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Delineating Juvenile Red Snapper Habitat on the Northern Gulf of Mexico Continental Shelf

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Abstract. A database of resource survey trawl samples was analyzed to determine if patterns in spatial variability of estimated density of juvenile red snapper *Lutjanus campechanus* in an approximately 15 × 10^3-km^2 area in the north–central Gulf of Mexico were consistent among years from 1991 through 2000. Areas that consistently produced high (n = 1), median (n = 2), or low (n = 1) estimated juvenile red snapper density during this time series then were mapped with digital side-scan sonar, and differences in acoustic reflectance of the seabed were groundtruthed with sediment analyses of boxcore samples. Spatial variability in juvenile density estimated from trawl samples (n = 80) in summer and fall 2001 were similar to historic patterns. Juvenile density was significantly higher in areas with shell rubble or sponge habitat, thus indicating juveniles require habitat with small-scale (cm to m) complexity. Results of this study indicate our mapping techniques were effective in delineating juvenile red snapper habitat, but future studies also should examine diet, growth, and mortality of juveniles to distinguish suitable versus essential habitats.

Introduction

One of the most pressing federal fisheries management concerns in the Gulf of Mexico (GOM) region of the United States is the overfished status of red snapper *Lutjanus campechanus*. Since the 1980s, increased knowledge of GOM red snapper life history and population dynamics, improvements in stock assessment methods, and federal legislation have resulted in changes to red snapper stock biomass rebuilding schedules and management regulations. However, two themes have remained omnipresent throughout the evolution of federal management during the past two decades. The first is that despite increased fishery regulations, estimated spawning potential ratio has remained dangerously low (<10%) for the stock (Schirripa and Legault 1999). The second persistent theme is bycatch of age-0 and age-1 red snapper by the GOM shrimp fleet has been the greatest source of mortality to red snapper (Goodyear 1995; Ehrhardt and Legault 1998; Schirripa 1998; Schirripa and Legault 1999).

Fishery biologists conjectured as to the possible role of shrimp trawl bycatch in declining red snapper abundance as early as the 1960s (Moe 1963; Bradley and Bryan 1975; Gutherz and Pellegrin 1986). Recent estimates indicated mortality of juvenile red snapper due to shrimp trawls approached 90% (prior to implementation of bycatch reduction devices [BRDs]) (Goodyear 1995). Results from simulation analyses also indicated that without significant reduction (i.e., >> 50%) of juvenile red snapper bycatch in shrimp trawls, the directed red snapper fisheries must be severely restricted or closed (Goodyear 1995; Schirripa 1998; Schirripa and Legault 1999). These results provided im-

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petus for the Gulf of Mexico Fishery Management Council to require BRDs in shrimp trawls to reduce bycatch of juvenile red snapper (GMFMC 1996), and BRDs became mandatory in the western GOM beginning in May 1998 (U.S. Office of the Federal Register 63:71[April 14, 1998]:18139–18147).

The decision to require GOM shrimpers to install BRDs in their nets was supported by National Marine Fisheries Service (NMFS) trawl experiments that demonstrated a BRD design, known as the EE-Fisheye, reduced juvenile red snapper bycatch by 59% (Watson et al. 1997). More recent analyses call to question whether the EE-Fisheye, or BRDs in general, will sufficiently reduce bycatch by excluding juveniles from shrimp trawls (Engaas et al. 1999; Gallaway and Cole 1999; Rogers 1999). New concerns also have been raised regarding the fate of juveniles excluded from trawls. Additional mortality may result from embolism after being brought from depth (I. Workman, NMFS Pascagoula Laboratory, personal communication) or from predation by piscivores following the net (Broadhurst 1998). In both of these cases, survival of excluded red snapper will be less than 100%, and the effectiveness of BRDs would be compromised (Crowder and Murawski1998).

Therefore, the problem of juvenile red snapper bycatch in shrimp trawls may not have a wholly technological solution. To achieve reductions in bycatch required to increase spawning stock biomass of red snapper, it may be necessary to augment the BRD program with shrimp trawl time–area closures that would provide refuges for juvenile red snapper (Gallaway and Cole 1999; Gallaway et al. 1999). Essential to any consideration of shrimp trawl time–area closures is a fundamental understanding of juvenile red snapper habitat requirements and knowledge of where juvenile GOM red snapper essential fish habitat exists.

Juvenile red snapper (age-0 and age-1 fish) have been reported from a variety of habitats including open sand, relict shell rubble, and artificial structures with vertical relief, but results of habitat preference studies have been equivocal (Bradley and Bryan 1975; Holt and Arnold 1982; Workman and Foster 1994; Szedlmayer and Howe 1997; Gallaway et al. 1999; Szedlmayer and Conti 1999). Laboratory and small-scale in situ experiments have demonstrated juvenile red snapper display an affinity for low-relief shell rubble habitat (Szedlmayer and Howe 1997; Lee 1998; Szedlmayer and Conti 1999). Results from mesoscale (km^2) and large-scale (100 km^2) studies on the shelf, however, indicated no difference in juvenile abundance between sand-silt and shell rubble bottom types and that vertical relief was a nonsignificant factor in explaining GOM-wide variance in juvenile red snapper abundance (Workman and Foster 1994; Gallaway et al. 1999).

Our study was conducted to gain greater understanding of juvenile red snapper habitat requirements in an area on the north-central GOM continental shelf that historically has supported a range of juvenile catch rates in annual resource surveys. The objectives of our study were to (1) determine if patterns existed in the spatial and temporal variability in juvenile red snapper density estimates from NMFS trawl surveys conducted over several years; (2) map shelf areas that historically supported high, median, and low juvenile densities with digital side-scan sonar; and (3) relate geotechnical properties of the seabed to historic and contemporary juvenile red snapper density. A priori, we hypothesized the seabed in areas that historically supported high densities of juvenile red snapper would be characterized by shell rubble habitat. To test this hypothesis, we characterized the seabed of selected areas with a combination of side-scan sonar and boxcore sediment samples and then related sediment type to historic and contemporary juvenile red snapper density estimates.

