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Modeling the spatial distribution of commercially important reef fishes on the West Florida Shelf

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ABSTRACT

Understanding the spatial distribution of a species is an important precondition to successfully managing marine populations. For reef fishes, this is of particular importance due to the patchy nature of reef communities. This study estimated the spatial distribution of five reef fish species on the West Florida Shelf: gag grouper (*Mycteroperca microlepis*), mutton snapper (*Lutjanus analis*), red grouper (*Epinephelus morio*), red snapper (*Lutjanus campechanus*), and vermilion snapper (*Rhomboplites aurorubens*). Estimation was done by combining large-scale fishery-dependent catch per unit of fishing effort with small scale fishery-independent video survey observation. Catch per unit of fishing effort was obtained from vessel logbook data while video observations of reef fish presence–absence and relative abundance were made by stratified random sampling on known reef and hard-bottom habitat in the Gulf of Mexico. Relative abundance estimates showed different abundance patterns for the five species depending on depth and geographical area. Variogram modeling suggested that gag grouper, mutton snapper, and red grouper were spatially autocorrelated on reef or hard-bottom habitats at short ranges of between 0.87 and 0.95 km, while red and vermilion snapper were found to be randomly distributed. Range estimates for gag grouper, mutton snapper and red grouper were supported by variograms of depth soundings in the Gulf which produced range estimates of between 1.56 and 6.34 km. Combining the relative estimates of abundance from catch per unit of effort with the spatial autocorrelation parameters from video surveys allowed us to provide stochastic fish abundance estimates at scales of about 2 km^2.

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1. Introduction

The spatial distribution of marine fish populations is important for developing appropriate management strategies such as defining essential fish habitat (Manderson et al., 2002) and establishing marine reserves (Jones, 2002). This is particularly true for reef fish assemblages, which can be characterized on multiple scales, typically occupying various patchy habitats during the course of their life, as well as being subjected to spatially heterogeneous predatory threats and environmental conditions (Sale, 1998). A large amount of information is available describing the spatial ecology of reef fish behavior including observations of feeding (Bullock and Smith, 1991; McCawley and Cowan, 2007), social behavior (Mueller et al., 1994; Lindberg et al., 2006), and reproduction (Coleman et al., 1996; Domeier and Colin, 1997). Reef fish spatial distribution and habitat use have been studied by analyzing fish stomach content, fish maturity state, tagging data, seasonal changes in spatial catch per unit of effort, and behavioral observations in the field (Ciannelli et al., 2008; Pittman and Brown, 2011; Topping and Szedlmayer, 2011). This wide body of information is useful for developing hypotheses about potential mechanisms by which fish are spatially distributed in a particular fashion at a given time.

As fisheries stock assessment and marine resource management moves toward a more holistic ecosystem approach (Link, 2002; Garcia et al., 2003), information that can be used to quantify how reef fish species are spatially distributed will become more necessary. In the absence of this information, many regional planners have historically used maps of "hard-bottom" as a proxy for marine biodiversity or spatial abundance patterns, due to the high correlation between these factors and hard-bottom habitat (DeBlieu et al., 2005; Ferdana et al., 2006). In many cases, however, the absence of this information has forced managers and biologists to ignore space altogether in population modeling and management, by assuming, for example, that all fishes have similar life history parameters throughout their range, and all are equally susceptible to fishing gear. These are poor assumptions because although it is possible to define the parameters that characterize a system at any scale, these parameters may be highly scale dependent. This is particularly

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important for reef fish systems, which are characterized by high variability in time and space (Chesson, 1998).

The spatial pattern of distribution of an organism can be characterized by its numerical abundance in a given location, and the degree to which the abundance in one location is related to other locations. This pattern of spatial relatedness or spatial autocorrelation is often quantified by a statistical tool called the variogram. Spatial autocorrelation measures how dependent or related observations are in geographic space. The variogram reflects the strength and shape of spatial autocorrelation and is an essential tool for mapping and statistically-based interpolation. Given a known abundance and a calculated variogram, it is possible to map the observed spatial distribution of an organism, and create simulated spatial datasets that reflect the abundance and distribution of a resource. These simulated datasets are useful tools for evaluating sampling strategies, bioeconomic modeling, and management strategy evaluation.

The objective of this study is to model the spatial distribution of five reef fish species on the West Florida Shelf in the Gulf of Mexico: gag grouper (*Mycteroperca microlepis*), mutton snapper (*Lutjanus analis)*, red grouper (*Epinephelus morio*), red snapper (*Lutjanus campechanus*), and vermilion snapper (*Rhomboplites aurorubens*). This is done in a two-step process by coupling the estimation of a spatial catch per unit effort (CPUE) index of abundance with a Gaussian random field simulation that uses the variogram parameter estimates (Cressie, 1993) from video survey data. Results of these analyses are contrasted with current knowledge on the ecology and biology of these reef fish species and with the spatial autocorrelation characteristics of reef and hard bottom habitats of the West Florida Shelf. Ultimately, the analysis was conducted to provide a spatial distribution of reef fish abundance to a spatially explicit individual-based bioeconomic model that represents the interaction between fisher behavior and fish population dynamics on the West Florida Shelf.

