the Florida Keys and Dry Tortugas coral reef ecosystems supports a multibillion dollar industry for tourism and fishing (Ault et al. 2005a). A retrospective multispecies assessment of coral reef fish stocks has shown that the snapper-grouper complex has been serially overfished since the late 1970s, with many of these stocks below federal standards for sustainability (Ault et al. 1998, 2005b). In 2007, a 158 km² no-take 'Research Natural Area' (RNA) was implemented in Dry Tortugas National Park (DTNP) as a shallow-water complement to the 391 km² no-take Tortugas Ecological Reserve (ERs) network, established in 2001 by the Florida Keys National Marine Sanctuary (FKNMS).

There is a broad scientific and management interest in understanding how the NTMRs of the Tortugas region will perform as tools for rebuilding the lucrative snapper-grouper fisheries. Previously, I have described the development of a mechanistic model of fish movements (Chapter 4) driven by empirical data (Chapter 3) collected within a calibrated array of hydroacoustic receivers in Dry Tortugas National Park, Florida (Chapter 2). In this chapter, I extend this model of reef fish movement into an individual-based, object-oriented Spatial Management Performance Assessment (SMPA) simulation model parameterized for black grouper (*Mycteroperca bonaci*), red grouper (*Epinephelus morio*), and mutton snapper (*Lutjanus analis*) populations in the Dry Tortugas, Florida. SMPA is a discrete time-step (Δt) model that extends traditional population dynamics methods into a spatial context to allow simulation of spatially-explicit processes such as the protection of fish stocks using NTMRs.

SMPA was used to evaluate the interactions and impacts of a variety of life histories, movement patterns and speeds, and management regulations upon NTMR performance using metrics of long-term stock sustainability, as measured by annual changes in spawning potential ratio (*SPR*), and long-term stock productivity, as measured by annual changes in fisheries yield-in-weight per recruit (Y_w/R). Specifically, SMPA was used to quantitatively evaluate what changes in sustainable yields should be expected from reserve establishment, how movement strategy and speed impact these yields, and how these impacts vary by species. As such, this model provides a quantitative assessment of the implications of realistic fish movements on NTMR performance as fisheries management tools.

Methods

Model Overview

The SMPA model was written in Java 6.10 (Sun Microsystems, Inc., Santa Clara, CA) using the Repast Agent Modeling Toolkit (North et al. 2006; Fig. 5.1). The model uses three primary Java classes; one representing an individual fish; one representing the Tortugas region of 193 x 147 distinct grid cells, each corresponding to a 200 m x 200 m Reef Visual Census primary sampling unit (Ault et al. 2007a); and one controlling the trajectory of the modeled population through time (Fig. 5.2). Each primary sampling unit in the region is assigned a habitat type (see Franklin et al. 2003) as determined by RVC surveys and aerial photography; a depth as determined by RVC surveys, Light Detecting and Ranging surveys (LIDAR), and multibeam sonar bathymetry data; and a protection status (fishable or unfishable).

Model Implementation

The model was initialized using equilibrium age-class vectors for each species of interest, with individual fish distributed in two-dimensional space (x, y) following the best available data from the fisheries-independent Reef Visual Census (RVC). The RVC is a diver-based visual survey of reef fish abundance conducted biannually in the Tortugas region since 1999 (Ault et al. 2006, 2007a). The model was initialized using RVC data from 1999 – 2000; prior to no-take marine reserve establishment (Table 5.2). Equilibrium age-class vectors were proportionally allocated to specific reef habitats (see Chapter 3, Franklin et al. 2003) within two major geographic zones ('Tortugas Bank' and 'Dry Tortugas National Park'). As such, the initial allocation of individual fish in each cell was a factor of both the zone containing the cell, and the dominant habitat type within the cell. Cells for which habitat type was unknown were assumed to contain 'Isolated Low-Relief' reef habitat, which contained the lowest relative abundance of individuals.

Simulations were run on one-day time steps for 21 years. Population dynamic processes (e.g. birth, death, growth, reproduction) and fishery yields (e.g. weight at time fish was landed) were tracked on an individual level and aggregated across individuals on an annual basis to create model outputs. Population abundance was tracked following a partial-differential equation based on conservation of mass expressed in terms of population i cohort abundance as a function of age a , time t , and two dimensional space (x and y), $N_{i(a, t, x, y)}$, following (Ault & Olson 1996; Ault et al. 1999, 2003a; Wang et al. 2003; Humston et al. 2004; Moorcroft & Lewis 2006):

$$\frac{dN_i}{dt} = \underbrace{\left(\frac{\partial N_i}{\partial a} \right)}_{\text{reaction kinetics}} + \underbrace{\left(D \nabla^2 u_{\mathbf{x},t}^i \right)}_{\text{random motion}} N_i - \underbrace{\left(\nabla \cdot \left[c u_{\mathbf{x},t}^i \vec{\mathbf{x}}_i \right] \right)}_{\text{directed motion towards center of home range}} N_i \quad (\text{Eqn. 5.1})$$

where $u(\mathbf{x},t)$ is the two-dimensional probability density function for the location of an individual at time t where \mathbf{x} is a vector indicating the (x, y) position of the individual, D is a diffusion term, c is an advection term, and ∇ denotes the spatial derivative operator in two dimensions. Thus, following Ault et al. (2003a), dN_i/dt is a material derivative expressing the local rate of change and advection of N_i as a function of:

- 1) reaction kinetics, i.e. births minus deaths in time, where birth rates (recruitments) are modulated by adult population size in the preceding generation, and death rates ($Z = F + M$) are a function of both natural (M) and fishing (F) mortality, where F varies in space due to management regulations
- 2) random diffusion
- 3) behavioral migrations and movements modulated by an affinity towards a home range center (see Chapter 4).

Each individual ‘Fish’ stores specific information about its morphometrics, reproductive output, and spatial location. Simulation outputs were filtered by spatial position to examine impacts of spatial protection and movement. Age was the primary driver for recruitment and fishing mortality; female fish reaching age of maturity (t_m) began producing eggs, and all fish reaching age of first capture (t_c) became susceptible to the fishing mortality ($F_{(x,y)}$) at their spatial location. Age-specific growth and survivorship were based upon the best population dynamic parameters available from the literature (Table 5.1), and were represented individually. For a list of symbols and abbreviations see Appendix A.1.

Growth in Length

Although growth is a stochastic process, to simplify comparisons between models by reducing variability, we modeled growth in length as deterministic following the von Bertalanffy growth equation,

$$L_{(a,t,x,y)} = L_{\infty} \left(1 - e^{-k(a_{t,x,y} - a_0)} \right) \quad (\text{Eqn. 5.2})$$

where $L_{(a,t,x,y)}$ is total length in the current time step, L_{∞} is the asymptotic length, k is the Brody growth coefficient, a_t is the current age, and a_0 is a constant scalar interpreted as the age at length zero.

Growth in Weight

Growth in weight was calculated from length using the power function

$$W_{(a,t,x,y)} = \alpha_{WL} L_{(a,t,x,y)}^{\beta_{WL}} \quad (\text{Eqn. 5.3})$$

where $W_{(a,t,x,y)}$ is weight (grams), $L_{(a,t,x,y)}$ is length (cm), and α_{WL} and β_{WL} are parameters from the literature (Ault et al. 2005b, 2007b). Weight estimates were used to generate estimates of spawning stock biomass (*SSB*) and yield-in-weight (Y_w).

Mortality

Although changes in water temperature, food availability, and protection status may lead to variability in natural mortality (MacPherson et al. 2000), for this initial modeling effort, natural mortality (M) was assumed constant both spatially and temporally. Estimates of M for each species were generated following Ault et al. (1998):

$$\hat{M} = \frac{-\ln[S(a_{\lambda})]}{a_{\lambda}} \quad (\text{Eqn. 5.4})$$

where, for an unexploited equilibrium, the probability of survivorship of recruits to the maximum age (a_i) is 5 percent (i.e., $S(a_i) = 0.05$), following Alagaraja (1984), with maximum age estimates from Ault et al. (2007b).

A spatially-averaged, region-wide estimate of fishing mortality rate (\bar{F}_t) for the Tortugas was calculated based on fisheries-independent estimates of ‘average size in the exploitable phase of the stock’ (Ault et al. 2006b, Ault et al. 2008). This regional fishing mortality rate was treated as the sum of the mean fishing mortalities generated by the commercial (\bar{F}_{com}) and recreational (\bar{F}_{rec}) fisheries:

$$\bar{F}_t = \bar{F}_{rec} + \bar{F}_{com} = \frac{(F_{com} * n_{com} + F_{rec} * n_{rec})}{(n_T)} \quad (\text{Eqn. 5.5})$$

where F_{com} and F_{rec} are fishing mortality from the commercial and recreational fisheries in cells open to fishing, respectively; n_{com} and n_{rec} are the number of cells open to commercial and recreational fishing, respectively, and n_T is the total number of cells in the model domain (Ω). This separation of fishing mortality into two fisheries was crucial to evaluate the Dry Tortugas fisheries, as Dry Tortugas National Park prohibits commercial fishing within its waters.

As fishing effort within any individual cell was the sum of the spatially-explicit value of F_{com} and F_{rec} for that cell:

$$F_{t,x,y} = F_{com,x,y} + F_{rec,x,y} \quad (\text{Eqn. 5.6})$$

Spatially-explicit modeling allowed for the establishment of reserves at various time steps during the simulation (e.g. $F_{t,x,y} = 0.0$) and the redistribution of fishing effort amongst the fishable subunits by proportionally increasing the level of F_{com} and F_{rec} in fishable cells.

During each one-day time step, the probability (p) of a fish dying was expressed as:

$$p(\text{death}_Z) = 1 - e^{-\left(\frac{M}{365} + \frac{F_{t,x,y}}{365}\right)} \quad (\text{Eqn. 5.7})$$

where $F = 0$ for unexploitable fish (e.g. below exploitable age or located within a no-take marine reserve). Deaths of exploitable fish were proportionally allocated towards total catch following:

$$p(\text{death}_F) = \frac{F_{t,x,y}}{Z} \quad (\text{Eqn. 5.8})$$

During each time step, SMPA records the yield in number ($Y_{n(a,t,x,y)}$) and biomass ($Y_{w(a,t,x,y)}$) of fish removed due to F :

$$Y_{n(a,t,x,y)} = F_{(a,t,x,y)} N_{(a,t,x,y)} \quad \text{and} \quad Y_{w(a,t,x,y)} = F_{(a,t,x,y)} B_{(a,t,x,y)} \quad (\text{Eqn. 5.9, 5.10})$$

Removal of fish due to fishing was assumed to occur at size of first capture (L_c) following a ‘knife-edged selectivity pattern’ (see Gulland 1983) for all fish at or above exploitable size at time t (e.g., $L_t \geq L_c$).

Maturity

Although stochasticity has been noted in the maturation process (Fitzhugh et al. 2006), for the purposes of these simulations, maturation was assumed to occur at size of first maturity (L_m) following a ‘knife-edged pattern’ for all fish at or above size at maturity at time t (e.g., $L_t \geq L_m$).

Gender

Because grouper are protogynous sequential hermaphrodites (Bannerot 1984), all red grouper began as females and transitioned to male following a probability function (θ_L) based on length (Brulé et al. 1999, Fitzhugh et al. 2006). Black grouper sexual transition followed length-at-transition checkpoints from Brulé et al. (2003). Mutton snapper gender was randomly assigned with a 1:1 sex ratio.

Fecundity

Spatially-explicit egg production was tracked for sexually-mature, egg-producing females. Females were allowed to produce eggs once during each spawning season, with timing of spawning season based upon the best available parameters from the literature. Fecundity was described by a power function suggested by Ault (1985) describing the volumetric relationship between fecundity and size (in weight):

$$E_{(a,t,x,y)} = \alpha_E (W_{(a,t,x,y)})^{\beta_E} \quad (\text{Eqn. 5.11})$$

where $E_{(a,t,x,y)}$ is the production of a viable ova for a female fish aged a at time t , $W_{(a,t,x,y)}$ is the weight of the fish in grams, and α_E and β_E are constant coefficients where $\beta_E > 1$. Spatially-explicit egg production was recorded in order to compare production between reserves and fishable areas.

Recruitment

Recruitment was assumed to be constant across the observed range of stock sizes (e.g. constant stock-recruitment relationship). Number of recruits (R_t) instantiated monthly into each cell was equal to initial abundance in the age 0 month class for that cell,

calculated from the equilibrium vector of the initial population for that cell's RVC proportionalized zone-habitat abundance. As such, number of recruits entering each cell (x,y) on a monthly basis remained constant throughout the simulation; consequently, the annual recruitment across the model domain (Ω) was also constant. The balance of long distance recruitment versus local retention depends upon poorly understood factors such as vertical migration, stratified current flows, and MPA location (Cowen et al. 2000). Assuming spatially- and temporally-constant recruitment eliminated recruitment variability from model analyses, facilitating quantification of the impacts of movement and life history upon reserve performance.

Movement

This model allowed for comparison of the impacts of no movement, random walk, and realistic movement scenarios upon marine reserve performance. As an individually-based model, SMPA allows for a comprehensive investigation of the stochastic impacts of movements of exploited fish within a management regime of spatially-heterogeneous fishing effort. The model also examined percent time spent inside vs. outside reserve boundaries and rates of movement across reserve boundaries for each population under a variety of management and movement scenarios.

For the random walk model, reef fish moved at every time step in random directions. Distance of movement was based upon a species-specific exponential distribution fit to empirical observations of movement. For the realistic movement scenario, reef fish movements within a home range were simulated as described in Chapter 4.

As movements on a 5-min time step would have required prohibitively high computational time, movements were aggregated on a daily time step. A species specific probability of movement was computed for each individual in the model domain, expressed as the number of 5-min intervals within the one-day time step that contained a detectable movement. This probability was modeled using 288 draws (e.g. number of 5-min intervals in one day) from a uniform random probability distribution ranging from 0 to 1, where a draw resulting in a number less than the species-specific probability of movement in a 5-min interval (see Chapter 4) represented a non-zero movement. If a particular one-day interval for the individual under examination contained non-zero movements, a distance of movement for a 5-min interval was selected from an exponential distribution fit to empirical tracking data (see Chapter 4) and then multiplied by the number of non-zero movements to scale for the one-day time step. A turning angle for this movement relative to the individual's home range center was randomly selected from a von Mises distribution fit to empirical tracking data (see Chapter 4). This process was repeated for all individuals of lengths greater than 40 cm (see Chapter 3) in the model domain for each time step. As movement distances and angles were randomly selected from distributions fit to acoustic telemetry data, movements represented a stochastic component in the SMPA simulations. This movement model was easily generalized to a variety of movement scales and affinities towards home range centers through scalar manipulation of distribution parameters.

Model Outputs

SMPA generated multiple management outputs calculated by summation across all individuals (i) and locations (x, y) within the model domain (Ω) on an annual basis. Outputs included the total number of individuals (N_t), number of individuals in the exploited phase ($N_{t_{exploited}}$), total egg production (E_t), egg production from reserves ($E_{t_{reserves}}$), average length in the exploited phase ($\bar{L}_{t_{exploited}}$; ‘Lbar’), and yield-in-numbers (Y_{N_t}).

To facilitate a parsimonious comparison between various model runs, preliminary analyses were focused upon two scaled management benchmarks: (1) yield-in-weight per recruit (Y_w/R); and, (2) spawning potential ratio (SPR).

Yield-in-weight (Y_{W_t}) was tracked continuously throughout the simulation as described previously (see ‘Mortality’). As recruitment was constant among simulation runs, Y_w/R serves as an index of fisheries production. Computing Y_w/R on an annual basis permitted an investigation of the transitional dynamics impacting the fishery.

Recognizing that US fisheries are currently mandated to ‘prevent overfishing while achieving, on a continuing basis, the optimum yield from each fishery’ (MSFCMA [Magnuson-Stevens Fishery Conservation and Management Act], Restrepo et al. 1998), the reproductive capacity of the stock was examined as an index of sustainability. As such, SMPA also output an important measure of stock reproductive potential, spawning stock biomass per recruit ($SSBR_t$), on an annual basis, by integrating across the spatial domain (Ω) the biomass of all individuals in the population between age of sexual maturity (a_m ; 50% maturity, assumed knife-edged) and the maximum age (a_λ):

$$SSBR(t) = \sum^{\Omega} \left[\frac{\int_{a_m}^{a_{\lambda}} B(a,t,x,y) da}{R_t} \right] \quad (\text{Eqn. 5.12})$$

This index of stock production was scaled to maximum spawning biomass, obtained under conditions of no fishing mortality. The resultant spawning potential ratio (SPR) is a management benchmark measuring a stock's potential to generate sustainable yields under present exploitation rates (Goodyear 1993):

$$SPR = \left(\frac{SSBR_{F_t}}{SSBR_{F=0}} \right) \quad (\text{Eqn. 5.13})$$

Estimated SPRs were compared to USA Federal standards, which define 30% SPR as the threshold for stock sustainability at current exploitation levels (see Gabriel et al. 1989, Restrepo et al. 1998). Additional outputs such as length-frequency and age-frequency distributions, population densities by zone-habitat categories, and measurements of flux across reserve boundaries were also examined.

Spatial Management Performance Assessment

To evaluate the contributions of the no-take marine protected areas of the Dry Tortugas region to fisheries sustainability, SMPA outputs were evaluated under numerous variable permutations intended to capture the impacts of various movement patterns, life history strategies, and management regimes (Fig. 5.3). Each model run began on Jan 1, 2000. For permutations where reserves were implemented in the simulation environment, ERs were implemented on Jan 1, 2001, and the RNA was implemented on Jan 1, 2007. Of the 22620 total grid cells in the model, implementation of the ERs closed 5603 (24.8% of the fishery), and implementation of the RNA closed an additional 3088 (13.7%), for a total closure of 8691 cells (38.4%).

Model Validation

SMPA was configured such that its spatial functionality could be disabled. Under the assumption of homogeneous space and uniform fishing effort throughout the region, we compared outputs of SMPA to the non-spatially-explicit REEFS model (Ault et al. 1998, 2006b) using the input parameters of Table 5.1. We also compared SMPA to REEFS given increases in L_c described by Ault et al. (2007b) to verify that 30% SPR was achieved. Finally, we investigated SPR achieved after a_λ years of full closure for each species.

Sustainability limit control rules were evaluated through comparison of current levels of fishing mortality and spawning stock biomass (e.g. biomass of mature individuals in the stock) to F_{msy} (F generating maximum sustainable yield, MSY) and B_{msy} (spawning stock biomass at MSY).

Spatial Protection

To determine impacts of spatial protection, we ran SMPA for black grouper, red grouper, and mutton snapper stocks over 22 years given the following assumptions: (1) $\bar{F}_{rec} = \bar{F}_{com}$; (2) \bar{F} constant; (3) no changes in L_c ; and, (4) realistic movement. We projected each stock given three levels of spatial protection: (1) no reserves, (2) ERs only, and (3) ERs and RNA together.

Movement Strategy

To examine impacts of movement strategy, we ran SMPA for black grouper, red grouper, and mutton snapper stocks over 22 years given the following assumptions: (1)

$\bar{F}_{rec} = \bar{F}_{com}$; (2) \bar{F} constant; and, (3) no changes in L_c . We projected each stock given three movement strategies: (1) no movement, (2) random movement, and (3) realistic movement. We further examined mutton snapper stocks under the ‘realistic’ movement scenario given three levels of mobility: (1) low mobility relative to observed movements ($\lambda = 0.5 * \lambda_{obs}$; $\kappa = 2 * \kappa_{obs}$), (2) realistic mobility (the default case: $\lambda = \lambda_{obs}$; $\kappa = \kappa_{obs}$), and, (3) high mobility relative to observed movements ($\lambda = 2 * \lambda_{obs}$; $\kappa = 0.5 * \kappa_{obs}$). Finally, we used paired t-tests for means to compare the rate of movement across reserve boundaries under the ‘realistic’ movement scenario given realistic mobility for all species.

Increased Size Limits

To determine the impacts of a change in L_c relative to spatial protection, we ran SMPA for red grouper stocks over 22 years given the following assumptions: (1) $\bar{F}_{rec} = \bar{F}_{com}$; (2) \bar{F} constant; (3) realistic movement. For these analyses, we projected the stock given a 15.0 cm increase (see Ault et al. 2007b) in L_c under three different levels of spatial protection: (1) no reserves, (2) ERs only, and (3) ERs and RNA together. We also ran SMPA for black grouper and mutton snapper stocks given 20.0 cm and 25.0 cm increases in L_c and ERs and RNA implemented.

Recreational Fishing Mortality

To investigate the impacts of increasing recreational fishing mortality (\bar{F}_{rec}), we ran SMPA for red grouper stocks over 22 years given the following assumptions: (1) $\bar{F}_{rec} = \bar{F}_{com}$; (2) no changes in L_c ; (3) realistic movement, (4) both ERs and RNA implemented. We compared the impacts of F_{rec} under two different assumptions: (1) \bar{F}_{rec}

remains constant and equivalent to \bar{F}_{com} over time ('Constant Fleet'), and (2) \bar{F}_{rec} begins equivalent to \bar{F}_{com} but grows linearly such that \bar{F}_{rec} doubles every 13 years, reflecting observed trends in growth of recreational fleet ('Growing Fleet'; see Ault et al. 2007b, Table 5.3).