Methods

Sample Area Selection

Historic juvenile red snapper catch data were obtained from the NMFS's Fall Groundfish Survey (FGS; SEAMAP Information System, National Marine Fisheries Service, Pascagoula, Mississippi), which is an annual resource survey conducted in the northern Gulf of Mexico since the early 1970s with standardized sampling gear (e.g., a single 12.8-m, four seam semiballoon shrimp trawl rigged with 2.4-m × 1-m doors, a 54.9-m bridle, and a tickler chain set 1.1 m shorter than the trawl footrope, towed at approximately 4.6 km/h). Juvenile red snapper catch data from individual trawl samples originally were sorted by time of collection (day or night; ratio of day versus night samples approximately 1:1) and imported into a geographic information system database. Trawl station locations within an area of approximately 15×10^3 km^2 off Alabama, Mississippi, and eastern Louisiana were inspected visually to determine their spatial coverage for years 1991–2000 for both day-collected and night-collected samples. We determined there was sufficient spatial replication in the annual distribution of trawl samples to permit examination of estimated juvenile red snapper density in 10' latitude by 10' longitude cells (approximately 350 km^2) as did Gallaway et al. (1999). Therefore, our original large area of the shelf was divided into 40 cells of this size. Preliminary analysis of annual differences in trawl catches within each cell revealed no consistent pattern of higher catches during day versus night sampling; thus, night and day samples were combined. After juvenile density (individuals/ha) was computed for all individual trawl samples in the combined data set, annual mean juvenile density was computed for each cell in each year of the time series.

Spatial and temporal variability in juvenile catch rates were examined to select cells that consistently produced high, median, or low juvenile densities. All cells were not sampled every year, however, and GOM red snapper year-class strength varied among years (Schirripa and Legault 1999). We attempted to account for these potential biases by standardizing annual cell-specific mean juvenile densities for a given year by scaling them to the mean density of all cells in that year. Resultant unitless values were treated as a standardized index of juvenile red snapper density. Mean index value was computed across the entire time series for cells that were sampled in at least 4 of the 10 years of the time series. These were plotted on a map of the sample region to examine visually the spatial variability in juvenile density.

Seabed Characterization

Based on results of the above analysis, the seabed of four cells that historically produced a range of juvenile red snapper density estimates was characterized by surveying an approximately 8-km² area at the center of each cell with digital side-scan sonar and then groundtruthing differences in acoustic reflectance with boxcore sediment samples. In adopting this strategy, we assumed the seabed of the center 8-km² area of each cell reflected the predominant sediment types found throughout the cell, which was based on prior studies that evidenced patterns in regional sediment characteristics were consistent over large areas (10s to 100s km²; Parker et al. 1992; Schroeder et al. 1995; Strelcheck 2001).

Our digital side-scan system consisted of a Klein (Salem, New Hampshire) model 2260NV dual frequency (100/500 kHz) tow fish, T2100 transceiver, and a high fidelity, low loss armored single conductor coaxial tow cable. Data were acquired simultaneously on port and starboard channels at 100 and 500 kHz using the Isis sonar system (version 5.75, Triton Imaging, Inc., Watsonville, California). Data from the side-scan tow fish and transceiver were georeferenced using a C&C Technologies (Lafayette, Louisiana) Ashtec global positioning system (GPS) receiver and a SatLoc (Scottsdale, Arizona) (sub-meter accuracy) differential beacon receiver. Real-time vessel position was superimposed on a nautical chart in ArcPad (ESRI, Inc., Redlands, California) and displayed to aid navigation. Following acquisition, the 100-kHz data were postprocessed using Isis and Delphmap (version 2.00.04, Triton Imaging, Inc.), and the resulting mosaic was exported as an 8-bit unsigned (0–255) georeferenced tagged image file format file. Overlapping lines were merged in mosaic creation using maximum shinethrough to preserve the most intense acoustic return.

Boxcores (45 × 45 cm) were located using differential GPS interfaced with previously acquired digital side-scan mosaics for core placement. Twenty to 25 boxcore samples were taken in groups of 3–5 replicates at 5–7 stations in each surveyed 8-km² area. Station location was stratified based on acoustic reflectance intensity. For example, if a large patch of highly reflective seabed was observed, a group of cores was collected from the center of the patch. Cores also were collected near transitions between contrasting reflectance patterns. Following collection, 2 subsamples (15-cm² area × 4-cm depth) were taken from each core for determination of sedimentologic properties (e.g., surficial grain size, organic carbon content, and carbonate content). Grain size was determined by wet sieving samples through 63-mm mesh, analyzing the fine fraction in a Micromeritics (Norcross, Georgia) Sedigraph particle-size analyzer, analyzing the coarse fraction in a Gilson (Lewis Center, Ohio) Autosiever sonic siever, and then merging the coarse and fine data sets. Organic carbon and calcium carbonate content were calculated from loss on ignition after 4 h at 500°C and 950°C, respectively (Carver 1971).

Spatial coverage of different seabed types within each cell was estimated by relating reflectance intensity from side-scan mosaics to either sand:mud ratio or calcium carbonate content depending on predominant surficial sediments. First, 10-m² areas were constructed around boxcore sample locations in side-scan mosaics. Mean pixel values then were computed for each area with Imagine (Erdas, Inc., Atlanta, Georgia) image analysis software. Linear regressions were computed to relate sand:mud ratio or percent calcium carbonate content (an index of shell content) to mean pixel value (an index of acoustic reflectance) (SAS Institute, Inc. 1996). Finally, linear regressions were applied to pixel values from side-scan mosaics to estimate percent coverage of sediment with either greater than 50% sand content or greater than 30% calcium carbonate content.