2. Materials and methods

2.1. Relative fish abundance from catch per unit of fishing effort

The National Marine Fisheries Service (NMFS) Coastal Logbook Program collects data by fishing trip on catch and effort for permit holding commercial fishing vessels in the Gulf of Mexico since 1993. Since the program's inception, participants have reported their spatial location as blocks of longitude and latitude rounded to the nearest degree. These one degree longitude by one degree latitude spatial areas, are referred to as NMFS statistical grids. The Coastal Logbook Program started to collect information on fishing depth starting in 2005. Since depth strata run parallel to the coast in the Gulf of Mexico, depth is spatially correlated to the distance away from the shore and can be used as proxy for distance offshore.

The intersection of NMFS statistical grids with contours of like depths can be used to define smaller spatial areas in the Gulf of Mexico in order to determine more precisely where fishing effort occurred. This more precise definition of space was used to estimate a CPUE index for various spatial partitions of the West Florida Shelf. Three years for which depth was recorded (2005 through 2007) were grouped together into fifteen different combinations of depth and statistical grid partitions, hereafter referred to as depth/area strata. These depth/area strata were defined by the interaction of five 20 m depth strata with the aggregation of NMFS statistical grids into three overall areas: grids 1 and 2, grids 3 through 7, and grids 8 through 10 (Fig. 1). Hereafter, the combination of grids 1 and 2 will be referred to as "southwest Florida," combination of grids 3 through 7 will be referred to as "West Florida", and combination of grids 8 through 10 will be referred to as "Florida pan-handle."

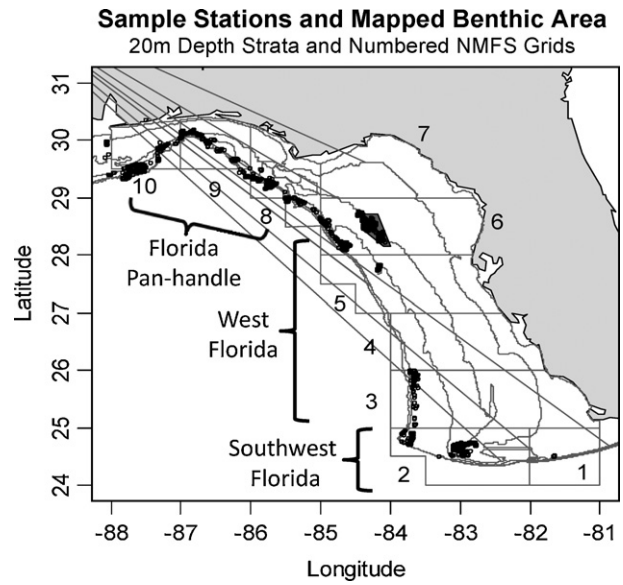

Fig. 1. West Florida Shelf in the Gulf of Mexico showing 20 m depth/area strata, small circles representing SEAMAP reef fish sampling stations, and gray polygon representing the benthic portion of the Gulf that was acoustically sampled.

This grouping was done to provide enough observations to each of the spatial stratifications. Generalized linear models (GLM) were developed using logbook data from these years and the least square means were estimated for each depth/area stratum.

The logbook data contained many zero observations because for a given species in the logbook data, there were a large number of unsuccessful units of effort, meaning strata that contained a positive effort value and zero catch. Analysis of such data using a standard GLM approach could lead to bias in the analysis. As a result, the delta-lognormal method (Pennington, 1983, 1996; Lo et al., 1992) was used to overcome this problem (Stefansson, 1996), where a binomial model was used to model whether the species of interest was encountered on a fishing trip, and a lognormal model was used to model the CPUE using records with positive catches for the species of interest. Results from these two models were then combined to generate an index of relative abundance (Hinton and Maunder, 2004).

CPUE from the commercial handline fleet was used to estimate each index, where catch equaled the kilograms of fish of a given species caught, and effort was a measure of the days away at sea times the number of crew on each vessel. Standardized CPUE for only the handline gear was estimated because this gear type was the most commonly used in the reef fish fishery. This assumed that a standardized index derived from handline data (73% of trips) alone provided an appropriate standardized index for all stocks considered. Other gears that participate in the commercial demeral fishery in the Gulf of Mexico include bottom longline (about 11% of trips), trolling (16% of trips), diving (5% of trips) and other (1% of trips).

2.2. Spatial autocorrelation of fish abundance

The Southeast Area Monitoring and Assessment Program (SEAMAP) is a joint state/federal program which conducts fishery independent surveys throughout the federal waters of the southeastern United States. One component of this program is the offshore reef fish video survey which samples reef fishes on the Gulf of Mexico hard bottom, reef areas, and banks, including ridges and pinnacles found on the continental shelf, shelf edge and slope (Dennis and Bright, 1988; Moe, 1963; Rezak et al., 1985; Smith et al., 1975). The survey uses a four camera array baited with squid, where