For the constant fleet, F_{rec} and F_{com} in cells open to fishing are computed as follows:

$$F_{com} = \left(\frac{(n_F * \bar{F})}{(1+s)} * \frac{1}{(n_{rec} * s + n_{com} - n_F * s)} \right) * \frac{n_T}{n_F} \quad (\text{Eqn. 5.14})$$

$$\text{and } F_{rec} = \left(s * \frac{F}{(1+s)} \right) * \frac{n_T}{n_F} \quad (\text{Eqn. 5.15})$$

where n_F is the number of cells open to any fishing and is equivalent to n_{rec} (a valid assumption for the Tortugas region); \bar{F} is the overall mean fishing effort for the region; and s is the scalar multiple for recreational to commercial fishing effort. For the growing fleet, the computation for F_{com} remains the same, as does the computation for F_{rec} in the first year of simulation (t_0), but F_{rec} in subsequent years is computed from F_{rec} in the previous year as follows:

$$F_{rec}(t) = \left(F_{rec}(t-1) * \left(s + \left(s * \frac{(t-t_0)}{13} \right) \right) \right) * \frac{n_T}{n_F} \quad (\text{Eqn. 5.16})$$

As the contribution of the recreational fleet to the overall estimated fishing mortality (\bar{F}) in the Tortugas region (Ault et al. 2008) is unknown, we examined the impacts of \bar{F}_{rec} when scaled (Table 5.4) at reduced (e.g. $s = 0.5$), equivalent (e.g. $s = 1$), and increased (e.g. $s = 2$) levels relative to commercial fishing mortality (\bar{F}_{com}), where

$$\bar{F}_{rec} = s * \bar{F}_{com} \quad (\text{Eqn. 5.17})$$

To examine transitional dynamics of the fishery as the stocks move to new equilibriums following implementation of the ERs in 2001 and the RNA in 2007, we examined transitional yields for red grouper stocks projected under the ‘Constant Fleet’ and ‘Growing Fleet’ assumptions outlined above.

Length Composition

To explore the impacts of spatial protection upon the length frequency composition of the red grouper stock, we projected the population under no, partial (e.g. ERs and RNA), and total closure scenarios, given the following assumptions: (1) $\bar{F}_{\text{rec}} = \bar{F}_{\text{com}}$; (2) \bar{F} constant; (3) no changes in L_c ; and, (4) realistic movement. Number of fish at length (1 cm intervals) within the spatial domain (Ω) was recorded at the end of each year, and comparisons were made between length-frequency compositions of stocks after 22 years of simulation.

Egg Production

To determine impacts of spatial protection upon egg production, we ran SMPA for black grouper, red grouper, and mutton snapper stocks over 22 years given the following assumptions: (1) $\bar{F}_{\text{rec}} = \bar{F}_{\text{com}}$; (2) \bar{F} constant; (3) no changes in L_c ; and, (4) realistic movement. We projected each stock given three levels of spatial protection: (1) no reserves, (2) ERs only, and (3) ERs and RNA together. Egg production within and outside of reserves was tracked continuously throughout each year and reported annually.

Results

Model Validation

Under the assumption of homogeneous space and uniform fishing effort throughout the region, SMPA replicates the output of the non-spatially-explicit REEFS model (Ault et al. 1998, 2006b; Table 5.5). Additionally, increases in L_c predicted by REEFS to result in 30% SPR produced identical results in SMPA, and a complete closure of the fishery resulted in 100% SPR after L_λ years for all species.

Limit control rule plots (see Ault et al. 2008) of non-spatial model outputs using $F = M$ as a proxy for F_{msy} (Quinn & Deriso 1999, Restrepo & Powers 1999) revealed that each species under examination is currently overfished, and overfishing continues (Fig. 5.4), with black grouper stocks currently fished at over 9 times sustainable levels.

Spatial Protection

Figure 5.5 illustrates changes in Y_w/R and SPR for simulated stocks of black grouper (Fig. 5.5A, D), red grouper (Fig. 5.5B, E) and mutton snapper (Fig. 5.5C, F) at three levels of spatial protection: (1) no reserves, (2) ERs only, and (3) ERs and RNA together. In general, implementation of the ERs alone provided only slight gains in SPR (4.2 times higher for black grouper, 1.5 times higher for red grouper, and 1.6 times higher for mutton snapper), whereas implementation of the RNA provided massive gains in long-term stock sustainability (8.3 times higher for black grouper, 2.2 times higher for red grouper, 1.6 times higher for mutton snapper). Conversely, near-term yields predicted for 2010 were much higher under the ‘no closure’ and ‘ERs only’ permutations as compared to the ‘ERs and RNA’ scenario (39% lower for black grouper, 36% lower

for red grouper, 22% lower for mutton snapper). Interestingly, long-term yields for mutton snapper were 7% higher with both the ERs and the RNA implemented. For black grouper, long-term yields were substantially reduced (30% lower) by implementation of the ERs and RNA. Current spatial closures appear substantial enough to restore red grouper stocks to 30% SPR by 2011, but are inadequate to bring black grouper and mutton snapper stocks to 30% SPR by 2021.

Movement Strategy

Figure 5.6 illustrates changes in Y_w/R and SPR for simulated stocks of black grouper (Fig. 5.6A, D), red grouper (Fig. 5.6B, E), and mutton snapper (Fig. 5.6C, F) under three different movement strategies: (1) no movement (dotted line); (2) random movement (dashed line); and (3) realistic movement (solid line). Expected long-term yields are much lower (44% for black grouper, 32% for red grouper, 105% for mutton snapper) and SPR is much higher (1.5 times for black grouper, 1.25 times for red grouper, 2.9 times for mutton snapper) under the no movement scenario as compared to realistic movement, suggesting movement rapidly erodes the protective benefits of reserves, but may serve to mitigate transitional losses in yield. Given no movement, black grouper stocks attain the target 30% SPR by 2015, but black grouper stocks moving realistically do not attain this target by 2021, despite impressive gains in SPR. Given no movement, red grouper stocks reach 30% SPR by 2009, and red grouper stocks moving realistically attain this target by 2011. Given no movement, mutton snapper stocks attain the target 30% SPR by 2014, but mutton snapper stocks moving realistically do not attain this target by 2021. Randomly moving stocks for all species are not projected to achieve

this goal under current spatial closures. Home range utilization clearly promotes fisheries production and stock sustainability, as mutton snapper moving realistically are highly mobile, yet attain nearly double the SPR and higher long-term yields as compared to randomly moving mutton snapper stocks.

Figure 5.7 illustrates changes in Y_w/R (Fig. 5.7A), SPR (Fig. 5.7B), and $Lbar$ (Fig. 5.7C) for simulated mutton snapper stocks under assumptions of reduced, realistic, and high mobility. The realistic mobility scenario leads to the highest long-term yields. High mobility rapidly erodes benefits of spatial protection, leading to smaller mean sizes in the population and a reduced spawning potential ratio.

All species moved more frequently out of reserves than into reserves (Table 5.6). Over the course of a 21 year simulation, approximately 2% of the movements made by individuals in simulated black grouper and red grouper populations, and 8% of the movements made by individuals in a simulated mutton snapper population were across reserve boundaries.

Increased Size Limits

Figure 5.8 illustrates changes in Y_w/R (Fig. 5.8A), SPR (Fig. 5.8B), and $Lbar$ (Fig. 5.8C) over time for simulated red grouper stocks given a 15.0 cm increase in L_c starting in 2000 (black lines). Outputs versus time are presented for three different levels of protection: no reserves (black dotted), ERs only (black dashed), and ERs and RNA (black solid). Compared to current management (e.g. ERs and RNA, $L_c = L_{c_{current}}$; gray line), increasing L_c results in massive short-term declines in Y_w/R followed by higher long-term Y_w/R and $Lbar$. A 15 cm increase in L_c coupled with implementation of the

ERs only is predicted to result in higher long term yields and SPR than implementation of the ERs and RNA without a change in L_c . For black grouper and mutton snapper, preliminary analyses suggested an increase in L_c between 20 – 25 cm, along with protection by ERs and RNA, would be required to restore stocks to 30% SPR by 2021 and would also lead to higher long-term yields as compared to projections under current management.

Recreational Fishing Mortality

Figure 5.9 illustrates changes in Y_w/R and SPR over time for simulated red grouper stocks assuming constant (solid line) and growing (dashed line) \bar{F}_{rec} . With a constant fleet, 30% SPR is achieved by 2010; whereas a growing fleet delays achievement of this goal until 2012.

For all species under all scenarios, reduced \bar{F}_{rec} relative to \bar{F}_{com} (e.g. $s = 0.5$) led to reduced overall yields and more rapid buildup of spawning stock biomass. Increased \bar{F}_{rec} relative to \bar{F}_{com} (e.g. $s = 2$) had the opposite effect – higher overall yields and delayed buildup of spawning stock biomass.

Implementation of the ERs in 2001 and RNA in 2007 has significant impacts upon the transitional dynamics of the fishery as the stocks move to a new equilibrium. Figure 5.10 illustrates predicted Y_n/R and Y_w/R relative to time for the ‘Constant Fleet’ and ‘Growing Fleet’ assumptions for red grouper. Assuming constant F_{rec} , Y_n/R_{2000} is exceeded 5 years after implementation of the ERs in 2001, but is not achieved again by 2021 following implementation of the RNA in 2007. Similarly, Y_w/R_{2000} is exceeded 5 years after implementation of the ERs and again 12 years after implementation of the

RNA. By contrast, if F_{rec} continues to grow following present trends, Y_n/R_{2000} is exceeded 5 years after ER implementation and again just 1 year after RNA implementation. Similarly, Y_w/R_{2000} is exceeded just 3 years following ER implementation, and although it declines following RNA establishment, it never decreases below 2000 levels. Ultimately, both scenarios result in higher long-term Y_w/R , although Y_w/R by 2021 is 11 times higher for the ‘Growing Fleet’ assumption versus the ‘Constant Fleet’ assumption.

Length Composition

Figure 5.11 illustrates changes in red grouper population length frequency composition under various management scenarios. Increased protection from fishing leads to increased proportional representation of larger size classes.

Egg Production

Between 2001 – 2021, population egg production for cells within reserves versus cells outside was significantly higher for black grouper ($t = 4.90$, $df = 20$, $p < 0.001$), red grouper ($t = 6.56$, $df = 20$, $p < 0.001$), and mutton snapper ($t = 5.38$, $df = 20$, $p < 0.001$). Figure 5.12 illustrates changes in black grouper (Fig. 5.12A), red grouper (Fig. 5.12B), and mutton snapper (Fig. 5.12C) population egg production over time given no reserves (dotted line), ERs only (dashed line), and ERs with RNA (solid line). Not surprisingly, overall reproductive output of the population is massively amplified by increased spatial protection. Overall population egg production is predicted to be approximately 13 times higher for black grouper and 3 times higher for red grouper and mutton snapper by 2019

with protection by ERs and the RNA relative to population egg production assuming no spatial protection over the same time period.

Discussion

Our modeling results suggested that any level of exchange across reserve boundaries rapidly degrades NTMR capacity for protection of SSB, and this rate of degradation increases with movement rate. Our results agreed with other modeling efforts suggesting that large movements of fish reduce the efficacy of marine reserves (Beverton & Holt 1957, Polacheck 1990, Bohnsack 1993, DeMartini 1993, Holland & Brazee 1996, Guénette & Pitcher 1999, Guénette et al. 2000); however, we found these reductions in NTMR efficacy were partially offset by affiliation to a home range center. Home range utilization minimized the actual displacement of mobile organisms, regardless of the frequency of movement.

Overall level of mobility had profound impacts upon sustainability because it regulated the scale of movements into the fishery for organisms with home range centers near reserve boundaries. Tracking studies of the simulated species noted spillover rates were highest when home range centers were near reserve boundaries (see Chapter 3). Previous modeling efforts have noted SSB decreases with increasing distance from the center of the reserve because mobile individuals with home ranges near reserve boundaries are more likely to cross over into the fishery (Rakitin & Kramer 1996, Walters 2000).

Our modeling results suggested that the realistic movements of snappers and groupers would significantly degrade the benefits of the Tortugas NTMR network for

protecting SSB, but also help mitigate transitional losses in yield. As such, movements might represent an optimized tradeoff for long-term productivity of the fishery, as enough fish are retained in the reserves to promote increased SSB, and enough fish spillover from reserves to maintain reasonably high yields. Ultimately, long-term yields were higher for the realistic mobility scenarios than for either the high or low mobility scenarios.

Numerous researchers have commented that community support is critical to the success of marine protected areas as management tools (White et al. 1994, Russ & Alcala 1996, Zeller & Russ 1998). NTMR establishment in the Florida Keys has faced strong opposition from members of the local fishing community, primarily due to a lack of evidence that the reserves would ultimately promote sustainability and enhanced yields (Suman et al. 1999). Our modeling efforts predicted reserve implementation would lead to substantial long-term increases in SPR (e.g. 8.3 times higher for black grouper, 2.2 times higher for red grouper, 1.6 times higher for mutton snapper) with targeted 30% SPR attained by the red grouper stock within 5 years following RNA establishment. Long-term yields were predicted to be higher for the mutton snapper and red grouper fisheries relative to baseline (e.g. year 2000) yields, with transitional losses in yields persisting for less than a decade. By contrast, the black grouper fishery, currently exploited at over 9 times sustainable levels, was predicted to remain below year 2000 yields following implementation of both ERs and RNA.

Our findings regarding the impacts of fish movement upon reserve effectiveness have significant implications upon the size and configuration of NTMRs necessary to achieve the desired gains in stock sustainability. In this modeling effort, nearly 40% of the spatial domain under examination was closed to fishing, yet high levels of mobility

still undercut a substantial proportion of the potential benefits of closure. Our results suggested that the reserves currently implemented, when coupled with current fisheries management regulations, would serve to restore SPR to 30% by 2012 for red grouper, but would be inadequate without additional external restrictions to achieve 30% SPR for black grouper or mutton snapper by 2021. Our results also suggested that even the 20% total area closures within the US EEZ proposed to the South Atlantic Fishery Management Council (Bohnsack 1990) may be inadequate to protect even moderately mobile species without additional management intervention.

Given the natural movement rates of larger reef fish such as groupers and snappers, we concur with Walters (2000) that it is wishful thinking that small NTMRs will act as effective “seed sources” for a population suffering from long-term recruitment overfishing, due to the high rate of loss across boundaries in reserves with a high perimeter-to-area ratio. Large reserves are more likely to contain a definable adult population, permit high densities of adults, and produce the high densities of larvae needed to seed the fished population outside the reserve (Allison et al. 1998, Dahlgren & Sobel 2000; Walters 2000). Smaller reserves may only be effective when designed to utilize natural boundaries to movement (e.g. land masses, deep sand trenches) to restrict movements across boundaries (Chapman & Kramer 2000; Eristhee & Oxenford 2001; Stewart & Jones 2001; Chapter 3, this volume). In a recent analysis of changes in reef fish density in FKNMS, Bartholomew et al. (2008) found the relative rate of density change was negatively correlated to the ratio of reserve boundary intersecting reef habitat/reef habitat area within the reserve. These findings suggest that natural landscape features may serve as deterrents to reef fish movement, amplifying the benefits of

reserves by reducing movements into the fishery (Bartholomew et al. 2008). In this analysis, we did not incorporate any behavioral responses to habitat into our movement model. Such responses might have altered the shape of animal home ranges and rates of flux across boundaries. By identifying critical habitats through a retroactive analysis of reef fish tracking data as higher-resolution habitat mapping of the region becomes available, this component could easily be incorporated into the model.

The biomass-overflow hypothesis (Edgar & Barrett 1999, Crowder et al. 2000) suggests that relaxation of fishing pressure within an NTMR results in a higher density and average size of targeted species, and this buildup leads to competition for resources followed by density-dependent emigration of juveniles and adults across reserve boundaries. We did not incorporate any density dependence in our present analysis; however, we observed increased flux out of the reserve relative to flux into the reserve as biomass within the reserve increased. The higher frequency of movement out of the reserve is probably explained by the majority of the population being contained within reserves at any given moment, as well as the higher probability of mortality outside of the reserve. Addition of density-dependent movement to the model would presumably increase yields to the fishery and delay recovery of SSB.

Our findings with regards to realistic fish movements are predicated upon those movements being realistic and representative across the size ranges examined. Sample sizes and length composition of fish tracked and tagged (see Chapter 3) were limited due to financial, technological, and logistic constraints. By ignoring movements for fish smaller than 40 cm, we reduced the need to extrapolate beyond our empirical observations of fish movement; reduced processing time; and retained the relationship

between fish abundance, habitat, and geographic region parameterized from the fishery-independent Reef Visual Census database.

Our findings suggested that controlling fishing pressure by increasing L_c can result in substantial gains in long-term yields and SPR when coupled with spatial protection in a multi-pronged management approach. Substantial increases in L_c resulted in a much larger average size fish in the population; however, they also resulted in extreme declines in short-term yields that may prove unacceptable for most fishermen, even relative to large-scale spatial closures. Additionally, increasing L_c in the absence of reserves does not provide the numerous subsidiary benefits of a spatial closure.

From a fisheries standpoint, an NTMR is preferable to an increase in L_c because although both shelter a large proportion of the mature stock, NTMRs provide the additional benefits of reducing bycatch mortality from barotrauma, gut-hooking, catch-and-release mortality, and associated risks. From a conservation standpoint, both NTMRs and increases in L_c may help protect spawning biomass, provide a recruitment source for surrounding areas, and restock fished areas through emigration (Bohnsack 1999, Bohnsack et al. 2004). Unlike a change in L_c , NTMRs potentially protect all species and size/age classes, eliminate by-catch, and protect habitat from fishing damage (Bohnsack 2000). They may also help to maintain genetic diversity within stocks that suffer selective fishing mortality (Plan Development Team 1990, Goodyear 1996, Bohnsack 1999, Trexler & Travis 2000).

Although the implementation of the RNA in 2007 resulted in substantial decreases in short-term yields, in the absence of other management intervention, it appeared to be critical for the restoration of the red grouper stock to the Federally-

mandated 30% SPR. For the highly overfished black grouper stocks (currently at 0.8% unexploited SPR), NTMR implementation facilitated massive gains in SPR but without additional management, was unable to bring stocks to 30% SPR by 2021. The high mobility of mutton snapper reduced the utility of the RNA for replenishing the population's SSB; as such, additional management measures such as an increase in L_c or a decrease in bag limits may be necessary to promote long-term sustainability of this overexploited stock. Simulations suggested an increase in L_c of 20 – 25 cm along with currently implemented NTMRs would bring both stocks to 30% SPR by 2021. These changes in L_c , while substantial, are far less than those recommended by Ault et al. (2007b) to rebuild these stocks in the absence of NTMR protection.

Our results suggested that the implementation of NTMRs is a useful tool for counteracting the process of 'juvenescence,' where increasing exploitation progressively eliminates older, more fecund size classes in a stock, resulting in an overall younger stock (Ricker 1963, Ault 1988). As the fecundity of individual fish increases exponentially with size (Berkeley et al. 2004b, Bobko & Berkeley 2004), older individuals produce larvae of higher quality (Berkeley et al. 2004a), and protogynous populations may become sperm-limited as larger individuals are selectively removed (Jennings & Lock 1996, Coleman et al. 1996), the protection of larger size classes may have tremendous implications for stock sustainability in the context of the stock-recruitment relationship.

Larger, more fecund individuals in reserves may 'seed' fishable areas with amplified recruitment (Crowder et al. 2000). For an aggregating, sequential hermaphrodite such as groupers, protection of larger size classes in reserves reduces the risks of sperm-limitation by protecting males, and may also elevate population densities

to a threshold level critical to initiate spawning migrations (Colin 1996, Alonzo & Mangel 2004). In this analysis, although exploited stocks demonstrated massively amplified egg production following reserve implementation (e.g. 13 times higher for black grouper, 3 times higher for red grouper and mutton snapper), a constant stock-recruitment relationship was assumed across observed stock sizes. Increases in recruitment due to enhanced egg production would accelerate the population (and fishery) recoveries we have described and might help black grouper and mutton snapper stocks attain 30% SPR without additional restrictions on fishing mortality or increases in L_c .

For this analysis, we assumed that recruitment was constant in both space and time – each month, the same number of age 0 fish recruited to the same location. High levels of local retention of larvae have been reported around islands (Cowen et al. 2000, Paris & Cowen 2004). Larval retention in the Tortugas might be supported by local currents such as the Tortugas Gyre and the Pourtales Gyre (Lee et al. 1994, Roberts 1997b, Lee & Williams 1999, Dahlgren & Sobel 2000). Given the long planktonic duration (1 – 2 mo) of most snapper and grouper species, the Florida Current might provide a mechanism to deliver amplified larval production from the reserves to habitats between the Dry Tortugas and the middle Florida Keys (Lee et al. 1994, Roberts 1997b, Dahlgren & Sobel 2000).

The importance of quantifying dispersal rates when evaluating the utility of marine protected areas was recognized as early as Beverton and Holt (1957); however, most models of marine protected areas have used simplifying assumptions concerning interchange among management zones, removing the spatial pattern of the population

from explicit consideration (Polacheck 1990, DeMartini 1993, Rakitin & Kramer 1996, Sumaila 1998, Fogarty 1999, Guénette & Pitcher 1999, Xiao 2000, Pitcher et al. 2000, Sladek-Nowlis 2000, Watson et al. 2000, Sanchirico & Wilen 2001). This is the first quantitative assessment of NTMR performance incorporating fish movements parameterized from empirical tracking data. Being individually-based, SMPA is sensitive to the unique spatial configuration of the NTMRs relative to fishable areas and is better able to express the actual movements and population dynamics of the wild population.

This modeling effort indicated reserve implementation will provide long-term benefits for overall grouper and snapper stock sustainability and fisheries productivity. Increased abundance, density, and average size within no-take reserves has been empirically demonstrated for numerous exploited species in the Florida Keys and Dry Tortugas fisheries (Ault et al. 2004, Ault et al. 2007a, Bartholomew et al. 2008). Our modeling results suggest that these benefits will extend to fishable areas through enhanced long-term yields and stock sustainability. Additionally, the species considered in this modeling effort have larger home ranges than most coral reef fish. As such, the benefits described by this paper would be amplified for less mobile stocks in the diverse Tortugas multispecies fisheries. Marine reserves are especially suited to applications in declining multispecies fisheries for three reasons: (1) a number of fisheries focus on stocks of related species with similar habitat requirements (Lindeman et al. 2000, Koenig et al. 2000); (2) reserves are the most effective approach towards preserving ecosystem structure and function (Peterson et al. 2000, Rosenberg et al. 2000); and (3) reserves

ameliorate the considerable problems of by-catch mortality that disrupt the local and regional ecosystem (Collins et al. 2000).