Trawl Sampling

Trawl sampling was conducted in our four study cells to examine contemporary juvenile red snapper habitat utilization patterns. Survey areas within each cell were divided into 20 stations measuring 200 m (north to south) by 2 km (east to west). Five fixed stations then were randomly selected within each cell for trawl sampling on four cruises conducted between August and December 2001. Trawl sampling was conducted onboard the NMFS's R/V *Caretta*, an 18-m former commercial shrimp trawler converted for research purposes. All samples were collected between 0.5 h after sunrise and 0.5 h before sunset. Trawls were rigged following FGS protocols as described above; however, two trawls were fished simultaneously, one each on starboard and port outriggers. Prior to trawling at a given station, a Sea-Bird (Bellvue, Washington) conductivity–temperature–depth (CTD) sensor was deployed to measure salinity, temperature, dissolved oxygen, and depth. Trawls then were deployed with an approximate scope of 6:1 cable distance to water depth and were towed at approximately 4.6 km/h for 20 min across the long (east to west) axis of trawl stations. Vessel position was superimposed on a nautical chart in ArcPad to aid navigation, and distance towed was estimated from GPS coordinates of the ship's path. Area sampled was estimated by multiplying distance towed by the combined distance of trawl openings (24 m).

Catches from both trawls were combined on deck and treated as a single sample. Samples were weighed to the nearest 0.1 kg. Following subsampling for species composition analysis (not detailed here), all reef fishes (including juvenile red snapper) and sponges (phylum porifera) were selected from the sample before it was returned to the sea. Sponges were weighed to the nearest 0.1 kg and discarded. All juvenile red snapper were frozen in plastic bags and transported back to the laboratory where they were thawed, weighed to the nearest 0.1 g, and measured to the nearest mm total length (TL).

Juvenile red snapper density was computed as the number of individuals divided by ha trawled and sponge density as mass divided by ha trawled. Differences in red snapper densities among cells and sampling cruises were tested with analysis of variance (ANOVA) (SAS Institute, Inc. 1996). Prior to analysis, density data were transformed as $Y = \log(\text{density} + 1)$ to meet the assumptions of normality and homogeneity of variances. The relationship between juvenile red snapper density and sponge density in cell 11 was tested with correlation analysis (SAS Institute, Inc. 1996).

Results

The NMFS FGS sampled 513 stations during 1991–2000 in the area of the northern GOM continental shelf bounded by 89°10'W longitude to the west and 88°W longitude to the east (Figure 1). The FGS survey design was stratified by depth. Therefore, two clusters of station locations are apparent in the data, one centered around 30°N latitude and one centered around 29°20'N latitude. The number of stations sampled in a given 10'-latitude by 10'-longitude cell in a given year ranged from 0 (many cells throughout the time series) to 10 (cells 22 and 34 in 1991 and 1999, respectively). The mean number of cells (±SE) in which at least one station was sampled in a given year was 18.1 (±1.65) (range = 14 in 1991 and 1999 to 29 in 1993), but only 26 of 40 cells were sampled in at least 4 years of the time series.

Mean juvenile density index values were highest for cells 23 and 33 (Figure 2); however, the high index value for cell 33 was skewed by one sample in 1993 for

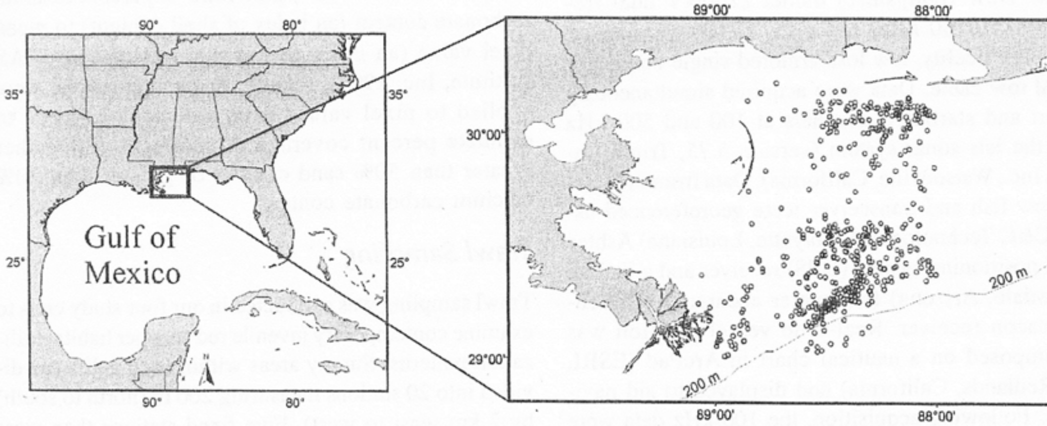

Figure 1. Map of the continental shelf in the north-central Gulf of Mexico depicting starting coordinates for trawl stations (n = 513) occupied by the National Marine Fisheries Service's Fall Groundfish Survey from 1991 to 2000. The 200-m isobath represents the shelf edge.