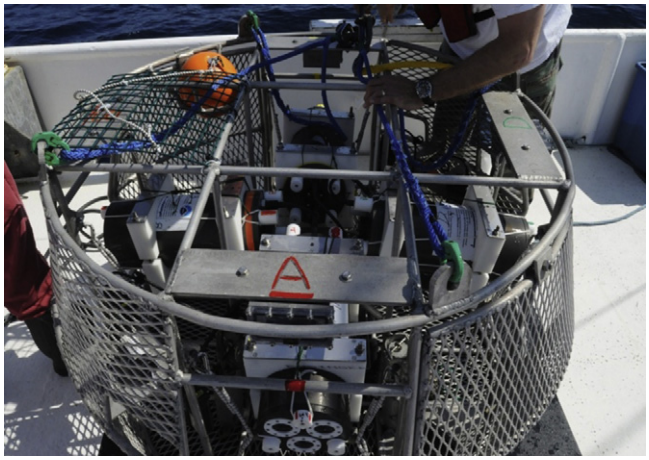

Fig. 2. Four camera array sampling gear used by the SEAMAP survey.

the four camcorders are mounted on the same platform orthogonal to each other (Fig. 2). For a given sampling station, all four cameras are placed at one depth about 20 cm from the seafloor facing reef structure. Depth is not changed during a survey event on a station. Variability in depth, however for the entire survey is achieved by sampling various stations of different depths ranging from 10 m to 200 m. Sampling time is 20 min. One of the four tapes are randomly selected (provided it offers a clear, unobstructed view), and samplers identify and enumerate all species. Sample sites are selected in two stages. Primary sampling units are blocks 10 min of latitude by 10 min of longitude and selected by stratified-random sampling. Secondary sampling units are approximately 100 m square and are randomly selected from those selected primary sampling units that are confirmed using acoustics to contain hard bottom habitat.

The data collected during this survey was used to estimate a variogram for each species. The variogram is a function which is used to quantify spatial autocorrelation. Variogram parameter estimates provide a statistical means of predicting abundance in locations that are not sampled, and allow for the creation of simulated patterns of abundance. There are two different types of variograms: the empirical and the theoretical variogram. The empirical variogram measures the geographic distance and correlation between each observation and all of the additional observations located within an a priori specified range. A plot of these distances and correlations is often called a variogram cloud (Cressie, 1993; Diggle and Ribeiro, 2007). In this study, the empirical variogram cloud was binned and a functional relationship called the theoretical variogram was fit to the binned empirical variogram data using ordinary least squares. For this study, a spherical relationship was fit to the variogram cloud, $V_Y(u) = \Gamma^2 + \sigma^2 \{1 - \rho(u)\}$ where $\rho(u) = \begin{cases} 1 - \frac{3}{2}\left(\frac{u}{\phi}\right) + \frac{1}{2}\left(\frac{u}{\phi}\right)^3 : 0 \le u \le \phi \\ 0 : u > \phi \end{cases}$ is a monotonic decreasing function. The spherical variogram has three parameters: the nugget (Γ), partial sill (σ), and range (ϕ). The variable u in the equation represents the binned distance between data points. The nugget parameter represents sampling variability at short distances that could not be described by the variogram. The partial sill, together with the nugget, represents the sample variance of the whole dataset. The range parameter represents the distance within which observations are spatially autocorrelated. Variogram modeling statistically assumes the data is stationary and has isotropy. Data violates the stationary assumption if there is another trend in the data where the mean and variance are not exclusively a function of location. Isotropy occurs when there are no directional trends in the data. Prior to fitting a variogram, data was tested to ensure it was stationary and had isotropy. Data that did not have isotropy was fit using an omni-directional variogram.

SEAMAP sampling efforts on the West Florida Shelf were divided into two main groups: one north of 27.5° latitude and the other south of 27.5° latitude with a spatial gap between the two groups. In order to avoid having this spatial gap potentially misinterpreted by the variogram, data was used from either north or south of the spatial gap depending on the species and its relative abundance in each region. Data from the northern group was used to fit variograms for gag grouper, vermilion snapper, and red snapper, while data from the southern group were used to estimate variograms for mutton snapper and red grouper. Data from 1996 to 2007 were included in our analysis, however in any given year, the number of presence observations was too sparse and it was not possible to estimate reasonable empirical variograms for each species by year. Aggregating the raw data across years is not appropriate due to annual changes in abundance and sampling location. Therefore, individual variogram clouds were estimated for each year and species, and aggregated by species across all years (Walter et al., 2007). Binned empirical variograms for each species were estimated from the combined variogram clouds.