Although marine reserve sites are often chosen opportunistically (Roberts 2000), our findings strongly suggest that reserve designs (e.g. proper sizes and configurations) must take into account the scales and patterns of movement exhibited by the exploited stocks they are intended to protect. Our modeling efforts also suggested reserves are not a panacea (Fogarty 1999); in order to promote sustainability for severely depleted stocks, they must be accompanied by an overall reduction in fishing capacity. Although important questions remain concerning the movements of reef fish in response to habitat and density dependent processes, our analyses of realistic reef fish behaviors suggest that the marine reserves of the Dry Tortugas region provide substantial protection of SSB and may promote enhanced long-term yields.

Table 5.1. Population dynamic parameters for species in model (from Ault et al. 2005b, 2007b).

Species Name		a_λ	K	L_{inf}	a_0	W_{inf}	L_m	t_m	L_c	t_c	L_{max}	M	F	α_{WL}	β_{WL}
Red Grouper	<i>Epinephelus morio</i>	29	0.16	854	-0.19	9.61	433.80	51	500	65	869.01	0.103	0.352	6.0E-09	3.1400
Black Grouper	<i>Mycteroperca bonaci</i>	33	0.169	1306	-0.768	41.43	826.00	62	600	36	1301.0	0.091	0.835	4.3E-06	3.2051
Mutton Snapper	<i>Lutjanus analis</i>	29	0.129	939	-0.738	14.02	275.78	24	400	44	797.75	0.103	0.515	1.6E-05	3.0112

Note: ' a_λ ' denotes maximum age in years, 'K' denotes Brody growth coefficient, ' L_{inf} ' denotes asymptotic length coefficient for von Bertalanffy growth equation, ' a_0 ' denotes theoretical age at length zero scaling parameter for von Bertalanffy growth equation, ' W_{inf} ' denotes theoretical maximum weight in kilograms, ' L_m ' denotes length (in mm) at maturity, ' t_m ' denotes age (in months) at maturity, ' L_c ' denotes length (in mm) at first capture, ' t_c ' denotes age (in months) at first capture, ' L_{max} ' denotes maximum length, 'M' denotes estimated instantaneous natural mortality, 'F' denotes estimated instantaneous fishing mortality, ' α_{WL} ' denotes alpha coefficient for length-weight conversions, and ' β_{WL} ' denotes beta coefficient for length-weight conversions.

Table 5.2. Relative abundance by region-habitat for species of interest, based on 2000 Reef Visual Census (Ault et al. 2007a).

Species	Region	Relative Abundance by Habitat				
		CHR	CLR	CMR	IHR	ILR
Black Grouper	DRTO	0.07	0.11	0.00	0.04	0.00
	Other	0.01	0.30	0.07	0.22	0.16
Red Grouper	DRTO	0.04	0.38	0.00	0.04	0.01
	Other	0.00	0.29	0.03	0.06	0.14
Mutton Snapper	DRTO	0.03	0.29	0.00	0.09	0.01
	Other	0.00	0.37	0.03	0.10	0.07

Note: ‘DRTO’ denotes Dry Tortugas National Park; ‘Other’ denotes Tortugas Bank, Riley’s Hump and other regions; ‘CHR’ denotes continuous high-relief; ‘CLR’ denotes continuous low-relief; ‘CMR’ denotes continuous medium-relief; ‘IHR’ denotes isolated high-relief; ‘ILR’ denotes isolated low-relief.

Table 5.3. Regional average fishing mortality (\bar{F}) and level of recreational (F_{rec}) and commercial (F_{com}) fishing mortality in cells open to fishing given \bar{F}_{rec} begins equivalent to \bar{F}_{com} (e.g. $\bar{F}_{rec} = \bar{F}_{com}$), given \bar{F}_{rec} doubles every 13 years, with associated increases in \bar{F} .

Year	n_{rec}	n_{com}	\bar{F}	s	F_{rec}	F_{com}
2000	22620	16147	0.352	1.00	0.176	0.247
2001	17017	10701	0.366	1.08	0.252	0.372
2002	17017	10701	0.380	1.15	0.270	0.372
2003	17017	10701	0.393	1.23	0.288	0.372
2004	17017	10701	0.407	1.31	0.306	0.372
2005	17017	10701	0.420	1.38	0.324	0.372
2006	17017	10701	0.434	1.46	0.342	0.372
2007	13929	10539	0.447	1.54	0.440	0.378
2008	13929	10539	0.461	1.62	0.462	0.378
2009	13929	10539	0.474	1.69	0.484	0.378
2010	13929	10539	0.488	1.77	0.506	0.378
2011	13929	10539	0.501	1.85	0.528	0.378
2012	13929	10539	0.515	1.92	0.550	0.378
2013	13929	10539	0.529	2.00	0.572	0.378
2014	13929	10539	0.542	2.08	0.594	0.378
2015	13929	10539	0.556	2.15	0.616	0.378
2016	13929	10539	0.569	2.23	0.638	0.378
2017	13929	10539	0.583	2.31	0.660	0.378
2018	13929	10539	0.596	2.38	0.682	0.378
2019	13929	10539	0.610	2.46	0.704	0.378
2020	13929	10539	0.623	2.54	0.726	0.378
2021	13929	10539	0.637	2.62	0.748	0.378
2022	13929	10539	0.651	2.69	0.770	0.378

Note: n_{rec} denotes number of cells open to recreational fishing; n_{com} denotes number of cells open to commercial fishing.

Table 5.4. Regional average fishing mortality (\bar{F}) and level of recreational (F_{rec}) and commercial (F_{com}) fishing mortality in cells open to fishing given different scales (s) of \bar{F}_{rec} relative to \bar{F}_{com} (e.g. $\bar{F}_{rec} = s * \bar{F}_{com}$), given assumption that \bar{F} remains constant through time.

Species	Reserves	n _{rec}	n _{com}	\bar{F}	s = 0.5		s = 1		s = 2	
					F _{rec}	F _{com}	F _{rec}	F _{com}	F _{rec}	F _{com}
Black grouper	None	22620	16147	0.835	0.278	0.780	0.417	0.585	0.557	0.390
	ERs only	17017	10701	0.835	0.370	1.177	0.555	0.882	0.740	0.588
	ERs and RNA	13929	10539	0.835	0.452	1.195	0.678	0.896	0.904	0.597
Red grouper	None	22620	16147	0.352	0.117	0.329	0.176	0.247	0.235	0.165
	ERs only	17017	10701	0.352	0.156	0.497	0.234	0.372	0.312	0.248
	ERs and RNA	13929	10539	0.352	0.191	0.504	0.286	0.378	0.382	0.252
Mutton snapper	None	22620	16147	0.515	0.172	0.481	0.258	0.361	0.343	0.240
	ERs only	17017	10701	0.515	0.228	0.726	0.342	0.544	0.456	0.363
	ERs and RNA	13929	10539	0.515	0.279	0.737	0.418	0.553	0.558	0.368

Note: n_{rec} denotes number of cells open to recreational fishing; n_{com} denotes number of cells open to commercial fishing.

Table 5.5. Equilibrium population parameters for average length of exploited phase fish (L_{bar} ; cm), yield-in-numbers per recruit (Y_n/R), yield-in-weight per recruit (Y_w/R), and spawning potential ratio (SPR) from non-spatial version of SMPA model, assuming constant fishing mortality at current levels, given input parameters listed in Table 5.1.

Species	L_{bar}	Y_n/R	Y_w/R	SPR
Black Grouper	71.9	0.69	4.51	0.008
Red Grouper	59.8	0.46	1.38	0.147
Mutton Snapper	49.2	0.62	1.11	0.063

Table 5.6. Mean number of movements across reserve boundaries for reef fish populations over a 21 year simulation given a realistic reserve implementation schedule and movements parameterized from empirical data.

Species	Flux In		Flux Out		t	df	sig.
	mean	se	mean	se			
Black grouper	884513.7	0.229874	888575.5	0.23114	-8.98447	20	p < 0.001
Red grouper	1212416	0.259328	1214490	0.259538	-11.6697	20	p < 0.001
Mutton snapper	2950513	0.346311	2953417	0.34691	-4.56073	20	p < 0.001

Note: ‘se’ denotes standard error, ‘df’ denotes degrees of freedom, and ‘sig’ denotes significance.

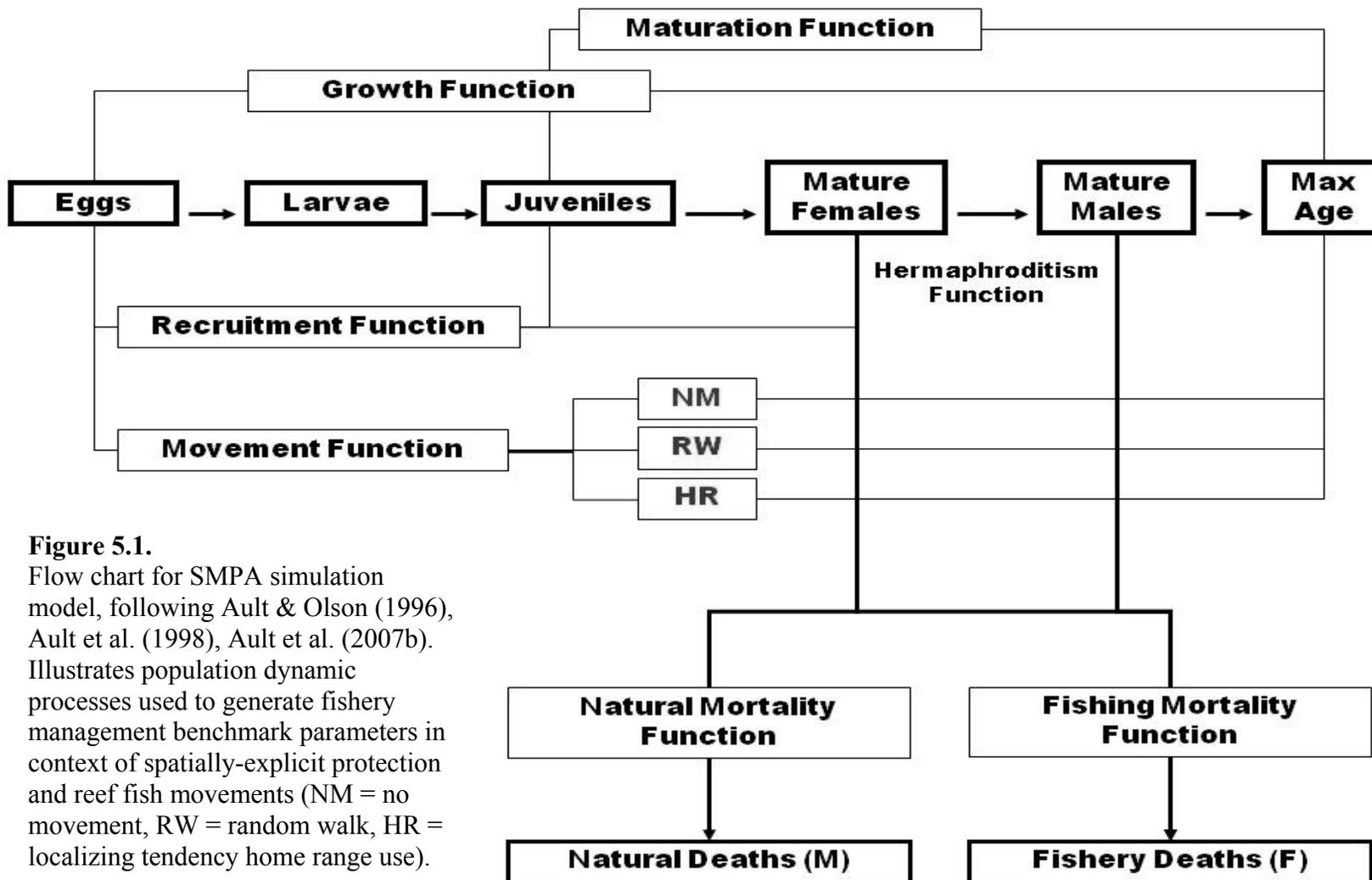
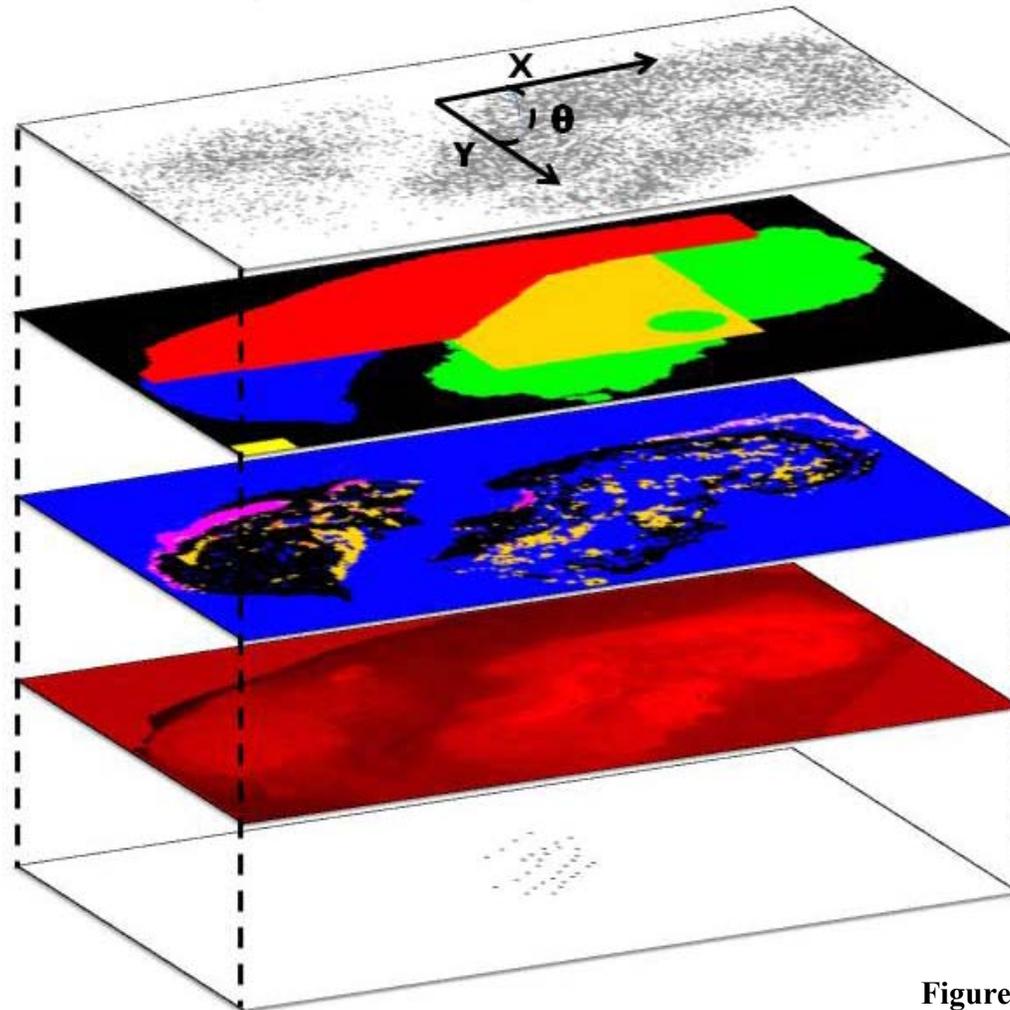


Figure 5.1. Flow chart for SMPA simulation model, following Ault & Olson (1996), Ault et al. (1998), Ault et al. (2007b). Illustrates population dynamic processes used to generate fishery management benchmark parameters in context of spatially-explicit protection and reef fish movements (NM = no movement, RW = random walk, HR = localizing tendency home range use).



FISH –
Traditional Population
Dynamics + Movement

FISHERY –
Spatial protection +
Multiple fisheries

HABITAT –
Unique proportional
allocation of initial
population + recruits

DEPTH –
Impacts receiver
detection range

RECEIVERS –
Validate simulated
movements

Figure 5.2. Spatially-explicit layers of SMPA Model.

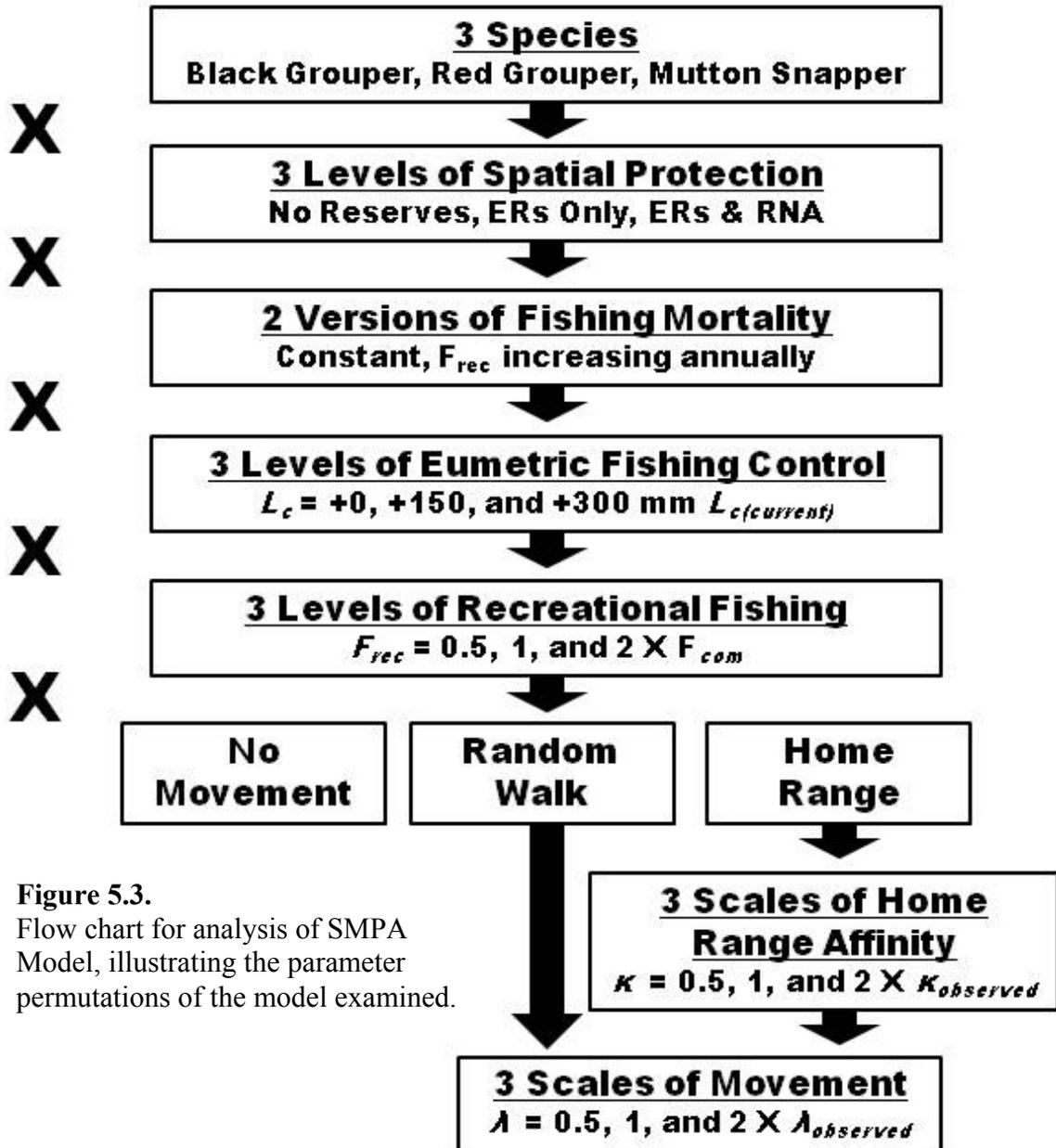


Figure 5.3.
Flow chart for analysis of SMPA Model, illustrating the parameter permutations of the model examined.