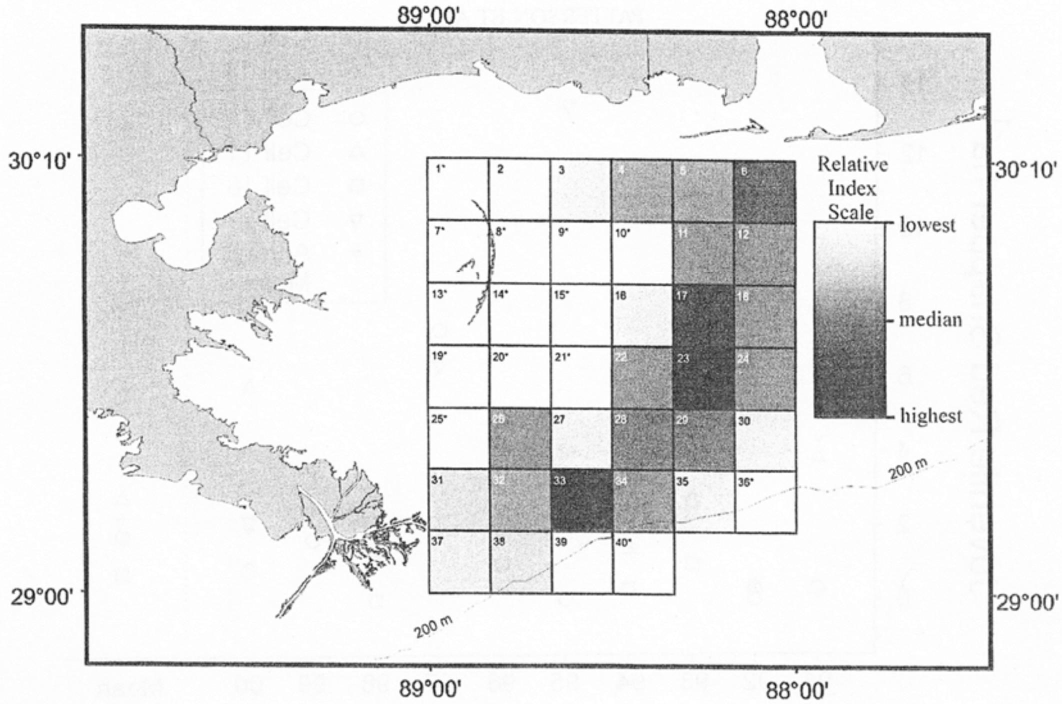

Figure 2. Map of the north-central Gulf of Mexico shelf with 10' latitude by 10' longitude cells demarcated by numbered rectangles. The relative index scale (from the figure legend) refers to annual mean juvenile red snapper among all cells for years 1991–2000 (see text for details). An asterisk following a cell's number indicates insufficient data to compute a mean index value.

which estimated juvenile density was 178.1 fish/ha. This value was 5.5-fold greater than any other trawl sample in 1993 and 2.6-fold greater than the next highest estimated density among all other samples. Therefore, cell 23 was selected as our high juvenile density cell. Cells 5 and 11 were selected randomly from a group of 10 cells whose average index values were near the median for the time series, and cell 16 was selected as our low juvenile density cell based on its low mean index value and proximity to the other three cells. Examination of juvenile density estimates for these four cells revealed cell 16 density estimates were always below the annual mean and cell 23 density estimates, while much more variable than those of cell 16, were always greater than annual mean (Figure 3). Juvenile density estimates for cells 5 and 11 also were variable, but annual mean density estimates for both were near the mean throughout the time series.

The center approximately 8-km^2 of cells 5 and 11 were surveyed with digital side-scan sonar on August 14–15, 2001, but due to technical difficulties, cells 16 and 23 were not surveyed until May 21–22, 2002. After side-scan sonar mosaics were created, boxcore samples from cells 5 and 11 were obtained during August 22–24, 2001, and for cells 16 and 23, during May 23–25, 2002. Side-scan data revealed spatial heterogeneity of seabed acoustic reflectance in cells 5 and 23, but much more uniform reflectance patterns existed in cells 11 and 16 (Figure 4).

Cells 5 and 23 were characterized by regions with both high and low reflectance corresponding to high (shell rubble) and low (sand) $CaCO_3$ content, respectively (Table 1; Figure 4). Mud content of surficial sediments in both blocks was between 3% and 10% in both shell rubble and sand habitat types. Surficial sediments of shell rubble habitats contained approximately 50% $CaC0_3$ (Table 1), which consisted mostly of fragments and entire valves of the estuarine oyster *Crassostrea*, along with a range of fully marine species, including the genera *Strombus*, *Murex*, and *Oliva*. Shell rubble habitat in both blocks tended to have 1–2 m of positive relief above the surrounding seabed. In cell 5, shell rubble habitat occurred in ridges that were 100–200 m wide, kms in length, and were oriented along northwestern to southeastern axes. The orientation of shell rubble habitat in cell 23 was more irregular than in cell 5 but comprised nearly a quarter of the area surveyed.

Side-scan data from cell 11 indicated a relatively homogeneous seabed with minimal relief. All boxcore

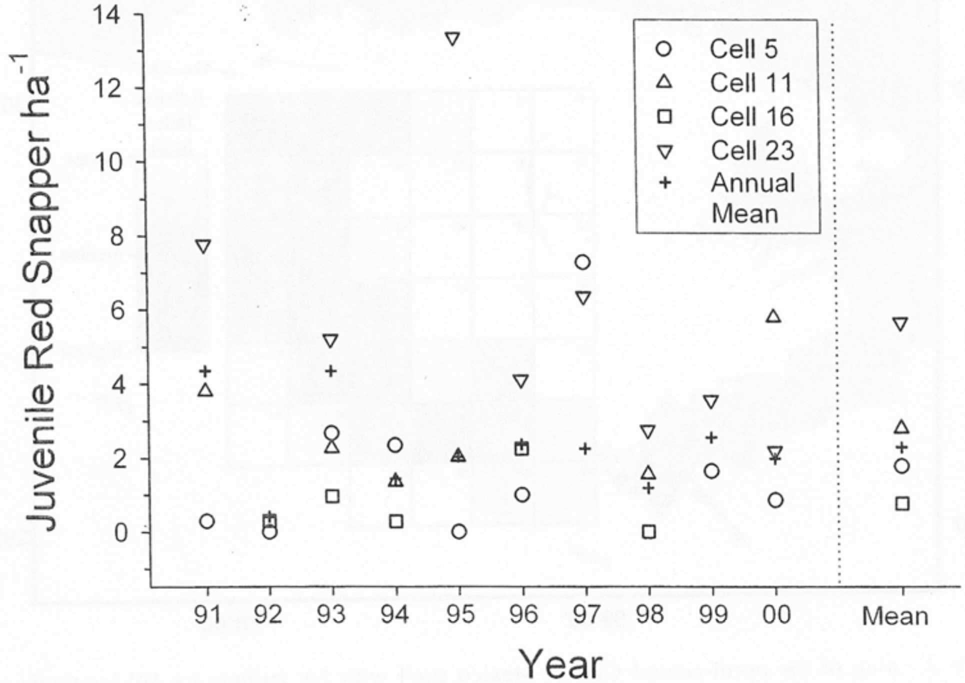

Figure 3. Annual and overall mean juvenile red snapper density estimates from the National Marine Fisheries Service's Fall Groundfish data for cells selected for seabed characterization.