For the five species considered, the statistical distribution of the SEAMAP video survey minimum count (abundance) data was highly skewed toward low values due to the high number of zero observations. Therefore, the spatial structure of fish abundance was difficult to describe with variograms calculated from the abundance data. The presence of such zero inflated data is a common issue in ecology and must be modeled appropriately (Martin et al., 2005). Many ecological applications of spatial statistics have used both presence–absence and abundance data when present, to estimate discrete variograms (Warren, 1998; Kint et al., 2003; Wagner, 2003; Bellier et al., 2007). These studies have found that both a variogram using presence–absence information and a variogram of un-transformed relative abundance that does not model zeros produce similar range estimates, and proportional nugget and sill estimates. Consequently only presence–absence information was used to fit empirical and theoretical variograms in this study. The binned empirical variograms contained a large amount of variance. As a result, the fit of the spherical theoretical variogram model to the empirical variogram was highly sensitive to the initial starting guess values of the three parameters (range, partial sill, and nugget). Consequently, a sensitivity analysis was conducted to determine initial starting guesses and bounds to fit the theoretical variogram, and bin interval to smooth the empirical variogram. A series of corresponding empirical and theoretical variograms were fit using all possible combinations from an array of potential starting parameters. Starting range values were 1.0, 2.0, and 3.0 km based on the knowledge that adult snapper and grouper species typically have a short distanced home range, in which they spend most of their time (Sale, 1998; Chapman and Kramer, 2000; Meyer and Holland, 2005; Jones, 2007; Pina-Amargos and Gonzalez-Sanson, 2009; Munoz et al., 2010). Starting nugget values were 0, 0.2 times the partial sill, and 0.4 times the partial sill. For each combination of starting parameter, the following bin sizes over which to aggregate the variogram cloud were considered: 30, 25, 20, 15, and 10. Bounded non-linear least squares (Bates and Watts, 1988) was used for our analysis where the parameter starting guesses and bounds of the fitting algorithm were informed by results of the sensitivity analysis.

2.3. Stochastic spatial simulation of fish abundance

Estimates of fish abundance on the West Florida Shelf were modeled stochastically by combining the results from the standardized Delta model of CPUE with those from the variogram estimates of video survey data. This was done by stochastically apportioning

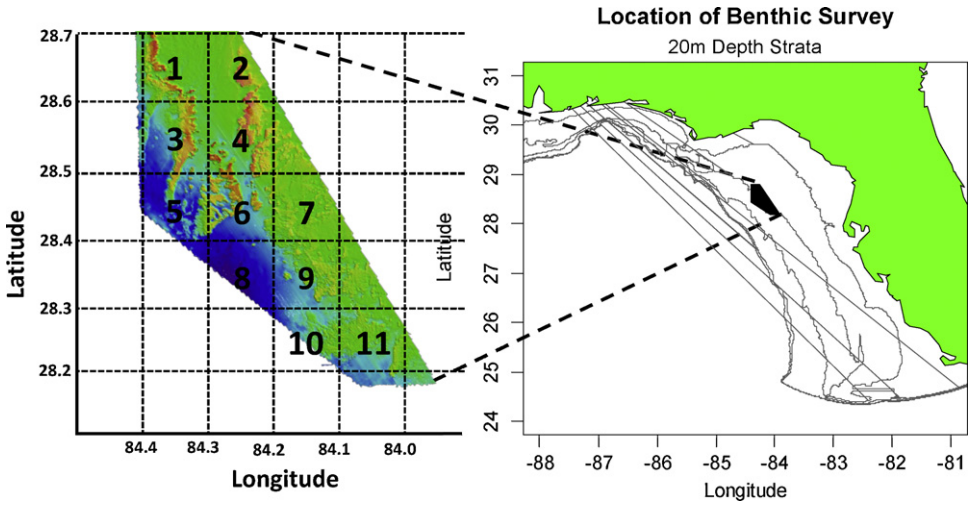

Fig. 3. Benthic portion of the West Florida Shelf sampled where darker shades represent areas of shallower relief. Sample space is partitioned into the 11 areas for the estimation of variograms.

the relative fish abundance for each area/depth strata into 1 min latitude by 1 min longitude grids. On the grid within each area/depth strata, a Gaussian model was used to simulate a random field using the species-specific variogram parameters (range, sill, and nugget) (Wood and Chan, 1994; Diggle and Ribeiro, 2007). These simulations were done using a Cholesky decomposition of the covariance matrix of parameters estimated by each variogram to spatially distribute adult abundance (Golub and Van Loan, 1996). The resulting random field was used to apportion abundance to each grid cell. The function called "Gaussian Random Field" (Ribeiro and Diggle, 2001) in The R Project for Statistical Computing (R Development Core Team, 2011) was used to conduct these simulations.

2.4. Benthic analysis

Estimates for the range of autocorrelation of reef fish habitat were obtained by fitting variograms to ocean seafloor depth sounding data collected from a portion of the Florida Middle Grounds (Grids 3 through 7 in Fig. 1). Data were collected along a continuous swath perpendicular to ship direction using a Kongsberg Simrad EM3000 (300 kHz) multibeam sonar system. The data were cleaned of bad navigation and depth soundings, and the resulting soundings were gridded onto a common grid (Weaver et al., 2006). The gridded depth sounding data of the sample area was stratified into 11 groups (Fig. 3). For each group, a variogram was estimated using 30,000 randomly selected samples of data soundings. Data was parsed in this manner to obtain a representative sample of the area studied while satisfying the memory constraints of the estimating variogram algorithm.

3. Results

Spatial CPUE indicated that in southwest Florida and the Florida pan-handle, gag and red grouper were more abundant at deeper depths, with a peak in abundance around 60 m, whereas on the Florida middle grounds, where they are more widely distributed, gag and red grouper were more abundant at shallower depths (20–40 m) (Fig. 4). Mutton snapper was most abundant in southwest Florida, with higher abundances at depths less than 80 meters. In west Florida, mutton snapper abundance was highest at deeper depths (80 m), with little abundance found in the Florida pan-handle. Red and vermilion snapper were more abundant in the Florida panhandle, with abundance increasing with depth for vermilion snapper, and decreasing with depth for red snapper. For southwest Florida and west Florida, highest relative abundances of red and vermilion snapper were both found at depths of between 60 and 100 m.