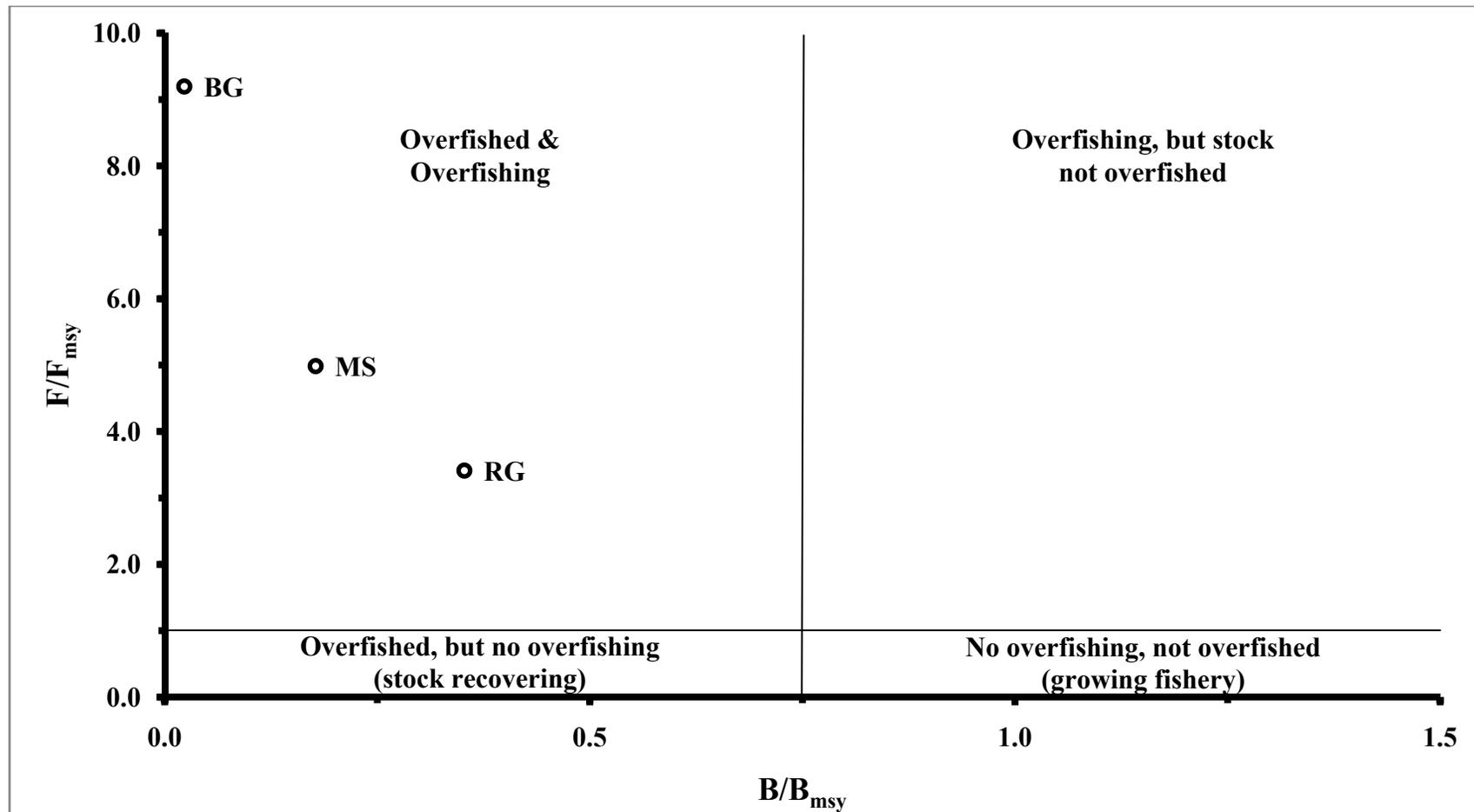


Figure 5.4. Conceptual diagram showing limit and target control rules with current positions of black grouper (BG), red grouper (RG), and mutton snapper (MS) fisheries in Dry Tortugas region. Limit control rules indicate levels of fishing above which there is unacceptable risk for serious or irreversible harm to the resource. Implementation of reserves and/or reduction of overall fishing mortality are required to promote sustainability.

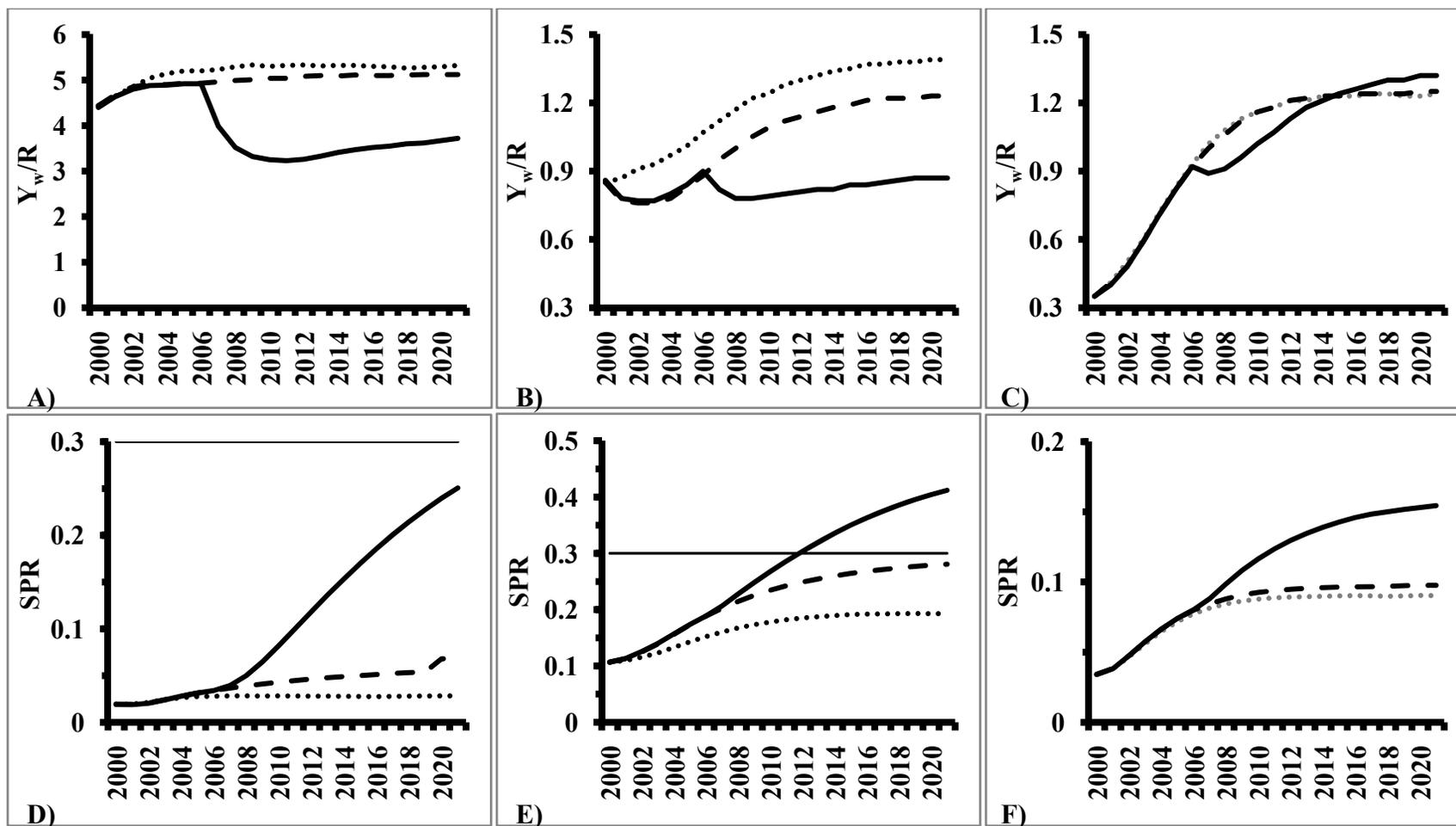


Figure 5.5. Predicted (A-C) yield in weight (Y_w/R) and (D-F) spawning potential ratio (SPR) for black grouper (A, D), red grouper (B, E) and mutton snapper (C, F) stocks with no reserves (dotted line), Ecological Reserves (ERs) only (dashed line), and ERs with Research Natural Area (RNA; solid line); given establishment of ERs in 2001 and RNA in 2008. Solid line in (D-F) denotes target 30% SPR.

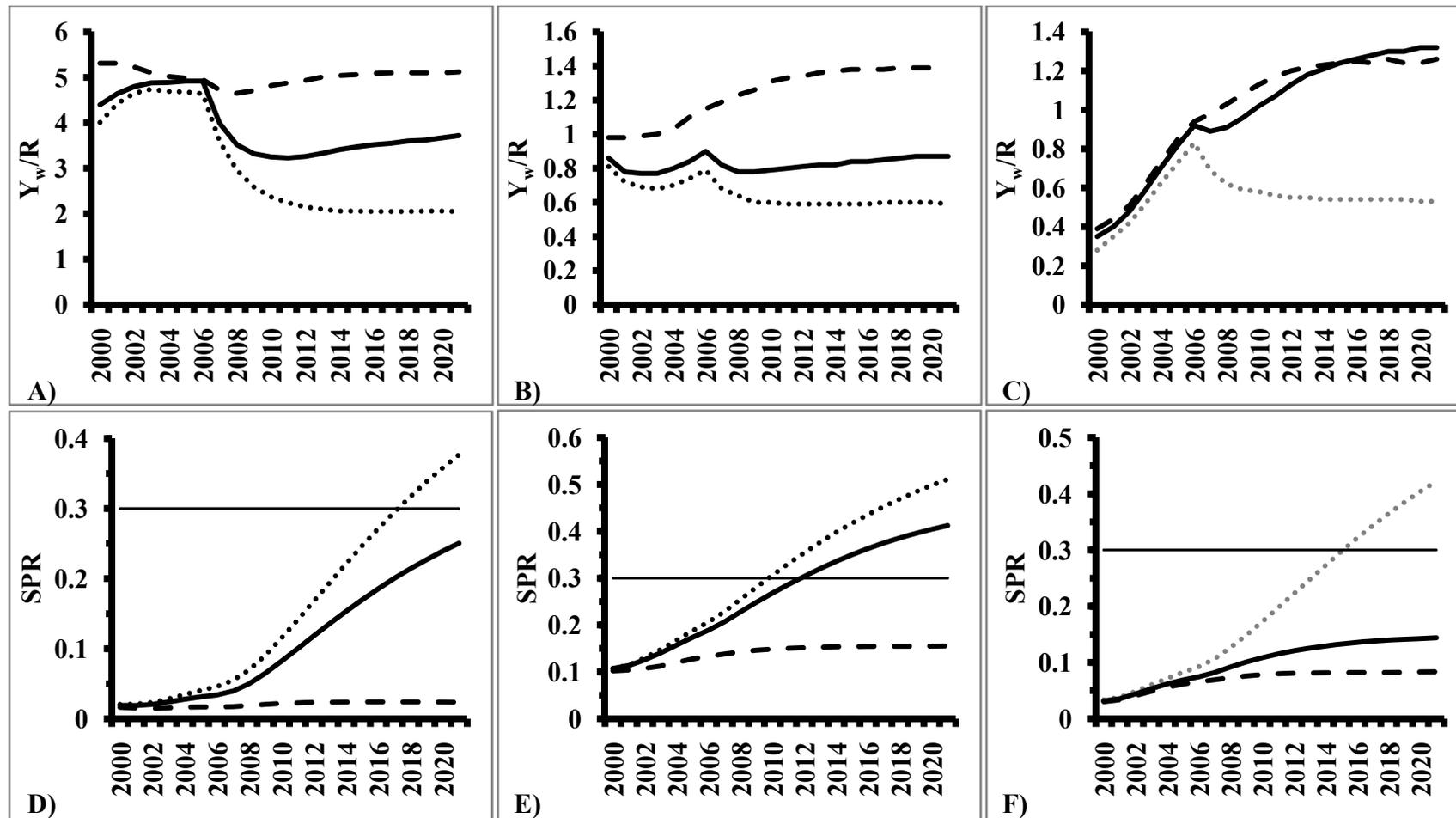


Figure 5.6. Predicted (A-C) yield in weight (Y_w/R) and (D-F) spawning potential ratio (SPR) for black grouper (A, D), red grouper (B, E) and mutton snapper (C, F) stocks given assumptions of no movement (dotted line), random movement (dashed line), and realistic movement (solid line) with establishment of Ecological Reserves in 2001 and Research Natural Area in 2008. Solid line in (D-F) denotes target 30% SPR.

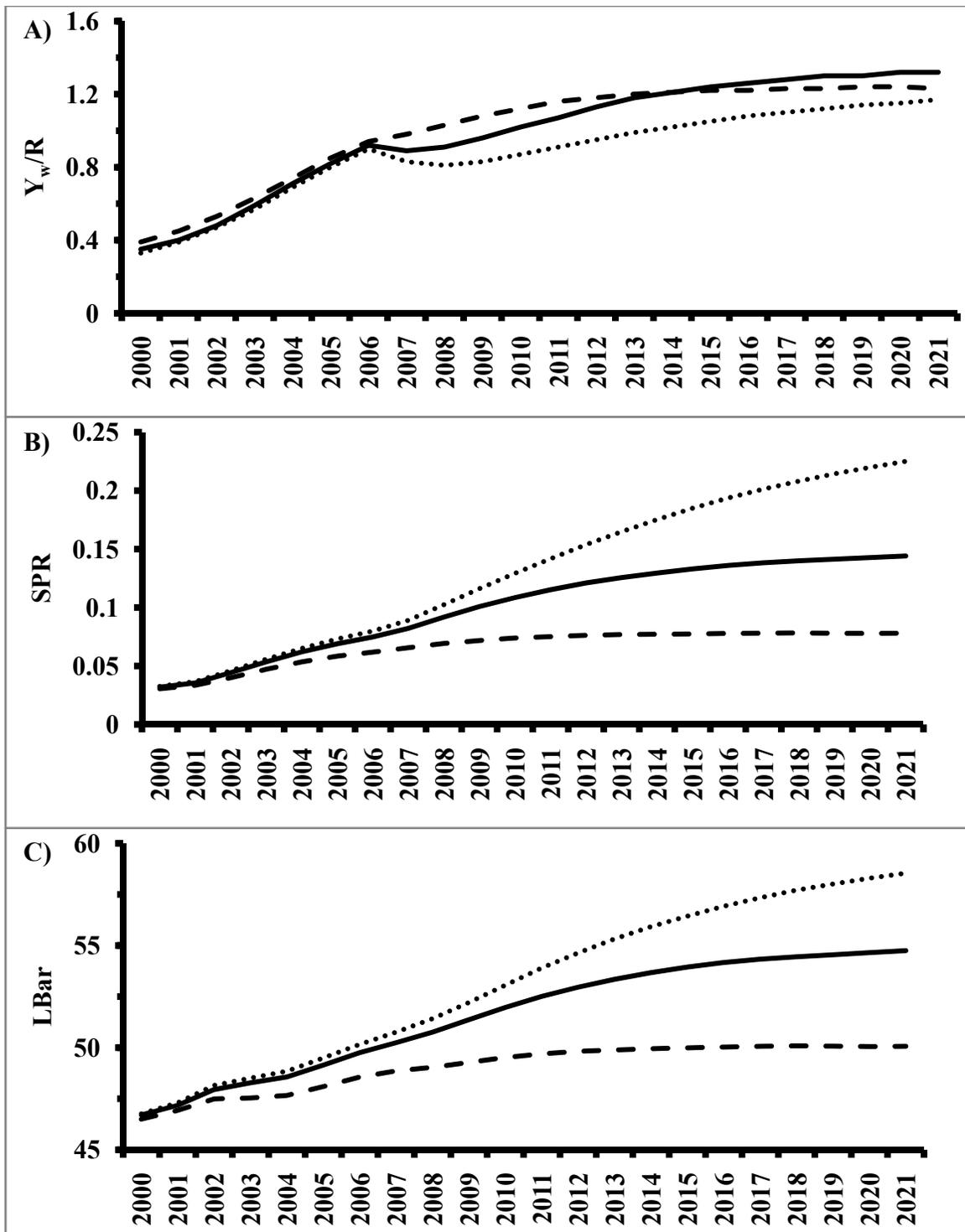


Figure 5.7. Predicted A) yield in weight (Y_w/R), B) spawning potential ratio (SPR), and C) average length in exploited phase (LBar) for mutton snapper stocks under assumptions of high movement (dotted line, $\lambda = 2 * \lambda_{obs}$; $\kappa = 0.5 * \kappa_{obs}$), realistic movement (solid line, $\lambda = \lambda_{obs}$; $\kappa = \kappa_{obs}$), and low movement (dashed line, $\lambda = 0.5 * \lambda_{obs}$; $\kappa = 2 * \kappa_{obs}$) following establishment of Ecological Reserves in 2001 and Research Natural Area in 2008.

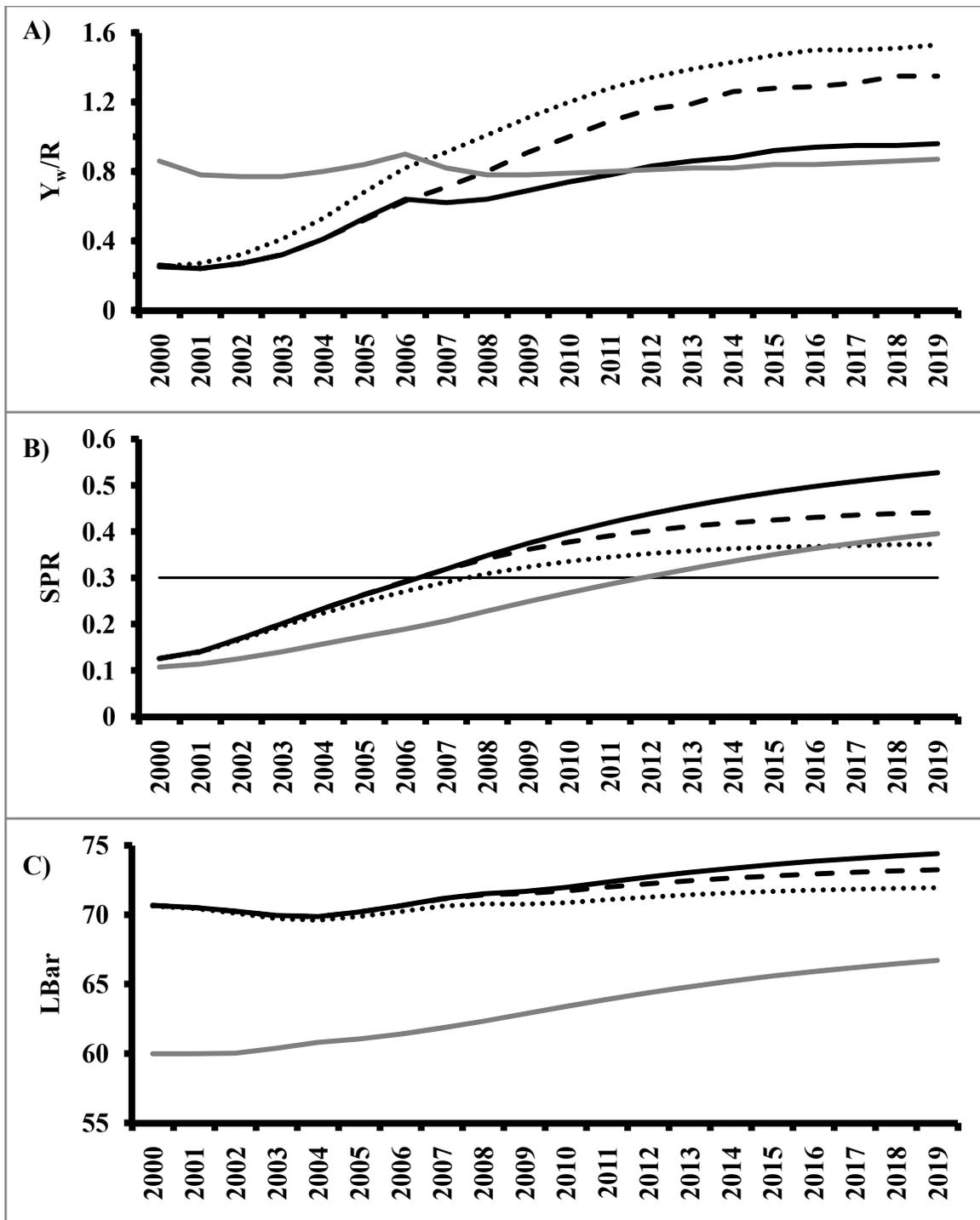


Figure 5.8. Predicted A) yield in weight (Y_w/R), B) spawning potential ratio (SPR), and C) average length in exploited phase (LBar) for red grouper stocks with 15 cm increase in L_c under assumptions of no reserves (dotted line), Ecological Reserves (ERs) only (dashed line), and ERs with Research Natural Area (RNA; solid line); given establishment of ERs in 2001 and RNA in 2008. Line in (B) shows target 30% SPR. Gray line indicates predictions for stock with no change in L_c .

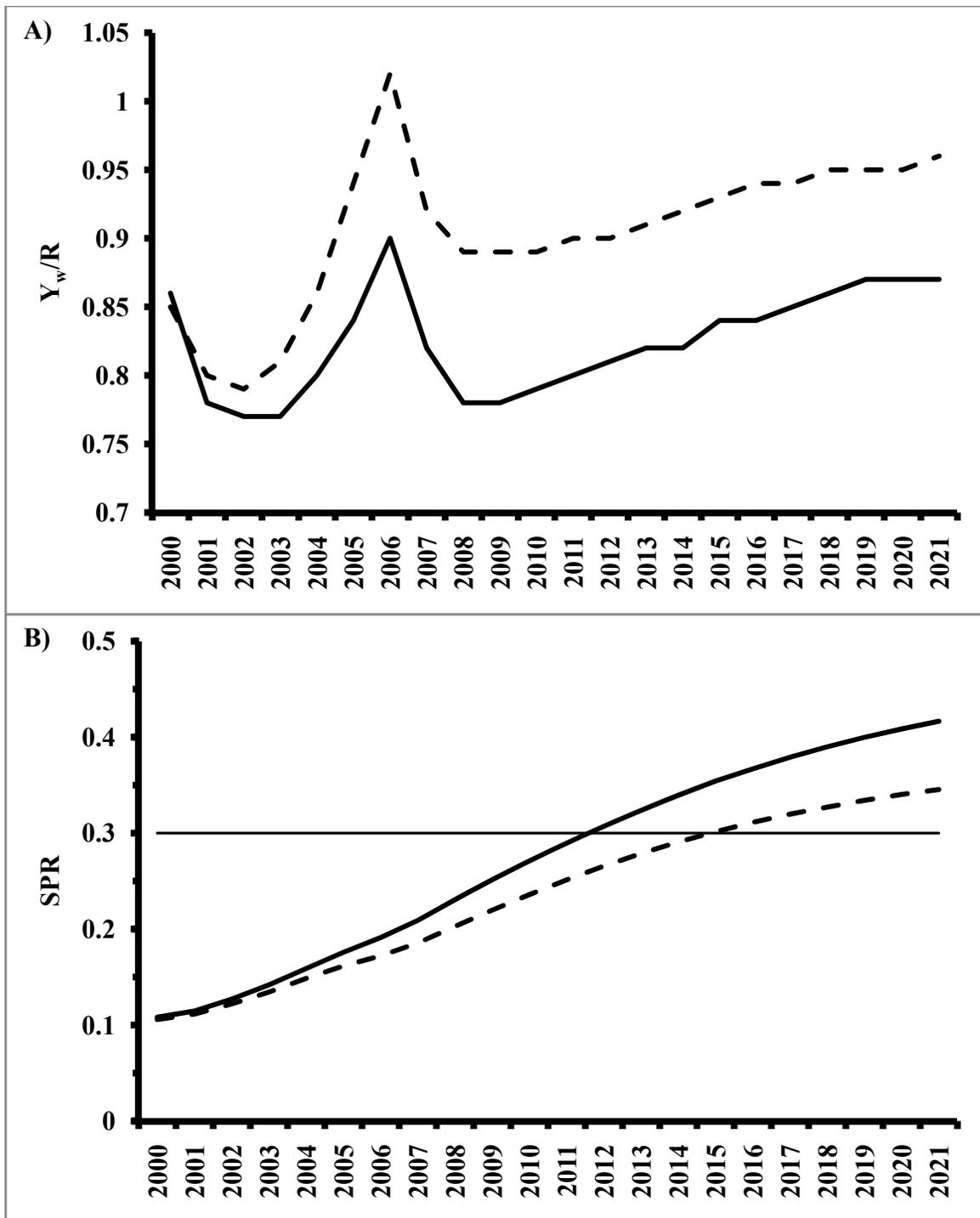


Figure 5.9. Predicted A) yield-in-weight per recruit and B) spawning potential ratio for red grouper population over time following implementation of Ecological Reserves in 2001 and Research Natural Area in 2007, assuming a constant (solid lines) or growing (dashed lines) recreational fleet. Note black dotted line denotes 30% spawning potential ratio, a USA Federal minimum standard for sustainability.