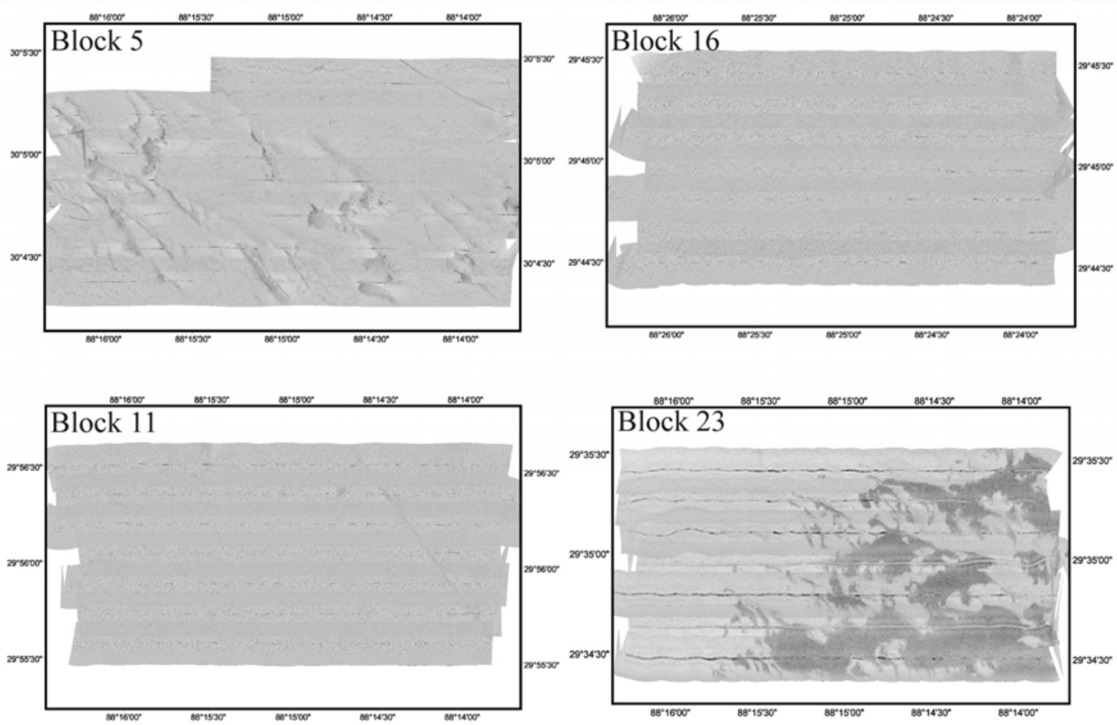

Figure 4. Acoustic reflectance mosaics of the center approximately 8-km² area of four 10' latitude by 10' longitude cells.

Table 1. Seabed geotechnical properties estimated from sediment analyses of boxcore samples taken in study cells. Percentage of survey area reported for each seabed type was extrapolated from application of linear regression equations relating sand:mud ratio (cell 16) or % CaCO3 (cells 5, 11, and 23) to reflectance (pixel) values from side-scan mosaics.

Cell	Seabed type	Mean % mud	Mean % sand	Mean % organic content	Mean % $CaCO_3$	% survey area
5	Sand	8.33	79.48	2.43	9.77	95.2
	Shell rubble ($CaCO_3$ > 30%)	7.12	38.58	3.06	51.25	4.8
11	Sand (sand:mud > 1.0)	20.23	63.63	2.62	13.52	100
16	Mud (sand:mud < 1.0)	58.22	24.51	7.75	9.52	65.7
	Sand (sand:mud > 1.0)	28.32	61.13	3.08	7.47	34.2
23	Sand	4.03	89.51	0.90	5.56	76.4
	Shell rubble ($CaCO_3$ > 30%)	3.78	45.64	3.47	47.11	23.6

samples taken in cell 11 were collected from regions with less than 30% $CaCO_3$ content and mud content of approximately 20% (Table 1). Cell 16 also was relatively low-relief and homogeneous but consisted of much muddier sediments with low $CaCO_3$ content (7–10%) (Table 1). The linear regression model computed to relate sand:mud ratio to acoustic reflectance intensity in cell 16 was

$$\text{sand:mud ratio} = 0.11 \times (\text{8-bit pixel value}) - 5.75$$
$$(F_{1;19} = 5.96, P = 0.025, R^2 = 0.36).$$

The linear regression model computed to relate carbonate content to reflectance intensity in cells 5, 11, and 23 was

$$\%CaCO_3 = 0.78 \times (\text{8-bit pixel value}) - 32.6$$
$$(F_{1;68} = 8.08; P < 0.001; R^2 = 0.66).$$

Application of these models to acoustic reflectance data allowed estimation of percent coverage of different seabed types in each cell (Table 1).

Trawl sampling cruises conducted to examine juvenile red snapper habitat utilization patterns occurred on August 19–21, September 18–20, November 6–8, and December 4–6, 2001. Mean water depths were approximately 19.5, 32.5, 36.0, and 39.5 for cells 5, 11, 16, and 23, respectively. Mean salinities measured 1 m off the bottom ranged from 33.6 to 36.3 p.s.u., and mean temperature ranged from 20.8°C to 28.7°C among all cells and cruises (Table 2). Mean dissolved oxygen generally was measured to be greater than 3.5 mg/L for all cells on all four cruises, except for cells 16 and 23 during September.