Prior to fitting variograms, tests for isotropy indicated that for gag grouper, the majority of the spatial autocorrelation was present in the 45° direction. As a result, variogram analysis for gag grouper utilized a directional variogram. No violation of the isotropy assumption was found for mutton snapper, red grouper, vermilion snapper, or red snapper. As a result, omnidirectional variograms were fit for the other species. During the sensitivity tests for vermilion snapper and red snapper, the model was not able to estimate parameter values and instead returned the starting parameters as the final parameter estimates. This suggests that the presence or absence of vermilion and red snapper in space may not be autocorrelated within the spatial scales explored using the video survey data. For those species found to exhibit spatial autocorrelation (gag grouper, mutton snapper, and red grouper), starting parameter values had little effect on the estimation. When left unbounded, however, the algorithm provided a fit with nugget and range parameter values that seemed unreasonably high. In order to obtain a biologically meaningful set of theoretical variogram parameters, while ensuring objectivity in the model fit, bounded non-linear least squares was used for our analysis. The results of the sensitivity analysis were used to provide the non-linear least squares fitting algorithm a range of bounds and a starting value for fitting the theoretical variogram.

The empirical variogram data for each species supported the placement of the nugget at zero, given the presence of data at or near the origin. Fixing the nugget at zero is a common practice in geostatistical modeling due to the large number of factors which may influence the estimation of the nugget including measurement error, unmeasured short-range spatial variation, sampling effects, and the choice of model fitted to the sample variogram (Cressie, 1993; Atkinson, 1997; Chiles and Delfiner, 1999; Fortin and Dale, 2005). Limited sampling at short distances, where much of the strongest spatial correlation frequently occurs, contributed to this decision. Final model fits estimated the range as 0.90 km for gag grouper, 0.87 km for mutton snapper, and 0.95 km for red grouper. Sill estimates were 0.14 for gag grouper, 0.31 for mutton snapper, and 0.31 for red grouper (Fig. 5). Due to the difficulty in estimating the nugget parameter, we recommend the SEAMAP program