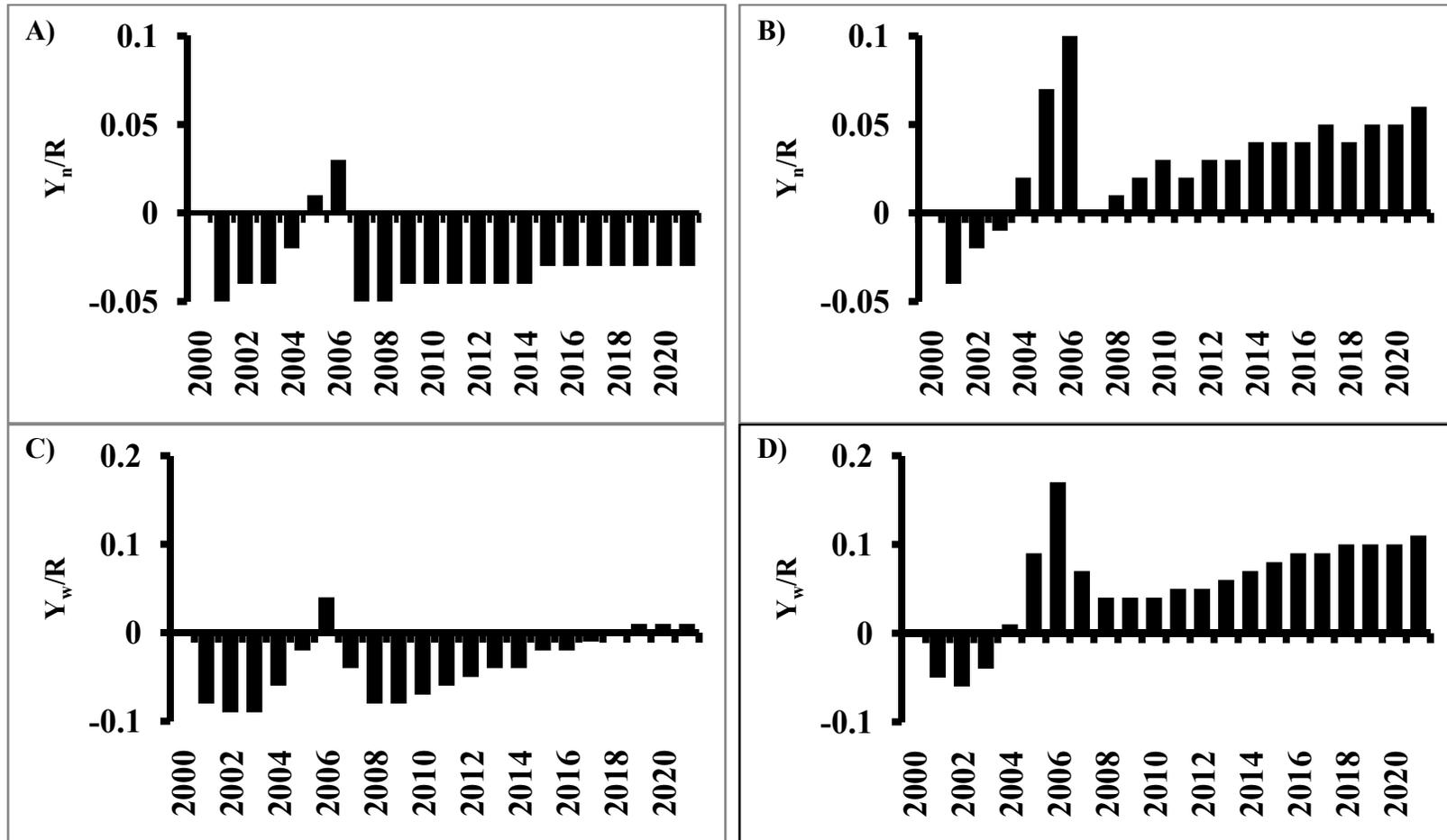


Figure 5.10. Transitional dynamics of red grouper fishery yields scaled to year 2000 values following implementation of Ecological Reserves in 2001 and Research Natural Area in 2007, illustrating changes in yield per recruit in numbers (Y_n/R) and weight (Y_w/R) under assumptions of constant recreational fleet size (A, C) and growing recreational fleet (B, D).

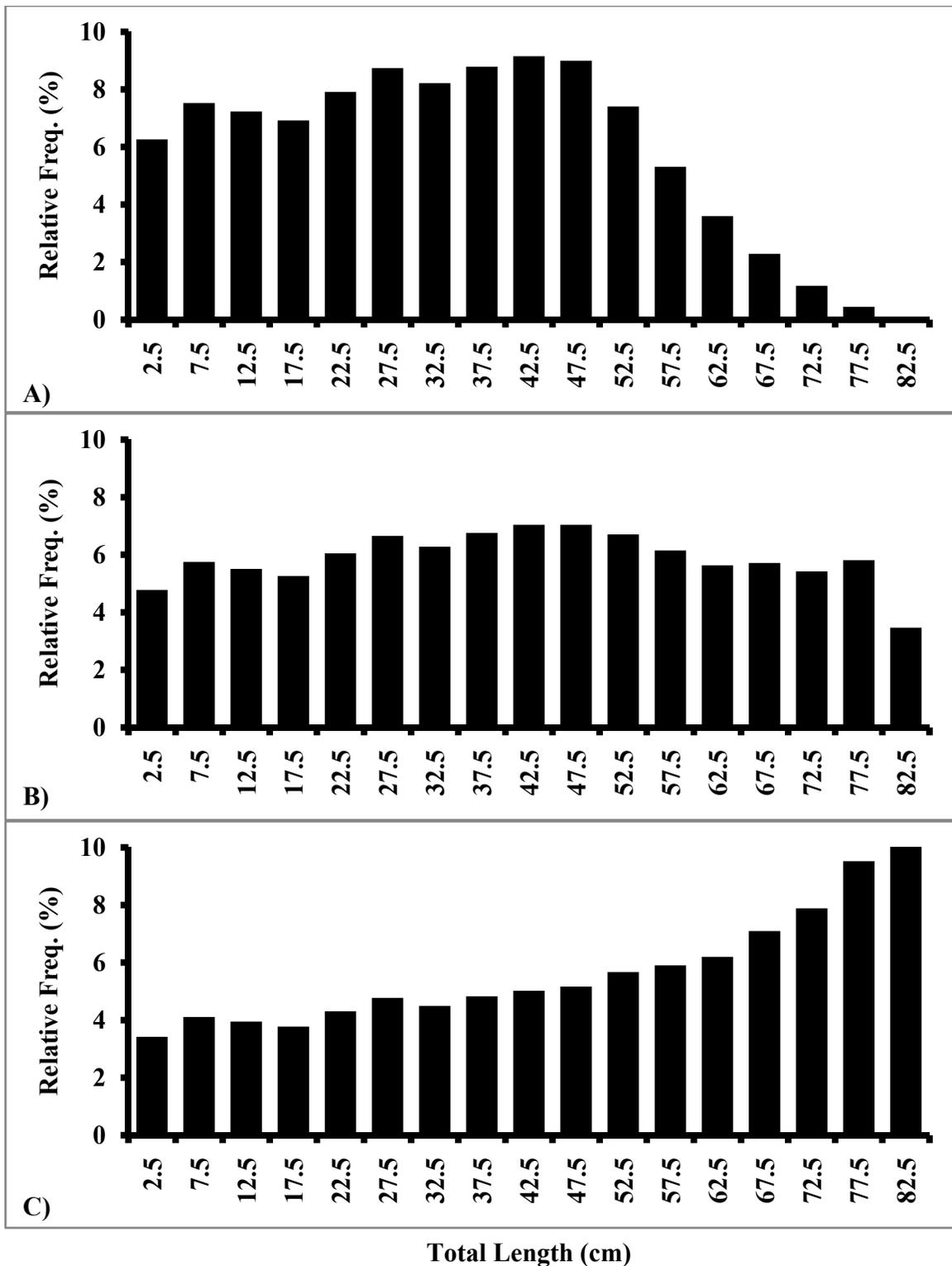


Figure 5.11. Length-frequency histograms for red grouper stocks assuming A) year 2000 population structure at current exploitation; B) year 2020 population structure at current exploitation with Ecological Reserves and Research Natural Area implemented; C) equilibrium structure given no exploitation.

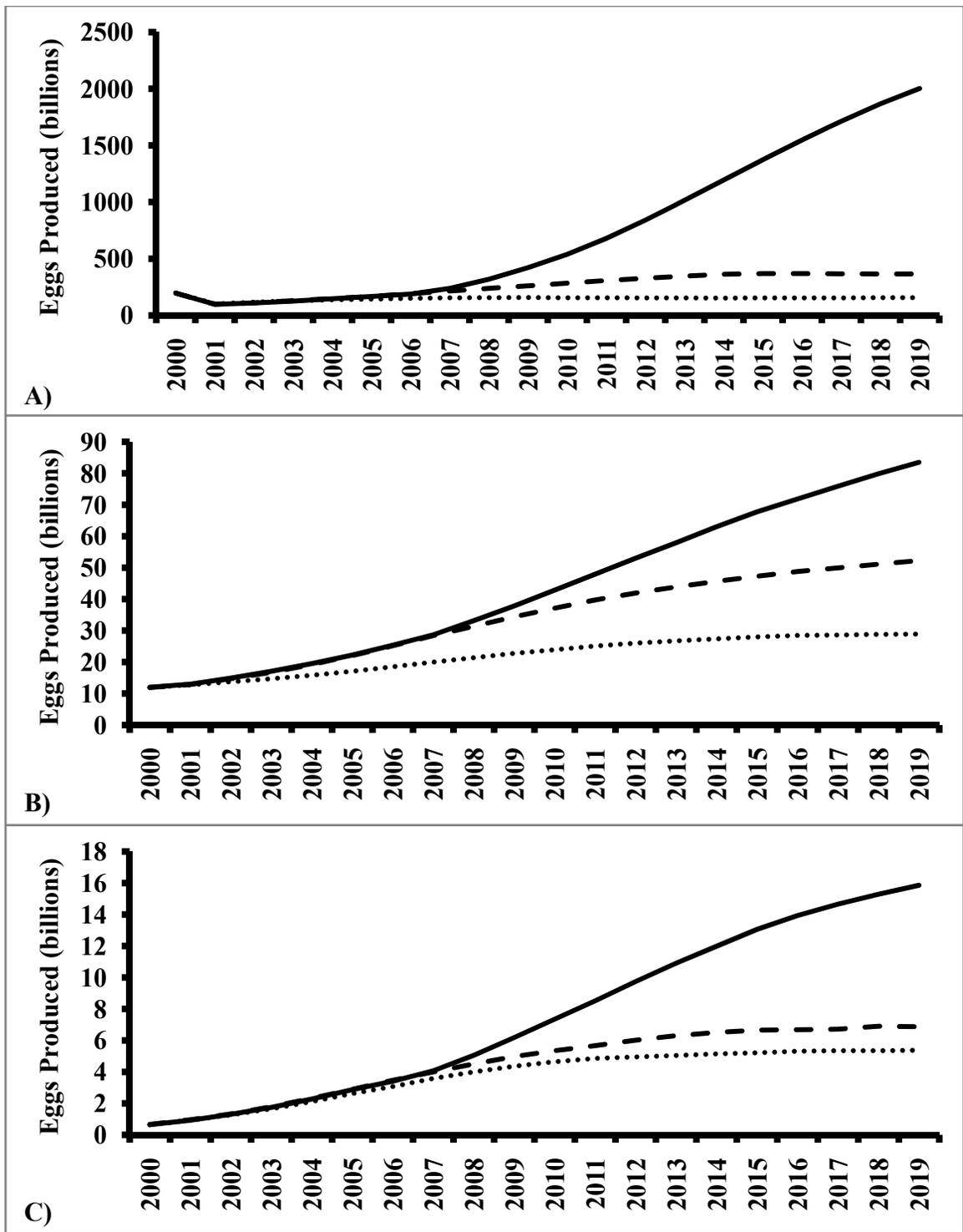


Figure 5.12. Total population egg production for A) black grouper, B) red grouper, and C) mutton snapper stocks under assumptions of no reserves (dotted line), Ecological Reserves (ERs) only (dashed line), and ERs with Research Natural Area (RNA; solid line), given establishment of ERs in 2001 and RNA in 2008.

WORKS CITED

- Abesamis, R.A. and Russ, G.R. 2005. Density-dependent spillover from a marine reserve: Long-term evidence. *Ecological Applications*, 15(5): 1798-1812.
- Alagaraja, K. 1984. Simple methods for estimation of parameters for assessing exploited fish stocks. *Indian Journal of Fisheries*, 31: 177-208.
- Alcala, A.C. and Russ, G.R. 1990. A direct test of the effects of protective management on abundance and yield of tropical marine resources. *Journal du Conseil International pour l'Exploration de la Mer*, 46: 40-47.
- Allison, G.W., Lubchenco, J., and Carr, M.H. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecological applications*, 8: 79-92.
- Allman, R.J. and Grimes, C.B. 2002. Temporal and spatial dynamics of spawning, settlement, and growth of gray snapper (*Lutjanus griseus*) from the West Florida shelf as determined from otolith microstructures. *Fisheries Bulletin*, 100: 391-403.
- Alonzo, S.H. and Mangel, M.. 2004. The effects of size-selective fisheries on the stock dynamics of and sperm limitation in sex-changing fish. *Fisheries Bulletin*, 102:1-13.
- Ambrose, H.W., III. 1972. Effect of habitat familiarity and toe clipping on rate of owl predation in *Microtus pennsylvanicus*. *Journal of Mammalogy*, 53: 909-919.
- AMIRIX. 2007. Understanding the performance of VEMCO 69 kHz single frequency acoustic telemetry. Technical White Paper, Document #: XDOC-004372 Version 04. Available at www.vemco.com.
- Armstrong, D.P. 1991. Aggressiveness of breeding territorial honeyeaters corresponds to seasonal changes in nectar availability. *Behavioural Ecology and Sociobiology*, 29: 103-111.
- Aronson, L.R. 1951. Orientation and jumping behavior of the gobiid fish, *Bathygoblis soporator*. *American Museum Novitates* 1486: 1-22.
- Aronson, L.R. 1971. Further studies on orientation and jumping behavior in the gobiid fish, *Bathygoblis soporator*. *Annals of the New York Academy of Sciences*, 188: 378-392.
- Attwood, C.G. and Bennett, B.A. 1994. Variation in dispersal of galjoen (*Coracinus capensis*) from a marine reserve. *Canadian Journal of Fisheries & Aquatic Science*, 51: 1247-1257.
- Atwood, T.C. and Weeks, Jr., H.P. 2003. Spatial home-range overlap and temporal interaction in eastern coyotes: the influence of pair types and fragmentation. *Canadian Journal of Zoology*, 81: 1589-1597.

- Ault, J.S. 1985. Some quantitative aspects of reproduction and growth of the red abalone, *Haliotis rufescens* Swainson. *Journal of the World Mariculture Society*, 16: 398-425.
- Ault, J.S. 1988. Nonlinear numerical simulation models for assessing tropical fisheries with continuously breeding multicohort populations. Ph.D. Dissertation, University of Miami, Rosenstiel School of Marine and Atmospheric Science, 242 p.
- Ault, J.S., Bohnsack, J.A., and Meester, G.A. 1998. A retrospective (1979-1996) multispecies assessment of coral reef fish stocks in the Florida Keys. *Fishery Bulletin* 96(3): 395-414.
- Ault, J.S., Bohnsack, J.A., Smith, S.G., and Luo, J. 2005a. Towards sustainable multispecies fisheries in the Florida USA coral reef ecosystem. *Bulletin of Marine Science* 76(2): 595-622.
- Ault, J.S., Luo, J., Smith, S.G., Serafy, J.E., Wang, J.D., Humston, R., and Diaz, G.A. 1999. A spatial dynamic multistock production model. *Canadian Journal of Fisheries and Aquatic Sciences*, 56(Suppl. 1): 4-25.
- Ault, J.S., Luo, J., and Wang, J.D. 2003a. A spatial ecosystem model to assess spotted seatrout population risks from exploitation and environmental changes. Chapter 15, Pages 267-296 in *Biology of Spotted Seatrout*. S.A. Bortone (ed.). CRC Press, Boca Raton, Florida.
- Ault, J.S. and Olson, D.B. 1996. A multicohort stock production model. *Transactions of the American Fisheries Society*, 125(33): 343-363.
- Ault, J.S., Smith, S.G., and Bohnsack, J.A. 2005b. Evaluation of average length as an indicator of exploitation status for the Florida coral reef fish community. *ICES Journal of Marine Science* 62:417-423.
- Ault, J.S., Smith, S.G., Bohnsack, J.A., Luo, J., Harper, D.E., and McClellan, D.B. 2006. Building sustainable fisheries in Florida's coral reef ecosystem: Positive signs in the Dry Tortugas. *Bulletin of Marine Science*, 78(3): 633-654.
- Ault, J.S., Smith, S.G., Farmer, N.A., and Schmidt, T. 2007a. Fishery-independent monitoring of coral reef fishes, coral reefs, and macro-invertebrates in the Dry Tortugas. Final Report to the National Park Service. 95 p.
- Ault, J.S., Smith, S.G., Franklin, E., Luo, J., and Bohnsack, J.A. 2003b. Sampling design analysis for coral reef fish stock assessment in Dry Tortugas National Park. Final Report to NPS.

- Ault, J.S., Smith, S.G., Luo, J., Meester, G.A., Bohnsack, J.A., and Miller, S.L. 2001. Baseline multispecies coral reef fish stock assessments for the Dry Tortugas. NOAA Technical Memorandum NMFS-SEFSC-487. 117 p.
- Ault, J.S., Smith, S.G., Luo, J., Monaco, M.E., and Appeldorn, R.S. 2008. Length-based assessment of sustainability benchmarks for coral reef fishes in Puerto Rico. *Environmental Conservation*, 35(3): 221-231.
- Ault, J.S., Smith, S.G., and Tilmant, J.T. 2007b. Fishery management analyses for reef fish in Biscayne National Park: bag & size limits. National Park Service, Natural Resource Technical Report NPS/NRPC/WRD/NRTR—2007/064. 66 p.
- Ault, J.S., Smith, S.G., Tilmant, J.T., Bohnsack, J.A., Luo, J., and Kellison, G.T. 2009. Are the coral reef finfish fisheries of south Florida sustainable? *In*: Proceedings of the 11th International Coral Reef Symposium. Ft. Lauderdale, FL (in press).
- Bakun, A. 1996. Patterns in the ocean: Ocean processes and marine population dynamics. University of California Sea Grant, San Diego, California, USA, in cooperation with Centro de Investigaciones Biológicas de Noroeste, La Paz, Baja California Sur, Mexico. 323 pp.
- Bannerot, S.P. 1984. The dynamics of exploited groupers (Serranidae): An investigation of the protogynous hermaphroditic reproductive strategy. University of Miami Dissertation. 393 p.
- Baras, E., Togola, B., Sicard, B., and Bènech, V. 2002. Behaviour of tigerfish *Hydrocynus brevis* in the River Niger, Mali, as revealed by simultaneous telemetry of activity and swimming depth. *Hydrobiologia*, 483: 103-110.
- Barrett, N.S. 1995. Short- and long-term movement patterns of six temperate reef fishes (Families Labridae and Monacanthidae). *Marine and Freshwater Research*, 46: 853-860.
- Bartholomew, A., Bohnsack, J.A., Smith, S.G., Ault, J.S., Harper, D.E., and McClellan, D.B. 2008. Influence of marine reserve size and boundary length on the initial response of exploited reef fishes in the Florida Keys National Marine Sanctuary, USA. *Landscape Ecology*, 23: 55-65. DOI 10.1007/s 10980-007-9136-0.
- Beaumariage, D.S. 1969. Returns from the 1965 Schlitz Tagging Program including a cumulative analysis of previous results. Florida State Board of Conservation Marine Laboratory. Technical Series No. 59. St. Petersburg, FL. 38 p.
- Beaumariage, D.S., and Bullock, L.H. 1976. Biological research on snappers and groupers as related to fishery management requirements. Fla. Sea Grant Program, Report no. 17:86-94.