Juvenile red snapper density estimates from trawl samples were within the range of historic density estimates computed from NMFS data (Figures 3, 5). There was a significant difference in estimated juvenile density among cells (ANOVA: $F_{3;64} = 8.94$, $P < 0.001$), but neither cruise (ANOVA: $F_{3;64} = 1.69$, $P = 0.1790$) nor the interaction between cell and cruise (ANOVA: $F_{9;64} = 1.02$, $P = 0.4337$) were significant in the model. Tukey's studentized range test (a = 0.05) indicated estimated juvenile density was not significantly different among cells 5, 11, and 23, but densities in those three cells were significantly different than cell 16. In cell 11, juvenile red snapper density was significantly correlated with sponge density (Pearson's $r = 0.71$, $P < 0.001$) (Figure 6).

Total length frequency distributions indicate differences in size of juveniles captured in the different cells also existed, with two modes evident in the data (Figure 7). The first mode was between 75 and 100 mm TL in August, which shifted to between 125 and 150 mm TL by December. The second mode was between 200 and 250 mm TL in August, which shifted to greater than 250 mm TL by December. Analysis of sagittal otoliths of 20 fish sampled from each of these modes revealed otoliths of fish in the mode with shorter TL had no opaque zones (i.e., no annuli) and, thus, were judged to be age-0 juveniles (Patterson et al. 2001b). Sagittae of fish in the second mode contained one opaque and two translucent zones and, therefore, were judged to be age 1 (Patterson et al. 2001b).

In August, some age-1 fish were present in cells 5 and 11, but all fish in cell 23 appeared to be 1-year-olds. Age-0 fish were most abundant in cell 5 throughout the summer and fall but appeared to recruit to cell 11 starting in September when age-1 abundance decreased; fish sampled from cells 5 and 11 were predominantly age-0 individuals thereafter. Cell 23, on the other hand, contained mostly age-1 fish through September, but large, possibly early-spawned, age-0 fish began to recruit to this cell in November when numbers of age-1 appeared to be declining.

Table 2. Hydrographic parameters measured 1 m above the seabed during trawl sampling cruises in summer/fall 2001. Parameters are reported as the mean (SE) of 3 conductivity–temperature–depth casts made at each cell.

Cell	Date	Dissolved oxygen (mg/L)	Temperature (°C)	Salinity (psu)
5	Aug 21	No data	No data	No data
	Sep 19	3.88 (0.07)	28.7 (0.09)	33.6 (0.09)
	Nov 8	4.82 (0.12)	23.1 (0.01)	35.6 (0.01)
	Dec 4	4.85 (0.223)	20.8 (0.10)	35.1 (0.10)
11	Aug 20	No data	No data	No data
	Sep 20	4.11 (0.59)	28.4 (0.16)	35.2 (0.015)
	Nov 6	5.43 (0.14)	22.4 (0.04)	35.3 (0.01)
	Dec 5	4.99 (0.20)	21.9 (0.05)	35.9 (0.03)
16	Aug 20	3.45 (0.58)	25.0 (0.16)	36.2 (0.01)
	Sep 18	1.77 (0.03)	25.7 (0.12)	36.2 (0.03)
	Nov 7	4.83 (0.13)	23.4 (0.01)	35.7 (0.03)
	Dec 5	5.30 (0.54)	21.69 (0.17)	35.7 (0.07)
23	Aug 19	2.96 (0.19)	24.6 (0.11)	36.3 (0.02)
	Sep 18	1.84 (0.01)	25.5 (0.12)	36.1 (0.01)
	Nov 7	4.79 (0.32)	24.1 (0.01)	35.9 (0.01)
	Dec 6	5.08 (0.40)	22.7 (0.01)	36.1 (0.01)

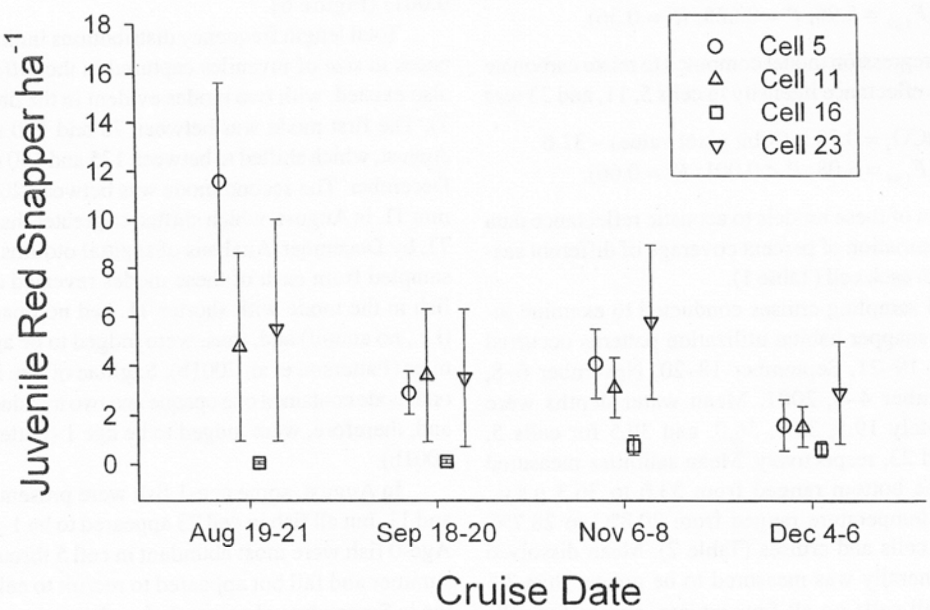

Figure 5. Mean (±SE) juvenile red snapper density (fish/ha) estimated from trawl samples taken from five stations within each of the four study cells during summer and fall 2001.