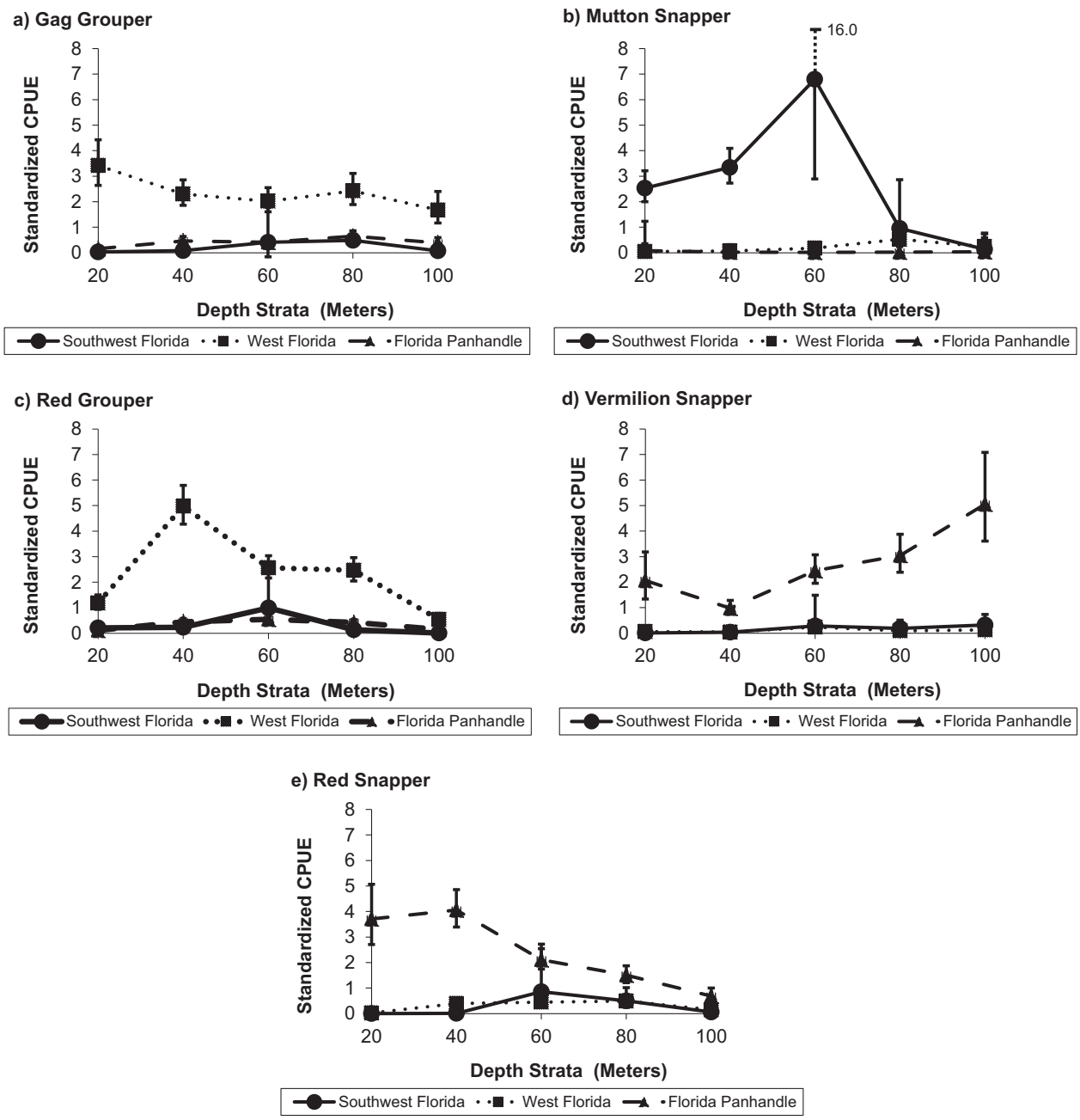

Fig. 4. Standardized spatial CPUE model fits with lower and upper confidence intervals by depth strata and grouped NMFS statistical grids on the West Florida Shelf.

increase sampling efforts at short distances in some places in order to increase the precision and accuracy of the nugget parameter estimate.

A realization of fine scale abundance distribution from the Gaussian random field simulation for one of the area/depth strata on the West Florida Shelf showed how the distribution of a spatially autocorrelated species (red grouper) would differ from one that, in the absence of a fitted variogram, we assumed to be randomly distributed (vermilion snapper) over the range explored with the video survey data (Fig. 6). Abundance on the simulated map for red grouper was concentrated into a number of small patches, as determined by the range parameter, where these patches were spatially distributed such that the location of one patch relative to another was spatially autocorrelated. In comparison, the abundance realization for vermilion snapper revealed more unpredictable changes where two adjacent locations may be assigned opposing abundances.

Variogram habitat estimates of depth soundings on the Florida Middle Grounds suggested that patches of habitat in the sampling domain were autocorrelated between 1.56 and 6.34 km, with a mean of 3.03 km and standard deviation 1.36 km (Fig. 7). These range parameters were within the same order of magnitude of those estimated by the variogram models fit to the video survey data for gag grouper, mutton snapper, and red grouper that had ranges of autocorrelation between 0.87 and 0.95 km.

4. Discussion

The results of this analysis demonstrate that the spatial distribution of a marine resource can be quantified by combining

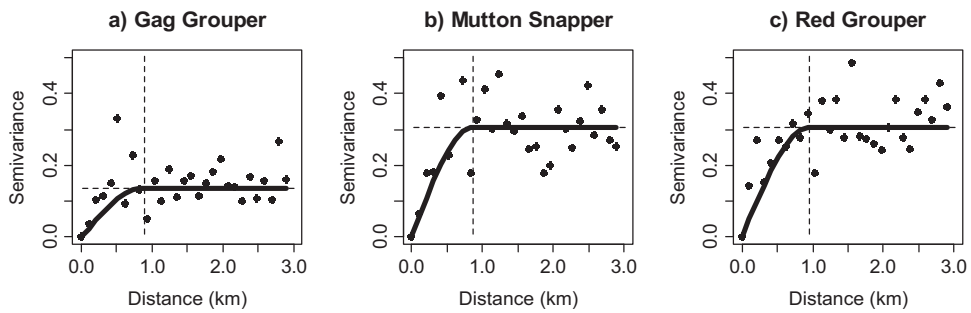

Fig. 5. Final variogram model fits for gag grouper, mutton snapper, and red grouper. Horizontal dashed lines represent the sill while vertical dashed lines represent the range. Range estimates are in kilometers, while the nugget and sill are represented in semivariance.

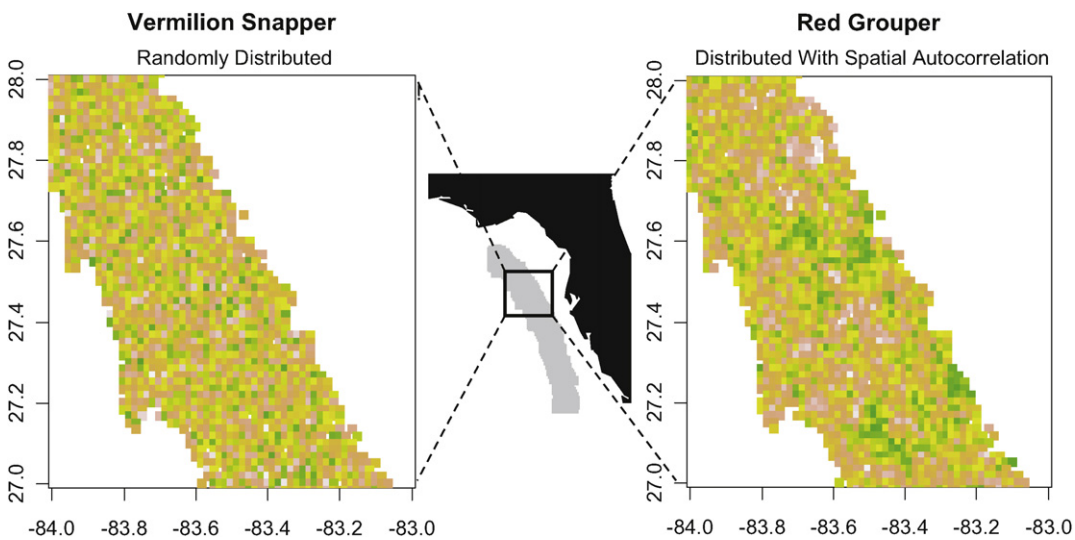

Fig. 6. One realization of fine scale abundance for a spatially autocorrelated and randomly distributed species on the Florida Middle Grounds using variogram parameters where darker shades represent areas of higher abundance. The plot with spatial autocorrelation shows grid cells with high and low abundance proximate to one another, whereas the randomly distributed plot does not show this pattern.