- Becker, R.A., Chambers, J.M., Wilks, A.R. 1988. The New S Language: a programming environment for data analysis and graphics. Wadsworth and Brooks/Cole Advanced Books and Software, Monterey, CA.
- Bell, T. and Kramer, D.L. 2000. Territoriality and habitat use by juvenile blue tangs, *Acanthurus coeruleus*. Environmental Biology of Fishes, 58: 401-409.
- Berkeley, S.A., Chapman, C., and Sogard, S.M. 2004a. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology, 85: 1258-1264.
- Berkeley, S.A., Hixon, M.A., Larson, R.J., and Love, M.S. 2004b. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries, 29: 23-32.
- Beverton, R. J. H. and Holt, S. J. 1957. On the dynamics of exploited fish populations, Fishery Investigations Series II Volume XIX, Ministry of Agriculture, Fisheries and Food.
- Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at <http://www.spatial ecology.com/htools>.
- Bobko, S.J. and Berkeley, S.A. 2004. Maturity, ovarian cycle, fecundity, and age-specific parturition of black rockfish (*Sebastes melanops*). Fisheries Bulletin, 102: 418-429.
- Bohnsack, J.A. 2000. A comparison of the short-term impacts of no-take marine reserves and minimum size limits. Bulletin of Marine Science, 66(3): 635-650.
- Bohnsack, J.A. 1998. Applications of marine reserves to reef fisheries management. Australian Journal of Ecology, 23: 298-304.
- Bohnsack, J.A. 1999. Incorporating no-take marine reserves into precautionary management and stock assessment. Proceedings, 5th NMFS NSAW. NOAA Tech. Memo. NMFS-F/SPO-40.
- Bohnsack, J.A. 1990. The potential of marine fishery reserves for reef fish management in the U.S. Southern Atlantic. Plan Development Team, Reef Fish Management Plan, South Atlantic Fishery Management Council, Coastal Resource Division CRD/89-90/04.
- Bohnsack, J.A. and Ault, J.S. 1996. Management strategies to conserve marine biodiversity. Oceanography, 9:73-82.
- Bohnsack, J.A., Ault, J.S., and Causey, B. 2004. Why have no-take marine protected areas? American Fisheries Society Symposium, 42:185-193.

- Bohnsack, J.A. and Harper, D.E. 1988. Length-weight relationships of selected marine reef fishes from the southeastern United States and the Caribbean. NOAA Technical Memorandum NMFS-SEFC-215. 31 p.
- Bohnsack, J.A., D.E. Harper, and McClellan, D.B. 1994. Fisheries trends from Monroe County, Florida. *Bulletin of Marine Science*, 54(3): 982-1018.
- Bolden, S.K. 2001. Nassau grouper (*Epinephelus striatus*, Pisces: Serranidae) movement in the Bahamas, as determined by ultrasonic telemetry. Ph.D. Dissertation, University of Miami, Miami, FL, USA.
- Botsford, L.W., Hasting, A., and Gaines, S.D. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecology Letters*, 4: 144-150.
- Bradbury, C., Green, J.M., and Bruce-Lockhart, M. 1995. Home range of female cunner, *Tautoglabrus adspersus* (Labridae), as determined by ultrasonic telemetry. *Canadian Journal of Zoology*, 73: 1268-1279.
- Bray, R.N. 1981. Influence of water currents and zooplankton densities on daily foraging movements of blacksmith, *Chromis punctipinnis*, a planktivorous reef fish. *US Fishery Bulletin*, 78: 829-841.
- Brown, J.L. 1964. The evolution of diversity in avian territorial systems. *Wilderness Bulletin*, 76: 160-169.
- Brulé, T., C. Déniel, T. Colás-Marrufo, and Sánchez-Crespo, M. 1999. Red grouper reproduction in the southern Gulf of Mexico. *Transactions of the American Fisheries Society*, 128: 385-402.
- Brulé, T., Renan, X., Colas-Marrufo, T., Hauyon, Y., Tuz-Sulub, A.N., Deniel, C. 2003. Reproduction in the protogynous black grouper from the southern Gulf of Mexico – *Mycteroperca bonaci* Poey. *Fishery Bulletin*, 101: 463-475.
- Bruylants, B., A. Vandelannoote, and Verheyen, R. 1986. The movement pattern and density distribution of perch, *Perca fluviatilis* L., in a channelized lowland river. *Aquaculture and Fisheries Management*, 17: 49-57.
- Burgos, J. M. 2001. Life history of the red grouper (*Epinephelus morio*) off the North Carolina and South Carolina coast. Master's Thesis. University of Charleston, South Carolina.
- Burkey, T. V. 1989. Extinctions in nature reserves: the effect of fragmentation and the importance of migration between reserve fragments. *Oikos* 55:75-81.

- Burnham, K.P. and D.R. Anderson. 2002. Model Selection and Multimodal Inference: An Information-Theoretic Approach. Springer-Verlag, New York City, New York, USA.
- Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, 24: 246-352.
- Burton, M.L., Brennan, K.J., Muñoz, R.C., and Parker, Jr., R.O. 2006. Preliminary evidence of increased spawning aggregations of mutton snapper (*Lutjanus analis*) at Riley's Hump two years after establishment of the Tortugas South Ecological Reserve. *Fishery Bulletin*, 103: 404-410.
- Buskirk, S.W. and McDonald, L.L. 1989. Analysis of variability in home range size of the American marten. *Journal of Wildlife Management*, 53: 997-1004.
- Carpenter F. L. 1987. Food abundance and territoriality: To defend or not to defend? *American Zoology*. 27:387-399.
- Carpenter, F.L. and MacMillen, R.E. 1976. Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. *Science*, 194: 639-642.
- Carpenter, F.L. and MacMillen, R.E. 1980. Resource limitation, foraging strategies and community structure in Hawaiian Honeycreepers. *Proceedings of the XVII International Ornithology Congress 2*: 1100-1104.
- Carr, G.M. and Macdonald, D.W. 1986. The sociality of foragers: a model based on resource dispersion. *Animal Behaviour*, 34: 1540-1549.
- Carr, M.H. and Reed, D.C. 1993. Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. *Canadian Journal of Fisheries and Aquatic Science*, 50: 2019-2028.
- Cato, D.H. 1980. Some unusual sounds of apparent biological origin responsible for sustained noise in the Timor Sea. *Journal of the Acoustic Society of America*, 68: 1056-1060.
- Chapman, M.R. and Kramer, D.L. 2000. Movements of fishes within and among fringing coral reefs in Barbados. *Environmental Biology of Fishes*, 57: 11-24.
- Clarke, M.F., Burke da Silva, K., Lair, H., Pocklington, R., Kramer, D.L., and McLaughlin, R.L. 1993. Site familiarity affects escape behaviour of the eastern chipmunk, *Tamias striatus*. *Oikos*, 66(3): 533-537.
- Claro, R., 1981. Ecología y ciclo de vida del pargo criollo, *Lutjanus analis* (Cuvier), en la plataforma cubana. *Academia de las Ciencias de Cuba, Inf. Científica Inst. Oceanológicos*, 186:1-83.

- Clay, C.S. and Medwin, H. 1977. Acoustical Oceanography: Principles and Applications. John Wiley and Sons, New York, NY.
- Clements, S., Jepsen, D., Karnowski, M., and Schreck, C.B. 2005. Optimization of an acoustic telemetry array for detecting transmitter-implanted fish. *North American Journal of Fisheries Management*, 25: 429–436.
- Coleman, F.C., Koenig, C.C. and Collins, L.A. 1996. Reproductive styles of shallow-water grouper (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Environmental Biology of Fishes*, 47: 129-141.
- Coleman, F.C., Koenig, C.C., Huntsman, G.R., Musick, J.A., Eklund, A-M., McGovern, J.C., Chapman, R.W., Sedberry, G.R., and Grimes, C.B. 2000. Long-lived reef fishes: the grouper-snapper complex. *Fisheries*, 25: 14-21.
- Colin, P.L. 1996. Longevity of some coral reef spawning aggregations. *Copeia*, 1996: 189-191.
- Colin, P.L., W.A. Laroche, and Brothers, E.B. 1997. Ingress and settlement in the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae), with relationship to spawning occurrence. *Bulletin of Marine Science*, 60(3): 656-667.
- Collins, L.A., Fitzhugh, G.R., Lombardi-Carlson, L.A., Lyon, H.M., Walling, W.T., and Oliver, D.W. 2002. Characterization of red grouper (Serranidae: *Epinephelus morio*) reproduction from the eastern Gulf of Mexico. NMFS Contribution Series 2002-07.
- Collins, M.R., Rogers, S.G., Smith, T.I.J., and Moser, M.L. 2000. Primary factors affecting sturgeon populations in the southeastern United States: Fishing mortality and degradation of essential habitats. *Bulletin of Marine Science*, 66(3): 917-928.
- Conover, D.O., Travis, J., and Coleman, F.C. 2000. Essential fish habitat and marine reserves: an introduction to the second Mote Symposium in fisheries ecology. *Bulletin of Marine Science*, 66(3): 527-534.
- Costello, T.J. and Allen, D.M. 1970. Synopsis of biological data on the pink shrimp, *Penaeus duorarum duorarum* Burkenroad, 1939. *FAO Fisheries Report*, 57(4): 1499-1537.
- Cote, I.M., Mosqueira, I., and Reynolds, J.D. 2001. Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *Journal of Fish Biology*, 59: 178-189.
- Cowen, R.K., Lwiza, K.M.M., Sponaugle, S., Paris, C.B., and Olson, D.B. 2000. Connectivity of marine populations: Open or closed? *Science*, 287(5454): 857-859.

- Crowder, L.B., Lyman, S.J., Figueira, W.F., and Priddy, J. 2000. Source-sink population dynamics and the problem of siting marine reserves. *Bulletin of Marine Science*, 66(3): 799-820.
- Dahlgren, C.P. and Eggleston, D.B. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology*, 81(8): 2227-2240.
- Dahlgren, C.P. and Sobel, J. 2000. Designing a Dry Tortugas Ecological Reserve: How big is big enough?...To do what? *Bulletin of Marine Science*, 66(3): 707-719.
- Davidson, R.J. 2001. Changes in population parameters and behaviour of blue cod (*Parapercis colias*; Pinguipedidae) in Long Island Kokomohua Marine Reserve, Marlborough Sounds, New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 11: 417-435.
- Davies, N.B. and Houston, A.I. 1981. Owners and satellites: the economics of territory defense in the pied wagtail, *Motacilla alba*. *Journal of Animal Ecology*, 50: 157-180.
- DeMartini, E.E. 1993. Modeling the potential for fishery reserves for managing Pacific coral reef fishes. *Fishery Bulletin*, 91(3): 414-427.
- Devillard, S., Aubineau, J., Berger, F., Léonard, Y., Roobrouck, A., and Marchandeu, S. 2008. Home range of the European rabbit (*Oryctolagus cuniculus*) in three contrasting French populations. *Mammalian Biology – Zeitschrift für Säugetierkunde*, 73(2): 128-137.
- Dixon, K.R. and Chapman, J.A. 1980. Harmonic mean measure of animal activity areas. *Ecology*, 61(5): 1040-1044.
- Domeier, M. L., Koenig, C. C., and Coleman, F. C. 1996. Reproductive biology of the gray snapper (*Lutjanus griseus*), with notes on spawning for other Western Atlantic snappers (Lutjanidae). *In* Biology and culture of tropical groupers and snappers (F. Arreguín-Sánchez, J. L. Munro, M. C. Balgos, and D. Pauly, eds.). ICLARM Conference Proceedings, 48: 189–201.
- Douglas, R.H. 1996. Goldfish use the angle of a familiar landmark to locate a food source. *Journal of Fish Biology*, 49: 532-536.
- Dresser, B.K. and Kneib, R.T. 2007. Site fidelity and movement patterns of wild subadult red drum, *Sciaenops ocellatus* (Linnaeus), within a salt marsh-dominated estuarine landscape. *Fisheries Management and Ecology*, 14(3): 183-190.
- Edgar, G.J. and Barrett, N.S. 1999. Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates, and plants. *Journal of Experimental Marine Biology and Ecology*, 242: 107-144.

- Eggleston, D.B., Grover, J.J., and Lipcius, R.N. 1998. Ontogenetic diet shifts in Nassau grouper: Trophic linkages and predatory impact. *Bulletin of Marine Science*, 63(1): 111-126.
- Eklund, A-M., McClellan, D.B., and Harper, D.E. 2000. Black grouper aggregations in relation to protected areas within the Florida Keys National Marine Sanctuary. *Bulletin of Marine Science*, 66(3):721-728.
- Elliot, J.M. 1994. *Quantitative ecology and the brown trout*. Oxford University Press, Oxford, UK. 286 pp.
- Eristhee, N. and Oxenford, H.A. 2001. Home range size and use of space by Bermuda chub *Kyphosus sectatrix* (L.) in two marine reserves in the Soufrière Marine Management Area, St. Lucia, West Indies. *Journal of Fish Biology*, 59(Supplement A): 129-151.
- Ewald, P.W. and Carpenter, F.L. 1978. Territorial responses to energy manipulations in the Anna hummingbird. *Oecologia*, 31: 277-292.
- Fabrizio, M.C.; Pessutti, J.P.; Manderson, J.P.; Drohan, A.F.; Phelan, B.A. 2005. Use of the Historic Area Remediation Site by black sea bass and summer flounder. U.S. Department of Commerce Northeast Fisheries Science Center Reference Document 05-06; 95 p. Available from: National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026.
- Fahrig, L., and Merriam, G. 1985. Habitat patch connectivity and population survival. *Ecology* 66:1762-1768.
- Fitzhugh, G.R., Lyon, H.M., Walling, W.T., Levins, C.F., and Lombardi-Carlson, L.A. 2006. An update of Gulf of Mexico red grouper reproductive data and parameters for SEDAR 12. NMFS Panama City Laboratory Contribution, 06-14.
- Fogarty, M.J. 1999. Essential habitat, marine reserves and fishery management. *Trends in Ecology & Evolution*, 14(4): 133-134.
- Forseth, T., Naesje, T.F., Jonsson, B., and Härsaker, K. 1999. Juvenile migration in brown trout: a consequence of energetic state. *Journal of Animal Ecology*, 68: 783-793.
- Francini-Filho, R.B. and Moura, R.L. 2008. Evidence for spillover of reef fishes from a no-take marine reserve: An evaluation using the before-after control-impact (BACI) approach. *Fisheries Research*, 93(3): 346-356.
- Franklin, E.C., Ault, J.S., Smith, S.G., Luo, J., Meester, G.A., Diaz, G.A., Chiappone, M., Swanson, D.W., Miller, S.L., and Bohnsack, J.A. 2003. Benthic habitat mapping in the Tortugas region. *Marine Geodesy*, 26:19-34.

- Freeman, M.C. 1995. Movements by two small fishes in a large stream. *Copeia*, 1995: 361-367.
- Frost, S.K. and Frost, P.G.H. 1980. Territoriality and changes in resource use by sunbirds at *Leonotis leonurus* (Labiatae). *Oecologia*, 45: 109-116.
- Funk, J.L. 1957. Movement of stream fishes in Missouri. *Transactions of the American Fisheries Society*, 85: 39-57.
- Gabriel, W.L., Sissenwine, M.P., and Overholtz, W.J. 1989. Analysis of spawning stock biomass per recruit: an example for Georges Bank haddock. *North American Journal of Fisheries Management*, 9: 383-391.
- Gallistel, C.R. 1990. *The Organization of Learning*. MIT Press, Cambridge, Massachusetts, USA.
- Gass, C.L. 1979. Territory regulation, tenure, and migration in rufous hummingbirds. *Canadian Journal of Zoology*, 57: 914-923.
- Gass, C.L., Angeher, G., and Cents, J. 1976. Regulation of food supply by feeding territoriality in the rufous hummingbird. *Canadian Journal of Zoology*, 54: 2046-2054.
- Gell, F.R. and Roberts, C.M. 2002. The fishery effects of marine reserves and fishery closures. World Wildlife Fund-US, Washington, D.C., USA.
- Gell, F. R. and Roberts, C. M. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology and Evolution* 18:448-455.
- Gerber, L.R., Botsford, L. W., Hastings, A., Possingham, H. P., Gaines, S. D., Palumbi, S. R., and Andelman, S. 2003. Population models for marine reserve design: a retrospective and prospective synthesis. *Ecological Applications* 13(Supplement): S47-S64.
- Gerber, L.R., Kareiva, P.M., and Bascompta, J.. 2002. The influence of life history attributes and fishing pressure on the efficacy of marine reserves. *Biological Conservation*, 106: 11-18.
- Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J., and Wilmers, C.C. 2007. LoCoH: Nonparametric kernel methods for constructing home ranges and utilization distributions. *PLoS ONE*, e207(2): 1-11.
- GMFMC. 2008a. Public hearing draft for Amendment 29 to the reef fish fishery management plan - Effort management in the commercial grouper and filefish fisheries. Gulf of Mexico Fishery Management Council, 2203 North Lois Avenue, Suite 1100, Tampa, Florida 33607. 256 p.

- GMFMC. 2008b. Reef Fish Amendment 30B: Gag – End Overfishing and Set Management Thresholds and Targets; Red Grouper – Set Optimum Yield, Total Allowable Catch, and Management Measures; Area Closures; and Federal Regulatory Compliance. Gulf of Mexico Fishery Management Council, 2203 North Lois Avenue, Suite 1100, Tampa, Florida 33607. 433 p.
- Giocalone, V.M., D'Anna, G., Garofalo, G., Collins, K., and Badalamenti, F. 2005. Estimation of positioning error from an array of automated omni-directional receivers in an artificial reef area. *In* Aquatic telemetry: advances and applications. Proceedings of the Fifth Conference on Fish Telemetry held in Europe, Ustica, Italy, 9-13 June 2003. *Edited by* M.T. Spedicato, G. Lembo, and G. Marmulla. FAO/COISPA, Rome, 295 p.
- Gill, F.B. and Wolf, L.L. 1975. Economics of feeding territoriality in the golden-winged sunbird. *Ecology*, 56: 333-345.
- Gilliam, J.F. and Fraser, D.F. 2001. Movement in corridors: enhancement by predation threat, disturbance, and habitat structure. *Ecology*, 82: 258-273.
- Goeden, G. 1978. A monograph of the coral trout. Research Bulletin Vol. 1. Queensland Fisheries Service, Brisbane, 42 pp.
- Goodyear, C.P. 1996. Minimum sizes for red grouper: consequences of considering variable size at age. *North American Journal of Fisheries Management*, 16: 505-511.
- Goodyear, C.P. 1993. Spawning stock biomass per recruit in fisheries management: Foundation and current use. *In*: Smith, S.J., Hunt, J.J., and Rivard, D. (eds.) Risk evaluation and biological reference points for fisheries management. *Can. Spec. Publ. Fish. Aquat. Sci.* 120. pp. 67-81.
- Goodyear, C.P., and Schirripa, M.J. 1991. The red grouper fishery of the Gulf of Mexico. *Natl. Mar. Fish. Serv., SEFC, Miami Lab. Contrib. no. MIA-90/91-86*, 80 p.
- Grant, J.W.A. 1997. Territoriality. pp. 81-103. *In*: Godin, J.-G.J. (ed.) *Behavioural ecology of teleost fishes*. Oxford University Press, New York, NY, USA.
- Grant, J.W.A., Chapman, C.A., and Richardson, K.S. 1992. Defended versus undefended home range size of carnivores, ungulates and primates. *Behavioral Ecology and Sociobiology*, 31(3): 149-161.
- Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T., and DeAngelis, D.L. 2005. Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. *Science*, 310: 987-991.
- Gudger, E.W. 1929. On the morphology, coloration and behavior of seventy teleostean fishes of Tortugas, Florida. *Carnegie Institute Wash. Pap. Tortugas Lab.*, 26: 149-204.

- Gu nette, S. and Pitcher, T.J. 1999. An age-structured model showing the benefits of marine reserves in controlling overexploitation. *Fisheries Research*, 39: 295-303.
- Gu nette, S., Pitcher, T.J., and Walters, C.J. 2000. The potential of marine reserves for the management of northern cod in Newfoundland. *Bulletin of Marine Science*, 66(3): 831-852.
- Gulland, J.A. 1983. *Fish stock assessment: A manual of basic methods*. Wiley, New York City, New York, USA. 223 p.
- Hanski, I. 1982. Dynamics of regional distribution: the core and satellite hypothesis. *Oikos* 38:210-221.
- Hanski, I. 1985. Single-species spatial dynamics may contribute to long-term rarity and commonness. *Ecology* 66:335-343.
- Harestad, A.S. and Bunnell, F.L. 1979. Home range and body weight—a reevaluation. *Ecology*, 60: 389-402.
- Harrigan, P., Zieman, J.C., and Macko, S.A. 1989. Food habitats of juveniles of spotted seatrout and gray snapper in western Florida Bay. *Bulletin of Marine Science*, 44(1): 155-162.
- Harris, S., Cresswell, W.J., Forde, P.G., Trehwella, W.J., Woollard, T., and Wray, S. 1990. Home-range analysis using radio-tracking data – a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review*, 20: 97-123.
- Harvey, P.H. and Clutton-Brock, T.H. 1981. Primate home-range size and metabolic needs. *Behavioural Ecology and Sociobiology*, 8: 151-155.
- Healy, S.D. and Hurly, T.A. 1995. Spatial memory in rufous hummingbirds (*Selasphorus rufus*)—a field test. *Animal Learning and Behavior*, 23: 63-68.
- Hedger, R.D., Martin, F., Hatin, D., Caron, F., Whoriskey, F.G., and Dodson, J.J. 2008. Active migration of wild Atlantic salmon *Salmo salar* smolt through a coastal embayment. *Marine Ecology Progress Series*, 355: 235-246. doi: 10.3354/meps07239.
- Heggenes, J., T.G. Northcote, and Peter, A. 1991. Spatial stability of cutthroat trout (*Oncorhynchus clarki*) in a small, coastal stream. *Canadian Journal of Fisheries and Aquatic Sciences*, 48: 757-762.
- Helfman, G.S. 1993. Fish behaviour by day, night, and twilight. pp. 479 – 512, In: Pitcher, T.J. (ed.) Behaviour of Teleost Fishes. Chapman and Hall, London.