Discussion

Historic and contemporary juvenile red snapper density estimates were highest in shelf habitats with structures that provided small-scale (centimeters to meters) habitat complexity. We expected areas of the northern GOM that historically produced high numbers of juvenile red snapper in NMFS trawl samples would be characterized by low relief shell rubble habitat while areas that produced low catches were expected to have mud or sand seabed

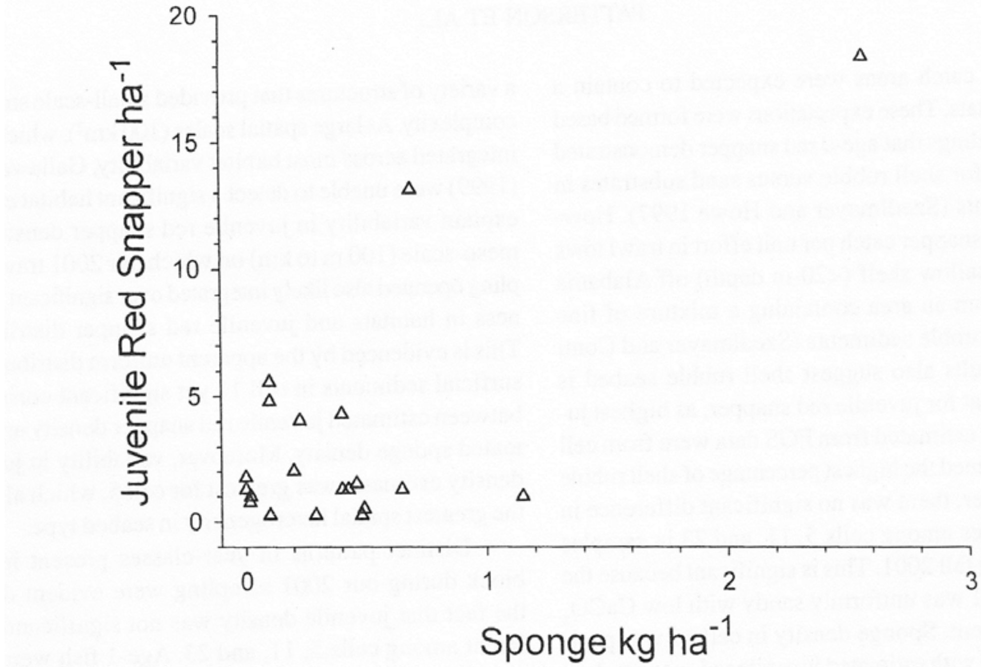

Figure 6. Scatterplot of estimated juvenile red snapper density (individuals/ha) versus estimated sponge density (kg/ha) from 20 trawl samples in cell 11 collecting during 2001 sampling cruises.

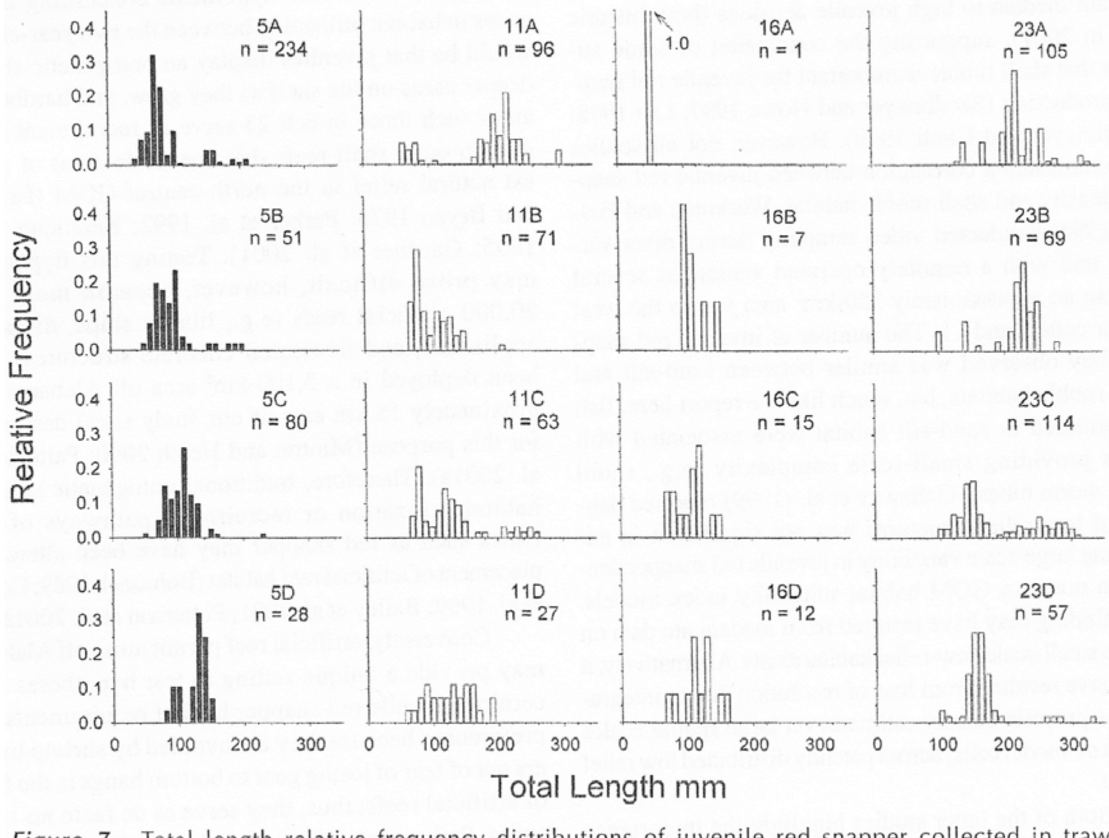

Figure 7. Total length relative frequency distributions of juvenile red snapper collected in trawl samples during 2001. Panel legends indicate cell, cruise (Cruise A, August 18–20; B, September 19–21; C, November 6–8; and D, December 4–6, 2001), and total sample size from five trawl stations.

types. Median catch areas were expected to contain a mixture of habitats. These expectations were formed based on previous findings that age-0 red snapper demonstrated a high affinity for shell rubble versus sand substrates in tank experiments (Szedlmayer and Howe 1997). However, age-0 red snapper catch per unit effort in trawl tows made on the shallow shelf (<20-m depth) off Alabama was highest from an area containing a mixture of fine sand and shell rubble sediments (Szedlmayer and Conti 1999). Our results also suggest shell rubble seabed is important habitat for juvenile red snapper, as highest juvenile densities estimated from FGS data were from cell 23, which contained the highest percentage of shell rubble habitat. However, there was no significant difference in juvenile densities among cells 5, 11, and 23 in samples collected during fall 2001. This is significant because the seabed in cell 11 was uniformly sandy with low $CaCO_3$ (i.e., shell) content. Sponge density in cell 11 was positively correlated with estimated juvenile red snapper density, thus suggesting sponges also supplied habitat complexity at a scale required by juvenile red snapper.