an estimate of fish abundance from large-scale fishery-dependent CPUE data with a simulated pattern of abundance from small scale fishery-independent video survey observation. Many natural resources exhibit patterns of spatial distribution on multiple scales (Levin, 1992; Sale, 1998). Reef fish populations are one such resource, with patchy distributions and spatial patterns that change both ontogenetically and seasonally (Sale, 1998; Chittaro, 2004). As a result, the analysis of spatial data must acknowledge the scale at which sampling took place and conform the scale used for sampling to the scale of the data analysis (Sale, 1998). Sampling and analyzing a resource at multiple spatial scales ensures that the analyst will capture both broader and finer spatial patterns of abundance that may occur. Due to the lack of extensive fine scale habitat mapping across much of the Gulf of Mexico, combining such course and fine scale observations to estimate spatial abundance is the best available approach to determine reef fish distributions in the region. Implementing a technique such as that presented in this paper can provide useful insight to managers, especially those responsible for spatial planning. This information could be particularly relevant during extreme events such as the Deepwater Horizon Oil Spill in the Gulf of Mexico by providing baseline information on the ecological state prior to the event, or by assisting economists and biologists in calculating the potential net loss in catch and revenue due to spatial fishing restrictions. Ultimately, this approach was developed and used to provide a spatial distribution of reef fish abundance to a spatially explicit individual-based bioeconomic model that represents the interaction between fisher behavior and fish population dynamics on the West Florida Shelf.

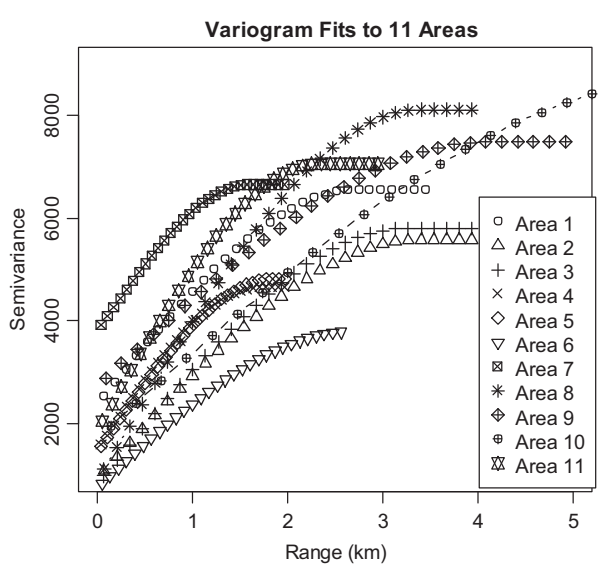

Fig. 7. Variogram fits to the 11 spatial areas shown in Fig. 2 partitioned from the benthic data.

In this study, the large scale spatial distribution of abundance across the West Florida Shelf as suggested by the spatial CPUE indices, was mostly driven by depth and latitudinal location, while

the small scale spatial autocorrelation that was calculated for each fish species (within 1 km) was found to be related to the distribution of suitable fish habitat. The fact that the range estimates for gag grouper, mutton snapper, and red grouper were within the scale of the range estimates for the benthic habitat suggests that two fish of the same species located within range distance of one another are likely to share the same benthic habitat or structure. In general, the primary determinant of reef fish presence or absence is the occurrence of suitable fish habitat (Bejarano et al., 2011; Yeager et al., 2011; Arias-Gonzalez et al., 2012). A fish's choice of habitat both throughout its life, and throughout the seasons of the year is probably a complex process determined in large part by the life history requirements of the animal.

The SEAMAP video sampling survey is an effective tool for capturing the spatial distribution of fishes that exhibit a high fidelity to reef or hard bottom structure. However, this gear largely ignores animals that may have some reef association, but live adjacent to the structure in neighboring soft bottom habitat due to the camera's focus on hard bottom. In addition, focusing sampling efforts specifically on reef areas may have confounded the autocorrelation of reef habitat with that of the fish. On the other hand, depth soundings are only a proxy for habitat so it is not unexpected that the range of autocorrelation for fish presence would be smaller than that for depth soundings. Depth soundings alone may not serve as a sufficient index of habitat quality for reef fishes. Other characteristics of the habitat, such as the type of benthos present or the relief of the habitat, in addition to other factors such as the presence of predators or prey, may better determine its suitability for these species of fish.