- Hettler, W.F., Jr. 1989. Food habits of juveniles of spotted seatrout and gray snapper in western Florida Bay. *Bull. Mar. Sci.* 44(1): 155-162.
- Heupel, M.R., Semmens, J.M. and Hobday, A.J. 2006. Automated acoustic tracking of aquatic animals: scales, design, and deployment of listening station arrays. *Marine and Freshwater Research*, 57: 1-13.
- Heupel, M.R., Simpfendorfer, C., and Lowe, C.G. 2005. Passive acoustic telemetry technology: Current applications and future directions. *In* Results of the VR2 workshop held on Catalina Island, Nov 28 – Dec 1, 2005. Mote Technical Report Number 1066. Mote Marine Laboratory, Sarasota, FL. Available from http://www.vemco.com/pdf/vr2_ws_proceedings.pdf [accessed November 28, 2007].
- Heupel, M.R., Simpfendorfer, C.A., and Hueter, R.E. 2004. Estimation of shark home ranges using passive monitoring techniques. *Environmental Biology of Fishes*, 71: 135-142.
- Hixon, M.A. 1987. Territory area as a determinant of mating systems. *American Zoologist*, 27: 229-247.
- Hobday, A.J. and Pincock, D. 2009. Estimating detection probabilities for linear acoustic monitoring arrays. *Advances in Fish Tagging and Marking Technology*, in review.
- Hobson, E.S. 1965. Diurnal-nocturnal activity of some inshore fishes of the Gulf of California. *Copeia*, 1965: 291-302.
- Hobson, E.S., McFarland, W.N., and Chess, J.R. 1981. Crepuscular and nocturnal activities of Californian nearshore fishes, with consideration of the scotopic visual pigments and the photic environment. *Fisheries Bulletin*, 79: 1-30.
- Holgate, P. 1971. Random walk models for animal behavior. In Patil, G., Pielou, E., and W. Walters (eds.), Statistical Ecology: Sampling and Modeling Biological Populations and Population Dynamics, vol. 2 of Penn State Statistics, pp. 1-12. Penn State University Press, University Park, Pennsylvania, USA.
- Holland, D.S. and Brazeel, R.J. 1996. Marine reserves for fisheries management. *Marine Resource Economics*, 11: 157-171.
- Holland, K.N., Lowe, C.G., and Wetherbee, B.M. 1996. Movements and dispersal patterns of blue trevally (*Caranx melampygus*) in a fisheries conservation zone. *Fisheries Research*, 25: 279-292.
- Holland, K.N., Peterson, J.D., Lowe, C.G., and Wetherbee, B.M. 1993. Movements, distribution and the growth rates of the white goatfish *Mulloidides flavolineatus* in a fisheries conservation zone. *Bulletin of Marine Science*, 52: 982-992.

- Hooge, P. N. and Eichenlaub, B. 2000. Animal movement extension to Arcview. ver. 2.0. Alaska Science Center - Biological Science Office, U.S. Geological Survey, Anchorage, AK, USA.
- Humston, R., Ault, J.S., Larkin, M.F., and Luo, J. 2005. Movements and site fidelity of bonefish (*Albula vulpes*) in the northern Florida Keys determined by acoustic telemetry. Marine Ecology Progress Series, 291:237-248.
- Humston, R., Ault, J.S., Lutcavage, M., and Olson, D.B. 2000. Schooling and migration of large pelagic fishes relative to environmental cues. Fisheries Oceanography, 9(2): 136-146.
- Humston, R., Olson, D.B., and Ault, J.S. 2004. Behavioral assumptions in models of fish movement and their influence on population dynamics. Transactions of the American Fisheries Society, 133: 1304-1328.
- Hunt von Herbing, I. and Hunte, W.. 1991. Spawning and recruitment in the bluehead wrasse, *Thalassoma bifasciatum*, in Barbados. Marine Ecology Progress Series, 72: 49-58.
- Jenness, J. 2008. Surface Tools (surf_tools.avx) extension for ArcView 3.x, v. 1.6b. Jenness Enterprises. Available from <http://www.jennessent.com/>.
- Jennings, S. and Lock, J.M. 1996. Population and ecosystem effects of fishing. *In*: M.R. Callum (ed.) Reef Fisheries. Chapman and Hall, London. pp. 193-217.
- Jennrich, R.I., and Turner, F.B. 1969. Measurement of non-circular home range. Journal of Theoretical Biology, 22: 227-237.
- Jory, D.E., and Iversen, E.S. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (south Florida): Red, black, and Nassau groupers. U.S. Fish & Wildlife Service Biological Reports, 82(11.110), 21 p.
- Kelt, D.A. and Van Vuren, D. 1999. Energetic constraints and the relationship between body size and home range area in mammals. Ecology, 80: 337-340.
- Kenchington, R.A. 1990. Managing Marine Environments. Taylor & Francis, New York, NY, USA.
- Kingsford, M.J., Leis, J.M., Shanks, A., Lindeman, K.C., Morgan, S.G., and Pineda, J. 2002. Sensory environments, larval abilities and local self-recruitment. Bulletin of Marine Sciences, 70(1): 309-340.
- Kodric-Brown, A. and Brown, J.H. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant rufous hummingbirds. Ecology, 59: 285-296.

- Koenig, C.C., Coleman, F.C., Grimes, C.B., Fitzhugh, G.R., Scanlon, K.M., Gledhill, C.T., and Grace, M. 2000. Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of shelf-edge reefs of Florida. *Bulletin of Marine Science*, 66(3): 593-616.
- Kramer, D.L. and Chapman, M.R. 1999. Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes*, 55: 65-79.
- Lacroix, G.L. and Voegeli, F.A. 2000. Development of automated monitoring systems for ultrasonic transmitters. *In Advances in Fish Telemetry. Edited by A. Moore and I. Russell*. CEFAS, Suffolk, U.K. pp. 37-50.
- Larimore, R.W., Childers, W.F., and Heckrotte, C. 1959. Destruction and reestablishment of stream fish and invertebrates affected by drought. *Trans. Am. Fish. Soc.*, 88: 261-285.
- Laundre, J.W. and Keller, B.L. 1984. Home range size in coyotes: a critical review. *Journal of Wildlife Management*, 84: 127-139.
- Lee, T.N. and Williams, E. 1999. Mean distributions and seasonal variability of coastal currents and temperature in the Florida Keys with implications for larval recruitment. *Bulletin of Marine Science*, 64: 35-56
- Lee, T.N., Clarke, M.E. Williams, E. Szmant, A.F. and Berger, T. 1994. Evolution of the Tortugas Gyre and its influence on recruitment in the Florida Keys. *Bulletin of Marine Science*, 54: 621-646.
- Leichter, J.J., Stewart, H.L., and Miller, S.L. 2003. Episodic nutrient transport to Florida coral reefs. *Limnol. Oceanography*, 48(4): 1394-1407.
- Leichter, J.J., Wing, S.R., Miller, S.L., and Denny, M.W. 1996. Pulsed delivery of subthermocline water to Conch Reef (Florida Keys) by internal tidal bores. *Limnol. Oceanogr.*, 41(7): 1490-1501.
- Lembo, G., Spedicato, M.T. Økland, F. Carbonara, P. Fleming, I.A. McKinley, R.S. Thorstad, E.B. Sisak, M. and Ragonese, S. 2002. A wireless communication system for determining site fidelity of juvenile dusky groupers *Epinephelus marginatus* (Lowe, 1834) using coded acoustic transmitters. *Hydrobiologia*, 483: 249-257.
- Lembo, G., Fleming, I.A., Økland, F., Carbonara, P., and Spedicato, M.T. 1999. Site fidelity of the dusky grouper *Epinephelus marginatus* (Lowe, 1834) studied by acoustic telemetry. *Marine Life*, 9: 37-43.

- Levin, S. and Pacala, S. 1996. Theories of simplification and scaling in ecological systems. *In*: Tilman, D. and Kareiva, P. (eds.). *Spatial ecology: The role of space in population dynamics and interspecific interactions*. Princeton, NJ: Princeton University Press.
- Lind, H. 1990. Strategies for spatial behaviour in *Helix pomatia*. *Ethology*, 86: 1-18.
- Lindeman, K.C., Pugliese, R., Waugh, G.T., and Ault, J.S. 2000. Development patterns within a multispecies reef fishery: Management applications for essential fish habitats and protected areas. *Bulletin of Marine Science*, 66(3): 929-956.
- Lokkeborg, S., Ferno, A., and Jorgensen, T. 2002. Effect of position fixing interval on estimated swimming speed and movement pattern of fish tracked with a stationary positioning system. *Hydrobiologia*, 483: 259–264.
- Løkkeborg, S., Skajaa, K., and Ferno, A. 2000. Food-search strategy in ling (*Molva molva* L.): crepuscular activity and use of space. *Journal of Experimental Marine Biology and Ecology*, 247: 195-208.
- Longhurst, A. and Pauly, D. 1987. *Ecology of tropical oceans*. Academic Press, San Diego, U.S.A. 407 pp.
- Longley, W.H. and Hildebrand, S.F. 1941. Systematic catalogue of the fishes of Tortugas, Florida, with observations on colour, habits and local distributions. *Carnegie Inst. Wash. Pap. Tortugas Lab.*, 34: 331 p.
- Lowe, C.G., Topping, D.T., Cartamil, D.P., and Papastamatiou, Y.P. 2003. Movement patterns, home range, and habitat utilization of adult kelp bass *Paralabrax clathratus* in a temperate no-take marine reserve. *Marine Ecology Progress Series*, 256: 205-216.
- Lubchenco, J., Palumbi, S.R. Gaines, S.D. and Andelman, S. 2003. Plugging a hole in the ocean: The emerging science of marine reserves. *Ecological Applications*, 13: S 3-7.
- Ludwig, D., Hilborn, R., and Walters, C. 1993. Uncertainty, resource exploitation, and conservation: Lessons from history. *Science*, 260(5104): 17 – 36.
- MacCall, A.D. 1990. *Dynamic geography of marine fish populations*. Washington Sea Grant Program, University of Washington Press, Seattle, Washington.
- MacDiarmid, A.B., and Breen, P.A. 1992. Spiny lobster population change in a marine reserve. *In*: Battershill C.N., Schiel D.R., Jones G.P., Creese R.G., MacDiarmid A.B. (eds). *Proceedings of the Second International Temperate Reef Symposium 7-10 January 1992, Auckland, New Zealand*. NIWA Marine: Wellington: 15-22.

- MacDonald, D. 1983. The ecology of carnivore social behavior. *Nature*, 301: 384-397.
- MacDonald, D., Ball, F., and Hough, N. 1980. The evaluation of home range size and configuration using radio tracking data. In C. Amlaner and D. Macdonald (eds.). *A handbook on biotelemetry and radiotracking*. Pergamon Press, Oxford, UK.
- Macpherson, E., García-Rubies, A., and A. Gordo. 2000. Direct estimation of natural mortality rates for littoral marine fishes using populational data from a marine reserve. *Marine Biology*, 137: 1067-1076.
- Mace, G.M., Harvey, P.H., and Clutton-Brock, T.H. 1983. Vertebrate home-range size and energetic requirements. pp. 32-53. *In: Swingland, I.R. & P.J. Greenwood (ed.) The Ecology of Animal Movement*, Clarendon Press, Oxford, U.K.
- Madison, D.M. 1980. Space use and social structure in meadow voles, *Microtus pennsylvanicus*. *Behavioral Ecology and Sociobiology*, 7: 65-71.
- Maher C. R. and Lott, D. F. 2000. A review of ecological determinants of territoriality within vertebrate species. *American Midland Naturalist*, 143:1–29.
- Major, P.F. 1977. Predator-prey interactions in schooling fishes during periods of twilight: a study of the silverside *Pranesus insularum* in Hawaii. *Fisheries Bulletin*, 75: 415-426.
- Mann, K.H. and Lazier, J.R. 1991. Dynamics of marine ecosystems: Biological-physical interactions in the oceans. Blackwell Publishing, U.S.A. 408 pp.
- May, R.M., J.R. Beddington, C.W. Clark, S.J. Holt, and Laws, R.M. 1979. Management of multispecies fisheries. *Science*, 205: 267-277.
- McCarthy, M.A. and Lindenmayer, D.B. 1998. Population density and movement data for predicting mating systems of arboreal marsupials. *Ecological Modeling*, 109: 193-202.
- McCauley, R.D. 1994. Distributions and levels of snapping shrimp noise in northern Australia. Report for the Defense Science and Technology Organization.
- McClanahan, T.R. and Mangi, S. 2001. The effect of a closed area and beach seine exclusion on coral reef catches. *Fisheries Management and Ecology*, 8: 107-121.
- McClellan, D.B. and Cummings, N.J. 1998. Fishery and biology of the yellowtail snapper, *Ocyurus chrysurus*, from the southeastern United States, 1962 through 1996. *Proceedings of the Gulf and Caribbean Fisheries Institute*, 49: 25-45.
- McLoughlin, P.D. and Ferguson, S.H. 2000. A hierarchical sequence of limiting factors may help explain variation in home range size. *Écoscience*, 7: 123-130.

- McLoughlin, P.D., Ferguson, S.H., and Messier, F. 2000. Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. *Evolutionary Ecology*, 14: 39-60.
- McManus, J.W., Ferrer, E.M., and Campos, W.L. 1988. A village-level approach to coastal adaptive management and resource assessment (CAMRA). Proceedings of the 6th International Coral Reef Symposium, Australia, 2: 381-386.
- McNab, B.K. 1963. Bioenergetics and the determination of home range size. *American Naturalist*, 97(894): 133-140.
- Meester, G.A., Ault, J.S., Smith, S.G., and Mehrotra, A. 2001. An integrated simulation modeling and operations research approach to spatial management decision making. *Sarsia*, 86: 543-558.
- Meester, G.A., Mehrotra, A., Ault, J.S., and Baker, E.K. 2004. Designing marine reserves for fishery management. *Management Science*, 50(8): 1031-1043.
- Metzgar, L.H. 1967. An experimental comparison of screech owl predation on resident and transient white-footed mice, *Peromyscus leucopus*. *Journal of Mammalogy*, 48: 387-391.
- Meyer, C.G. and Holland, K.N. 2005. Movement patterns, home range size and habitat utilization of the bluespine unicornfish, *Naso unicornis* (Acanthuridae) in a Hawaiian marine reserve. *Environmental Biology of Fishes*, 73: 201-210.
- Meyer, C.G., Holland, K.N., Wetherbee, B.M., and Lowe, C.G. 2000. Movement patterns, habitat utilization, home range size and site fidelity of whitesaddle goatfish, *Parupeneus porphyreus*, in a marine reserve. *Environmental Biology of Fishes*, 59: 235-242.
- Meyer, C.G., Papastamatiou, Y.P., and Holland, K.N. 2007. Seasonal, diel and tidal movements of green jobfish (*Aprion virescens*, Lutjanidae) at remote Hawaiian atolls: Implications for Marine Protected Area design. *Marine Biology*. 151: 2133-2143.
- Moe, M.A., Jr. 1972. Movement and migration of south Florida fishes. Fla. Dep. Nat. Resour. Tech. Ser. No. 69: 1-25 pp.
- Moe, M.A., Jr. 1969. Biology of the red grouper, *Epinephelus morio* (Valenciennes) from the eastern Gulf of Mexico. Florida Department of Natural Resources Marine Research Laboratory Professional Paper Series #10, 95 p.
- Moorcroft, P.R. and Lewis, M.A. 2006. Mechanistic Home Range Analysis. Princeton University Press, Princeton, New Jersey, USA. 174 pp.

- Mueller, K.W., Dennis, G.D., Eggleston, D.B., and Wicklund, R.I. 2005. Size-specific social interactions and foraging styles in a shallow water population of mutton snapper, *Lutjanus analis* (Pisces: Lutjanidae), in the central Bahamas. *Environmental Biology of Fishes*, 40(2): 175-188. 10.1007/BF00002544.
- Muller, R.G., Murphy, M.D., de Silva, J., and Barbieri, L.R. 2003. A stock assessment of yellowtail snapper, *Ocyurus chrysurus*, in the Southeast United States. FWC-FMRI Report: IHR 2003-10.
- Murawski, S.A., Brown, R., Lai, H.-L., P.J. Rago, and Hendrickson, L. 2000. Large-scale closed areas as a fishery-management tool in temperate marine systems: The Georges Bank experience. *Bulletin of Marine Science*, 66(3): 775-798.
- Musick, J.A., Harbin, M. M., Berkeley, S. A., Burgess, G. H., Eklund, A. M., Findley, L., Gilmore, R. G., Golden, J. T., Ha, D. S., Huntsman, G. R., McGovern, J. C., Sedberry, G. R., Parker, S. J., Poss, S. G., Sala, E., Schmidt, T. W., Weeks, H., and Wright, S. G. 2000. Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of salmonids). *Fisheries*, 25(11): 6-30.
- Myrberg, A.A., Jr., Montgomery, W.L., and Fishelson, L. 1989. The reproductive behavior of *Acanthurus nigrofuscus* (Forsk.) and other surgeon-fishes (Family Acanthuridae) off Eilat, Israel (Gulf of Aquba, Red Sea). *Ethology*, 79: 31-61.
- NRC (National Research Council). 1999. Sustaining marine fisheries. National Academies Press, Washington, D.C. 164 p.
- Nemtsov, S.C. 1997. Intraspecific variation in home range exclusivity by female razorfish, *Xyrichtys splendens* (family Labridae), in different habitats. *Environmental Biology of Fishes*, 50: 371-381.
- Norman, M.D. and Jones, G.P. 1984. Determinants of territory size in the pomacentrid reef fish *Parma victoriae*. *Oecologia*, 61:60-69
- North, M.J., Collier, N.T., and Vos, J.R. 2006. Experiences Creating Three Implementations of the Repast Agent Modeling Toolkit. *ACM Transactions on Modeling and Computer Simulation*, 16(1): 1-25.
- O'Dor, R., Lindholm, J., Oxenford, H., and Parsons, D. 2004. Acoustic tracking of fish: How continuous data on fish movement could change the planning of MPAs. *MPA News*, 5(9): 1-3.
- O'Neill, M.J. 1992. Effects of familiarity and place complexity on wayfinding in simulated buildings. *Journal of Environmental Psychology*, 12: 319-327.
- Odum, E.P. and Kuenzler, E.J. 1955. Measurement of territory and home range size in birds. *Auk*, 72: 128-137.

- Okubo, A. 1980. Diffusion and ecological problems: Mathematical models. Springer-Verlag, Berlin, Germany.
- Okubo, A. and Levin, S. 2001. Diffusion and ecological problems: Modern perspectives (2nd ed.), vol. 14 of Interdisciplinary Applied Mathematics. Springer-Verlag, Berlin, Germany.
- Ostfeld, R.S. 1990. The ecology of territory in small mammals. *Trends in Ecology and Evolution*, 5: 411-415.
- Owen-Smith, N. 1977. On territoriality in ungulates and an evolutionary model. *The Quarterly Review of Biology*, 52(1): 1-38.
- Palumbi, S.R. 2001. The Ecology of Marine Protected Areas. *In*: M.D. Bertness et al., (eds.) Marine Community Ecology. Sinauer, Sunderland, MA. pp. 509-530.
- Paris, C.B. and Cowen, R.K. 2004. Direct evidence of a biophysical retention mechanism for coral reef fish larvae. *Limnol. Oceanogr.*, 49: 1964-1979.
- Parrish, J.D. 1987. The trophic biology of snappers and groupers. *In*: J.J. Polovina and S. Ralston (eds.) *Tropical snappers and groupers: biology and fisheries management*. Westview Press, Boulder, Colorado. pp. 405-463.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, Jr., F. 1998. Fishing down marine food webs. *Science*, 275: 860-863.
- Payer, D.C. 1999. Influences of timber harvesting and trapping on habitat selection and demographic characteristics of American marten. Ph.D. dissertation, University of Maine, Orono.
- Peterson, J.T., and Bayley, P.B. 1993. Colonization rates of fishes in experimentally defaunated warmwater streams. *Transactions of the American Fisheries Society* 122: 199-207.
- Peterson, C.H., Summerson, H.C., Thomson, E., Lenihan, H.S., Grabowski, J., Manning, L., Micheli, F., and Johnson, G. 2000. Synthesis of linkages between benthic and fish communities as a key to protecting essential fish habitat. *Bulletin of Marine Science*, 66(3): 759-774.
- Piedra, G. 1969. Materials on the biology of the yellowtail snapper (*Ocyurus chrysurus* Black). *In*: A.S. Bogdanov (ed.). *Soviet-Cuban fishery research*. Translated from Russian: Israel Program for Scientific Translations, Jerusalem, Israel. pp. 251-269.
- Pincock, D.G. and Voegeli, F.W. 2002. A quick course in underwater telemetry systems. VEMCO Ltd., Nova Scotia, Canada.