These results may explain equivocal results from previous juvenile red snapper habitat studies. Shelf areas containing shell rubble habitat were estimated to contain median to high juvenile densities (both historic and in 2001), supporting the conclusion of some authors that shell rubble is important for juvenile red snapper production (Szedlmayer and Howe 1997; Lee 1998; Szedlmayer and Conti 1999). However, not all studies have indicated a correlation between juvenile red snapper density and shell rubble habitat. Workman and Foster (1994) conducted video sampling during diver surveys and with a remotely operated vehicle at several sites in an approximately 350-km^2 area just to the west of our cells 5 and 11. The number of juvenile red snapper they observed was similar between sand-silt and shell rubble habitats, but, much like we report here, fish encountered in sand-silt habitat were associated with items providing small-scale complexity (e.g., squid eggs, worm tubes). Gallaway et al. (1999) reported density of low relief structures was not significant in explaining large-scale variability in juvenile red snapper density in northern GOM habitat suitability index models. This finding may have resulted from inadequate data on where small-scale, low-relief habitat exists. Alternatively, it may have resulted from loss of resolution due to integration of juvenile density estimates on large spatial scales (334-km^2 model cells) across patchily distributed low relief habitat.

Both of the latter studies highlight the importance of choosing an appropriate scale of observation for the ecological process being observed. At small spatial scales (centimeters to meters), Workman and Foster (1994) reported juvenile red snapper were associated with a variety of structures that provided small-scale structural complexity. At large spatial scales (100 km^2), which likely integrated across most habitat variability, Gallaway et al. (1999) were unable to detect a significant habitat effect to explain variability in juvenile red snapper density. The meso-scale (100 m to km) on which our 2001 trawl sampling operated also likely integrated over significant patchiness in habitats and juvenile red snapper distribution. This is evidenced by the apparent uniform distribution of surficial sediments in cell 11 yet significant correlation between estimated juvenile red snapper density and estimated sponge density. Moreover, variability in juvenile density estimates was greatest for cell 5, which also had the greatest spatial heterogeneity in seabed type.

Distinct patterns in year-classes present in each block during our 2001 sampling were evident despite the fact that juvenile density was not significantly different among cells 5, 11, and 23. Age-1 fish were most abundant in cell 23, but larger age-0 fish began recruiting to this cell by late fall. It appears from these results, as has been suggested by other authors (Lee 1998; Bailey et al. 2001), that the scale of habitat complexity required by red snapper increases with fish size and age. An alternate hypothesis concerning differences in habitat utilization between the two year-classes would be that juveniles display an ontogenetic shift to deeper areas on the shelf as they grow, and hardbottom areas such those in cell 23 serve as recruitment corridors to outer shelf reefs that constitute areas of greatest natural relief in the north-central GOM (Bradley and Bryan 1975; Parker et al. 1992; Kennicutt et al. 1995; Gardner et al. 2001). Testing this hypothesis may prove difficult, however, because more than 20,000 artificial reefs (e.g., liberty ships, discarded appliances, and fabricated concrete structures) have been deployed in a 3,100-km^2 area off Alabama (approximately 15 km east of our study sites) designated for this purpose (Minton and Heath 2000; Patterson et al. 2001a). Therefore, traditional ontogenetic shifts in habitat utilization or recruitment pathways of reef fishes such as red snapper may have been altered by placement of artificial reef habitat (Bohnsack 1989; Cowan et al. 1999; Bailey et al. 2001; Patterson et al. 2001a).

Conversely, artificial reef permit areas off Alabama may provide a unique setting to test hypotheses concerning juvenile red snapper habitat requirements and preferences because they are avoided by shrimp trawlers out of fear of losing gear to bottom hangs in the form of artificial reefs; thus, they serve as de facto no-trawl zones. Parker et al. (1992) described shell rubble habitat analogous to that identified in our cell 23 in an approximately 20-km^2 area (30°02'N, 87°57'W) contained within an artificial reef area off Alabama. Strelcheck (2001) described shell ridge features similar to those in cell 5 from an approximately 25-km^2 area (29°59'N, 88°02'W) also within an artificial reef permit zone. Therefore, these de facto no-trawl zones may provide control habitat to test if trawls significantly affect the density and distribution of benthic invertebrate flora and fauna (e.g., soft corals, calcareous algae, sponges) that may add structural complexity not found in areas subjected to trawling.

Future studies also should address whether differences in juvenile feeding opportunity, growth, or survival exist among different seabed types, and the spatial extent of different seabed types on the shelf should be estimated. While this study provides evidence that trends in juvenile red snapper spatial distribution on the north-central GOM shelf are temporally consistent among years, and acoustic mapping techniques described herein enabled us to link high juvenile densities with habitats that provided structural complexity, further research is needed to determine what constitutes quality juvenile red snapper habitat. Studies examining diet, growth, and mortality should provide additional insight into what constitutes good versus poor juvenile red snapper habitat (i.e., what habitat conveys high versus low recruitment potential; Beck et al. 2001). However, our understanding of what habitats are essential will be incomplete without knowledge of the spatial extent of different habitats (Stunz et al. 2002). We envision an index of habitat quality may consist of the product of estimated survival in a given habitat, the density of individuals located there, and habitat dimension. Thus, habitat that exhibits only modest increases in juvenile survivorship and density will need to be expansive in order to contribute significantly to year-class strength. In contrast, habitat that dramatically increases potential survivorship and supports very high densities will be essential to juvenile production even if the total area of the habitat is small.

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