The three species for which spatial autocorrelation was successfully detected in the video survey data (gag grouper, mutton snapper, and red grouper) have life history characteristics that the SEAMAP sampling design was well suited to measure on a small spatial scale. Essentially, these three species exhibit strong site fidelity to areas characterized by some relief, reef, or hard-bottom structure. According to tagging studies, gag grouper are found on or a few meters above such habitat for extended periods of time (often greater than a year), either as a member of a small group or as solitary individuals (Bullock and Smith, 1991; Kiel, 2004; Lindberg et al., 2006). Red grouper occur mainly over rocky and muddy bottoms, occupying ledges, caverns and holes in limestone reefs; they are territorial and are typically found as solitary individuals with complete independence of movement from conspecifics (Jory and Iversen, 1989; Bullock and Smith, 1991; Hernandez and Seijo, 2003). Mutton snapper are also typically found solitary or in small groups where they associate with coral reefs and other rocky hard bottom areas typically near seagrass habitat where they tend to exhibit site fidelity once established (Bortone and Williams, 1986; Mueller et al., 1994; Domeier and Colin, 1997; Serafy et al., 2003).

Primary dietary choices for each of these species support their choice of habitat. Gag grouper were found to feed mostly on reef-associated fishes, epibenthic, or pelagic macroinvertebrates (Bullock and Smith, 1991; Lindberg et al., 2006). Red grouper tend to eat reef associated fishes and invertebrates (Jory and Iversen, 1989; Bullock and Smith, 1991). Mutton snapper exhibit variability in foraging style feeding in hierarchical groups on benthic crustaceans and other fish during the day and dispersing independently across seagrass beds at night to feed on nocturnally active crustaceans, the source of their primary nutrition (Mueller et al., 1994).

In contrast, vermilion and red snapper exhibit much weaker site fidelity, making it more difficult to detect spatial autocorrelation in these species using the video sampling protocol. For example, vermilion snapper may be described as generalists that spend time foraging on both benthic and planktonic invertebrates and small fishes (Grimes, 1979; Sedberry and Cuellar, 1993; Johnson et al., 2010). However, the planktonic foraging strategy employed part of the time by vermilion snapper within the water column may make this species difficult to detect by the SEAMAP video sampling array which is positioned on the benthos facing structural habitat. Therefore, the lack of spatial correlation in the SEAMAP data may be a sampling artifact and not reflective of the actual spatial distribution of this species. In order to better detect this species in the video survey, some sampling effort should be directed to the water column above and adjacent to reef areas.

Different from vermilion snapper, red snapper are more associated with hard bottom habitat, but exhibit low site fidelity (as adults) as they move from one habitat to another possibly in response to changes in food availability or seasonal changes in their environment such as passing cold fronts or changes in salinity (Diamond et al., 2007; Strelcheck et al., 2007; Diamond et al., 2010). Site fidelity in red snapper is stronger among juveniles when the threat of predation is higher. As individuals grow, age, and migrate to deeper offshore locations with lower habitat density (such as on the West Florida Shelf), site fidelity seems to decrease (Diamond et al., 2007; Patterson, 2007). Small groups of red snapper are also found to associate together and may also move together as members of sub-cohorts (Diamond et al., 2007). In addition, red snapper are opportunistic feeders which tend to forage on benthic organisms (such as portunid crabs, adult *S. empusa*), some fish, and pelagic zooplankton (Nelson, 1988; McCawley and Cowan, 2007). They deliberately leave structural relief areas for extensive periods of time, hovering a few meters off of soft or mud benthic areas in order to capture prey from the substrate (McCawley and Cowan, 2007). Due to the movement behaviors of red snapper, placement of the video camera on or facing reef locations may not effectively sample red snapper populations. Incorporation of sampling efforts on mud bottom areas adjacent to reef habitat may help improve the sampling of red snapper by the video survey.

5. Conclusion

At the larger spatial scale defined by the 15 areas classified using combined latitudinal blocks (NMFS statistical grids) and 60 foot depth increments, the spatial distribution of abundance was explained by differences in the bottom morphology of the shelf and coastal ecosystems. Some of these differences may include the gradient of the shelf slope, relative depth of the partition, and habitat type within each area. Fine scale presence–absence of reef fishes at small scales (1 km grid cells) appears to be specifically related to the presence of hard bottom habitat for the three species for which spatial autocorrelation was found in the data. Differences between species are related to the level of dependency between the presence of hard bottom and the ecology of adult reef fishes. In this paper, we have shown that knowledge on spatial distribution of abundance at these two separate scales can be combined into a spatial stochastic estimation model for relative abundance of reef fishes over the entire West Florida Shelf.

Kleisner et al. (2010) also showed that the spatial autocorrelation of pelagic fish abundance was related to the spatial autocorrelation of the habitat variables that structure the pelagic environment, namely depth and sea-surface temperature. It is worth noting that there are two orders of magnitude difference in the range of spatial autocorrelation found for pelagic fishes (50–100 km) by Kleisner et al. (2010), compared to that for demersal fishes (about 1 km) found in this paper. This is especially interesting because both studies refer to the same large marine ecosystem, the Gulf of Mexico. We believe that the results of studies such as ours, which characterize spatial autocorrelation of abundance at the population level, are critical in our attempts to match the scales of sampling, assessing and managing fish resources.

Matching such scales is clearly important to produce regulatory actions that are appropriate for the species being managed (Sale, 1998).

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