- Pitcher, T.J., Watson, R., Haggan, N., Guénette, S., Kennish, R., Sumaila, U.R., Cook, D., Wilson, K., and Leung, A. 2000. Marine reserves and the restoration of fisheries and marine ecosystems in the South China Sea. *Bulletin of Marine Science*, 66(3): 543-566.
- Plan Development Team. 1990. The potential of marine fishery reserves for reef fish management in the U.S. southern Atlantic. Snapper-Grouper Plan Development Team Report for the South Atlantic Fisheries Management Council. NOAA Technical Memo. NMFS-SEFC-261. National Oceanographic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Center, Miami, Florida. 45 p.
- Polachek, T. 1990. Year-round closed areas as a management tool. *Natural Resource Modeling*, 4: 327-354.
- Pollnac, R.B., McManus, J.W., del Rosario, A.E., Banzon, A.A., Vergara, S.G., and Gorospe, M.L.G. 2000. Unexpected relationships between coral reef health and socio-economic pressures in the Philippines: reefbase/RAMP applied. *Marine and Freshwater Research*, 51: 529-533.
- Pollock, B.R. 1982. Movements and migrations of yellowfin bream, *Acanthopagrus australis* (Gunther), in Moreton Bay, Queensland as determined by tag recoveries. *Journal of Fish Biology* 20:245-252.
- Popple, I.D. and Hunte, W. 2005. Movement patterns of *Cephalopholis cruentata* in a marine reserve in St. Lucia, W.I., obtained from ultrasonic telemetry. *Journal of Fish Biology*, 67: 981-992.
- Potthoff, M.T. and Allen, D.M. 2003. Site fidelity, home range, and tidal migrations of juvenile pinfish, *Lagodon rhomboides*, in salt marsh creeks. *Environmental Biology of Fishes*, 67: 231-240.
- Potts, G.W. 1990. Crepuscular behavior of marine fishes. pp. 221-227, In: Herring, P.J., Campbell, A.K., Whitefield, M., and L. Maddock (eds.) Light and Life in the Sea. Cambridge University Press, Cambridge, UK.
- Poucet, B. 1993. Spatial cognition maps in animals: new hypotheses on their structure and neural mechanisms. *Psychological Review*, 100: 163-182.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *American Naturalist*, 132: 652-661.
- Quinn, T.J. and Deriso, R.B. 1999. *Quantitative Fish Dynamics*. Oxford, UK: Oxford University Press: 542 pp.

- Quinn, J.F., Wing, S.R. and Botsford, L.W. 1993. Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. *American Zoologist*, 33: 537-550.
- Randall, J.E. 1967. Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography*, University of Miami, 5: 665-847.
- Rakitin, A. and Kramer, D.L. 1996. Effects of a marine reserve on the distribution of coral reef fishes in Barbados. *Marine Ecology Progress Series*, 131: 97-113.
- Restrepo, V.R. and Powers, J.E. 1999. Precautionary control rules in US fisheries management: specifications and performance. *ICES Journal of Marine Science*, 56: 846-852.
- Restrepo, V.R., Thompson, G.G., Mace, P.M., Gabriel, W.L., Low, L.L., MacCall, A.D., Methot, R.D., Powers, J.E., Taylor, B.L., Wade, P.R., and Witzig, J.F. 1998. Technical guidance on the use of precautionary approaches in implementing national standard 1 of the Magnuson-Stevens Fishery Conservation and Management Act. NOAA Technical Memorandum NMFSF/SPO-031, NOAA, USA: 54 pp.
- Ribble, D.O. and Stanley, S. 1998. Home ranges and social organization of syntopic *Peromyscus boylii* and *P. truei*. *Journal of Mammalogy*, 79: 932-941.
- Ricker, W.E. 1963. Big effects from small causes: two examples from fish population dynamics. *Journal of Fisheries Research Board of Canada*, 20: 257-264.
- Roberts, C.M. 1997a. Ecological advice for the global fisheries crisis. *Trends in Ecology and Evolution*, 12: 35-38.
- Roberts, C.M. 1997b. Connectivity and management of Caribbean coral reefs. *Science*, 278: 1454-1457.
- Roberts, C.M. and Polunin, N.V.C. 1991. Are marine reserves effective in management of reef fisheries. *Review of Fish Biology and Fisheries*, 1: 65-91.
- Robertson, D.R. 1981. The social and mating systems of two labrid fishes, *Halichoeres maculipinna* and *H. garnoti*, off the Caribbean coast of Panama. *Marine Biology*, 64: 327-340.
- Rosenberg, A., Bigford, T.E., Leathery, S., Hill, R.L., and Bickers, K. 2000. Ecosystem approaches to fishery management through essential fish habitat. *Bulletin of Marine Science*, 66(3): 535-542.
- Rothschild, B.J. 1986. *Dynamics of marine populations*. Harvard University Press, Boston, U.S.A. 271 pp.

- Russ, G.R. 2002. Yet another review of marine reserves as reef fishery management tools. Pages 421-443. *In* Sale, P.F. (ed.) Coral reef fishes, dynamics and diversity in a complex ecosystem. Academic Press, San Diego, California, USA.
- Russ, G.R. and Alcala, A.C. 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Phillipenes. *Marine Ecology Progress Series*, 132: 1-9.
- Russ, G.R., Alcala, A.C., Maypa, A.P., Calumpong, H.P., and White, A.T. 2004. Marine reserve benefits local fisheries. *Ecological Applications*, 14(2): 597-606.
- Sadovy, Y. 1994. Grouper stocks of the western central Atlantic: the need for management and management needs. *Proceedings of the Gulf and Caribbean Fisheries Institute*, 43: 43-64.
- Sadovy, Y. and Eklund, A.M. 1999. Synopsis of biological data on the Nassau grouper, *Epinephelus striatus* (Bloch, 1792), and the jewfish *E. itajara* (Lichtenstein, 1822). NOAA Technical Report. NMFS 146. 65 p.
- Sale, P.F. 1978. Reef fishes and other vertebrates: a comparison of social structures. pp. 313-346. *In*: Reese, E.S. and F.J. Ligher (eds.) Contrasts in Behaviour, Wiley and Sons, New York, NY, USA.
- Sale, P.F., Cowen, R.K., Danilowicz, B.S., Jones, G.P, Kritzer, J.P., Lindeman, K.C., Planes, S., Polunin, N.V.C., Russ, G.R., Sadovy, Y.J., and Steneck, R.S. 2005. Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology & Evolution*, 20: 74-80.
- Samoilys, M.A. 1997. Movement in a large predatory fish: coral trout, *Plectropomus leopardus* (Pisces: Serranidae), on Heron Reef, Australia. *Coral Reefs*, 16: 151-158.
- Samuel, M., Pierce, D., and Garton, E. 1985. Identifying areas of concentrated use within the home range. *Journal of Animal Ecology*, 54: 711-719.
- Sanchirico, J.N., and Wilen, J.E. 1999. Bioeconomics of spatial exploitation in a patchy environment. *Journal of Environmental Economics and Management*, 37: 129-150.
- Saunders, D. A., and Hobbs, R. J. 1991. *Nature conservation 2: the role of corridors*. Surrey Beatty, Chipping Norton, Australia.
- Schaefer, J. 2001. Riffles as barriers to interpool movement by three cyprinids (*Notropis boops*, *Campostoma anomalum* and *Cyprinella venusta*). *Freshwater Biol.* 46: 379-388.
- Schenkel, R. 1966. Zum Problem der Territorialitat und des Markierens bei Säugern – am Beispiel des Schwarzen Nashorns und des Löwens. *Z. Tierpsychol.*, 23: 593-626.

- Schirripa, M.J., C.M. Legault, and M. Ortiz. 1999. The red grouper fishery of the Gulf of Mexico: assessment 3.0. National Marine Fisheries Service, Southeast Fisheries Science Center, Sustainable Fisheries Division. SFD-98/99-56. 121 p.
- Schoener, T.W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics*, 2: 369-404.
- Schoener, T.W. 1981. An empirically-based estimate of home range. *Theoretical Population Biology*, 20: 281-325.
- Schoener, T.W. and Schoener, A. 1982. Intraspecific variation in home-range size in some *Anolis* lizards. *Ecology*, 63: 809-823.
- Schroeder, R.E. 1980. Philippine shore fishes of the western Sulu Sea. National Media Production Center, Manila, 226 p.
- Seton, E.T. 1909. Life histories of northern animals. Volume 1. Charles Scribner's Sons, New York, NY, USA.
- Shapiro, D.Y., Garcia-Molina, G. and Sadovy, Y. 1994. Social system of an inshore stock of the red hind grouper, *Epinephelus guttatus* (Pisces: Serranidae). *Environmental Biology of Fishes*, 41: 415-422.
- Sharp, G.D. 1995. It's about time: new beginnings and good old ideas in fisheries sciences. *Fish. Oceanogr*, 4: 324-341.
- Shulter, D. and P.J. Weatherhead. 1992. Surplus territory contenders in male red-winged blackbirds: where are the desperados? *Behavioral Ecology and Sociobiology*, 31: 97-106.
- Simpendorfer, C.A., Heupel, M.R., and Hueter, R.E. 2002. Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Canadian Journal of Fisheries and Aquatic Sciences*, 59: 23-32.
- Skellam, J. 1973. The formulation and interpretation of mathematical models of diffusional processes in population biology. In Bartlett, M. and R. Hiorns (eds.), The Mathematical Theory of the Dynamics of Biological Populations. Academic Press, New York City, New York, USA.
- Sladek-Nowlis, J.S. and Roberts, C.M. 1999. Fisheries benefits and optimal design of marine reserves. *Fishery Bulletin*, 97(3): 604-616.
- Smith, C.L. 1961. Synopsis of biological data on groupers (*Epinephelus* and allied genera) of the western North Atlantic. FAO Fish. Biol. Synop. No. 23. 61 pp.

- Smithson, E.B. and Johnston, C.E. 1999. Movement patterns of stream fishes in a Ouachita Highlands stream: An examination of the restricted movement paradigm. *Transactions of the American Fisheries Society*, 128: 847-853.
- Sobel, J.A. and Dahlgren, C.P. 2004. *Marine reserves: A guide to science, design, and use*. Island Press, Washington, D.C., USA.
- Sokal, R.R. and Rohlf, F.J. 1995. *Biometry: the principles and practice of statistics in biological research*. W.H. Freeman, New York, NY.
- St. Mary, C.M., Osenberg, C.W., Frazer, T.K., and Lindberg, W.J. 2000. Stage structure, density dependence and the efficacy of marine reserves. *Bulletin of Marine Science*, 66(3): 675-690.
- Stamps, J.A. 1992. Simultaneous versus sequential settlement in territorial species. *American Naturalist*, 139: 1070-1088.
- Stamps, J.A. and Krishnan, V.V. 1999. A learning based model of territory establishment. *The Quarterly Review of Biology*, 74(3): 291-318.
- Stander, P.E. 1991. Demography of lions in the Etosha National Park, Namibia. *Madoqua*, 18: 1-9.
- Starck II, W.A. 1971. Biology of the gray snapper *Lutjanus griseus* (Linnaeus), in the Florida Keys.
- Steingrimsson, S.Ó. and Grant, J.W.A. 2003. Patterns and correlates of movement and site fidelity in individually tagged young-of-the-year Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 60(2): 193-202.
- Stenger, J. 1958. Food habits and available food for ovenbirds in relation to territory size. *Auk*, 75: 335-346.
- Stewart, B.D. and Jones, G.P. 2001. Associations between the abundance of piscivorous fishes and their prey on coral reefs: implications for prey-fish mortality. *Marine Biology*, 138: 383-397.
- Stott, B. 1967. The movements and population densities of roach (*Rutilus rutilus* (L.)) and gudgeon (*Gobio gobio* (L.)) in the River Mole. *Journal of Animal Ecology*, 36: 407-423.
- Sumaila, U.R. 1998. Protected marine reserves as fisheries management tools: a bioeconomic analysis. *Fisheries Research*, 37: 287-296.

- Suman, D., Shivilani, M., and Milon, J.W. 1999. Perceptions and attitudes regarding marine reserves: a comparison of stakeholder groups in the Florida Keys National Marine Sanctuary. *Ocean & Coastal Management*, 42: 1019-1040.
- Swihart, R.K., Slade, N.A., and Bergstrom, B.J. 1988. Relating body size to the rate of home range use in mammals. *Ecology*, 69: 393-399.
- Syms, C. and Jones, G.P. 2001. Soft corals exert no direct effects on coral reef fish assemblages. *Oecologia*, 127: 560-571.
- Synder, W.D., Jensen, W., and Cheney, C.D. 1976. Environmental familiarity and activity: aspects of prey selection in a ferruginous hawk. *Condor*, 78: 138-139.
- Szedlmayer, S.T. and Schroepfer, R.L. 2005. Long-term residence of red snapper on artificial reefs in the northeastern Gulf of Mexico. *Transactions of the American Fisheries Society*, 134: 315-325.
- Thompson, R. and Munro, J.L. 1978. Aspects of the biology and ecology of Caribbean reef fishes: Serranidae (hinds and groupers). *Journal of Fish Biology*, 12: 115-146.
- Tobias, J. 1997. Asymmetric territorial contests in the European robin: the role of settlement costs. *Animal Behaviour*, 54: 9-21.
- Topping, D.T., Lowe, C.G., and Caselle, J.E. 2006. Site fidelity and seasonal movement patterns of adult California sheephead *Semicossyphus pulcher* (Labridae): an acoustic monitoring study. *Marine Ecology Progress Series*, 326: 257-267.
- Tremain, D.M., Harnden, C.W., and Adams, D.H. 2004. Multidirectional movements sportfish between an estuarine no-take zone and surrounding waters of the Indian River Lagoon, Florida. *Fishery Bulletin*, 102(3):533-544.
- Trexler, J.C. and J. Travis. 2000. Can marine protected areas restore and conserve stock attributes of reef fishes? *Bulletin of Marine Science*, 66(3): 853-873.
- Urick, R.J. 1983. *Principles of Underwater Sound*, 3rd Edition. New York. McGraw-Hill.
- van Rooij, J. M., Kroon, F. J., and Viedeler, J. J. 1996. The social and mating system of the herbivorous reef fish *Sparisoma viride*; one-male versus multi-male groups. *Environmental Biology of Fishes*, 47: 353-378.
- Vannini, M. and Cannicci, S. 1995. Homing behaviour and possible cognitive maps in crustacean decapods. *Journal of Experimental Marine Biology and Ecology*, 93: 67-91.
- Vincenty, T. 1975. Direct and Inverse Solutions of Geodesics on the Ellipsoid with Application of Nested Equations. *Survey Review*, 23 (176): 88-93.

- Voegeli, F.A. and Pincock, D.G. 1996. Overview of underwater acoustics as it applies to telemetry. *In Underwater Biotelemetry. Edited by E. Baras and J.C. Philippart.* University of Liege, Liege, Belgium, pp. 23-30.
- Walters, C.J. 2000. Impacts of dispersal, ecological interactions, and fishing effort dynamics on efficacy of marine protected areas: How large should protected areas be? *Bulletin of Marine Science*, 66(3): 745-757.
- Walters, C.J., Pauly, D., Christensen, V., and Kitchell, J.F. 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. *Ecosystems*, 3: 70-83.
- Wang, J.D., Luo, J., and Ault, J.S. 2003. Flows, salinity, and some implications for larval transport in South Biscayne Bay, Florida. *Bulletin of Marine Science*, 72(3): 695-723.
- Warburton, K. 1990. The use of local landmarks by foraging goldfish. *Animal Behaviour*, 40: 500-505.
- Watanabe, W.O. 2001. Species profile: Mutton snapper. Southern Regional Aquaculture Center, SRAG Pub. No. 725, 9 pp.
- Watson, R.A., Alder, J., and Walters, C. 2000. A dynamic mass-balance model for Marine Protected Areas. *Fish and Fisheries*, 1: 94-98.
- Weaver, D.C. 1996. Feeding ecology and ecomorphology of three sea basses (Pisces: Serranidae) in the northeastern Gulf of Mexico. M.S. Thesis, University of Florida, Gainesville, 93 p.
- Wenz, G.M. 1962. Acoustic ambient noise in the ocean: Spectra and sources. *Journal of the Acoustical Society of America*, 34:1936-1956.
- Wenz, G.M. 1964. Curious noises and the sonic environment in the ocean. *In Marine Bio-Acoustics. Edited by W.N. Tavolga.* Pergammon Press, New York, NY, pp. 101-119.
- White, A.T., Hale, L.Z., Renard, Y., and Cortesi, L. 1994. Collaborative and community-based management of coral reefs. Lessons from experience. Kumarian Press, Connecticut, USA.
- Wilkinson, D.A., Grigg, G.C., and Beard, L.A. 1998. Shelter selection and home range of echidnas, *Tachyglossus aculeatus*, in the highlands of south-east Queensland. *Wildlife Research*, 25: 219-232.
- Wilson E. O. Sociobiology: the new synthesis. Cambridge, MA: Belknap Press, 1975. 697 p.

- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, 70(1): 164-168.
- Xiao, Y. 2000. An individual-based approach to evaluating experimental designs for estimating rates of fish movement from tag recoveries. *Ecological Modeling*, 128: 149-163.
- Young, P.H. 1963. The kelp bass (*Paralabrax clathratus*) and its fishery, 1947-1958. *California Fish and Game Fisheries Bulletin*, 122: 1-67.
- Zeller, D.C. 1997a. Patterns of movement of *Plectropomus leopardus* (Serranidae) in relation to spawning aggregations and marine protected areas, as determined by ultrasonic telemetry. Ph.D. thesis, James Cook University, Townsville, Australia.
- Zeller, D.C. 1997b. Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). *Marine Ecology Progress Series*, 154: 65-77.
- Zeller, D.C. and Russ, G.R. 1998. Marine reserves: Patterns of adult movement of the coral trout (*Plectropomus leopardus* [Serranidae]). *Canadian Journal of Fisheries and Aquatic Science*, 55: 917-924.

APPENDIX

Appendix A.1. Symbols and abbreviations used in document.

Symbol	Units	Description	Symbol	Units	Description
NTMR	<i>n/a</i>	No-take marine reserve	<i>AIC</i>	<i>n/a</i>	Akaike information criterion
DRTO	<i>n/a</i>	Dry Tortugas National Park	N_i	<i>#fish</i>	Population abundance by cohort <i>i</i>
FKNMS	<i>n/a</i>	Florida Keys National Marine Sanctuary	N_r	<i>#fish</i>	Number of recruits
RNA	<i>n/a</i>	Research Natural Area	<i>Z</i>	<i>n/a</i>	Total instantaneous mortality
ER	<i>n/a</i>	Ecological Reserve	<i>F</i>	<i>n/a</i>	Fishing mortality rate
LT	<i>n/a</i>	Localizing tendency model	<i>M</i>	<i>n/a</i>	Natural mortality rate
MCP	<i>n/a</i>	Minimum convex polygon	<i>i</i>	<i>n/a</i>	Population cohort
<i>SSB</i>	<i>lbs</i>	Spawning stock biomass	<i>a</i>	<i>yrs</i>	Age
<i>SPR</i>	<i>n/a</i>	Spawning Potential Ratio	<i>x</i>	<i>dd</i>	X-coordinate (Longitude)
Ω	<i>n/a</i>	Model domain	<i>y</i>	<i>dd</i>	Y-coordinate (Latitude)
\bar{X}	<i>dd</i>	Harmonic mean longitude	L_∞	<i>cm</i>	Maximum size
\bar{Y}	<i>dd</i>	Harmonic mean latitude	<i>k</i>	<i>n/a</i>	Brody growth coefficient
X_i	<i>dd</i>	X-coordinate (Longitude) for receiver <i>i</i>	<i>L</i>	<i>mm</i>	Length
Y_i	<i>dd</i>	Y-coordinate (Latitude) for receiver <i>i</i>	a_0	<i>n/a</i>	Constant age parameter
R_i	<i>n/a</i>	Number of detections at receiver <i>i</i>	L_m	<i>mm</i>	Length at maturity
W_i	<i>n/a</i>	Weighting factor for receiver <i>i</i>	L_c	<i>mm</i>	Length at first capture
d_i	<i>m</i>	Max detection radius (receiver <i>i</i>)	<i>W</i>	<i>g</i>	Weight
d_{max}	<i>m</i>	Maximum detection radius (all receivers)	α_{WL}	<i>n/a</i>	Constant weight parameter
Δt	<i>min</i>	Change in time (step length specified)	β_{WL}	<i>n/a</i>	Constant weight parameter

t	<i>min</i>	Time	S	<i>n/a</i>	Survivorship
τ	<i>min</i>	Change in time (step length unspecified)	a_λ	<i>yrs</i>	Maximum age
$u(x,t)$	<i>%</i>	Individual location at time t (<i>pdf</i>)	q	<i>n/a</i>	Catchability coefficient
x	<i>dd</i>	Vector indicating (x, y) position of individual	f	<i>#vessels</i>	Fishing effort
$\vec{\mathbf{x}}$	<i>m</i>	Unit vector pointing towards home range center	I_0	<i>n/a</i>	Bessel function
c	<i>n/a</i>	Magnitude in bias in movement direction	p	<i>n/a</i>	Subunit incrementor
d	<i>n/a</i>	Diffusion coefficient	n	<i>n/a</i>	Total number of subunits
∇	<i>n/a</i>	Gradient operator	Y_n	<i>#fish</i>	Yield in numbers
X_H, Y_H	<i>dd</i>	Coordinates of home range center	Y_w	<i>lbs</i>	Yield in Weight
b	<i>n/a</i>	Localizing tendency parameter	m_L	<i>%</i>	Probability of sexually maturity at length L
K	<i>n/a</i>	Localizing tendency distribution	θ_L	<i>%</i>	Probability of being male at length L
κ	<i>n/a</i>	Concentration parameter	E	<i>#eggs</i>	Total egg production
ϕ	<i>radians</i>	Direction of movement	α_E	<i>n/a</i>	Fecundity parameter
$\hat{\phi}$	<i>radians</i>	Direction towards home range center	β_E	<i>n/a</i>	Fecundity parameter

VITA

Nicholas Alexander Farmer was born in Oceanside, California, on December 20, 1978. His parents are Paul Farmer and Kathryn Farmer. He graduated valedictorian from Lake Braddock Secondary School in Burke, Virginia in 1997. During the summer of 2000, he worked as a National Science Foundation Research Experience for Undergraduates research fellow at the University of Hawai'i at Manoa and the Hawai'i Institute of Marine Biology. He was a Murchison scholar at Trinity University in San Antonio, Texas and graduated Summa Cum Laude in 2001 with a B.S. in Honors Biology and a B.A. in English. In August 2001, he was admitted as a National Defense Science and Engineering Graduate Fellow and University of Miami Doctoral Fellow to the Graduate School of the University of Miami's Rosenstiel School of Marine and Atmospheric Science. He was awarded a Ph.D. in Marine Biology and Fisheries in May 2009.

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