

Assessment of a shell bank and associated substrates as nursery habitat of postsettlement red snapper

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Abstract

Trawl surveys were conducted in 2000 and 2001 to examine patterns of distribution and abundance of postsettlement red snapper (*Lutjanus campechanus*) on a shell bank, Freeport Rocks Bathymetric High (FRBH), in the northwestern Gulf of Mexico. In addition, otolith-based methods were used to determine age, hatch-date, growth and mortality of new recruits associated with FRBH. Date and region were significant factors affecting density of red snapper in 2000. Peak densities of red snapper were observed in July and August, and mean density among habitat types (shell bank, inshore mud, offshore mud) was similar (range: 50–52 ind hectare⁻¹) in 2000. Alternatively, a habitat effect was detected during a limited survey conducted in 2001, with density higher on the shell bank than inshore or offshore mud habitat. Postsettlement red snapper were first detected at approximately 16 mm standard length, and individuals less than 20 mm were present in all habitats. Estimated ages of red snapper ranged from 26 to 121 d, with new settlers (≤ 20 mm) typically less than 28 d. Predicted hatch dates ranged from early April to mid August with a single peak occurring from late May to early June. Growth rate for the April–May cohort (0.817 mm d⁻¹) was similar to the June–July cohort (0.830 mm d⁻¹). Habitat-specific differences in growth were observed, and rates were highest for individuals from the inshore habitat (0.881 mm d⁻¹). Mortality rates (Z) during the early post-settlement period were approximated using catch curves, and early life mortality of red snapper was 12.1% d⁻¹ ($Z = 0.129$). While the difference in mortality between cohorts was negligible, a habitat-specific difference in mortality was observed. Mortality rate of red snapper inhabiting the inshore mud habitat ($Z = 0.045$, 4.4% d⁻¹) was lower than rates observed for individuals on the shell bank ($Z = 0.120$, 11.9% d⁻¹) or offshore ($Z = 0.099$, 9.3% d⁻¹) habitat. Individuals residing in the inshore habitat had significantly higher growth rates and significantly lower mortality rates, suggesting that recruitment potential was higher for these individuals.

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1. Introduction

Red snapper (*Lutjanus campechanus*) supports valuable commercial and recreational fisheries throughout its range, particularly in the Gulf of Mexico (Gallaway et al., 1999). Red snapper is arguably the most valuable reef fish in the Gulf, and populations are presently classified as over fished (GMFMC, 2000). Potential yield of this species in the northern Gulf is well below its estimated long-term potential yield and, based on

current levels of total allowable catch, red snapper stocks are not expected to fully recover within the next decade (Goodyear, 1995). Declining red snapper stocks have been attributed in part to overexploitation by commercial and recreational fisheries. Further, incidental catch of juvenile red snapper by the shrimp fishery is responsible for substantial mortality (Gutherz and Pellegrin, 1988).

To fully understand the dynamics of fishing activity on the recruitment of red snapper, essential nursery areas must be delineated, and these data are prerequisite to employing habitat-based management strategies (i.e. time and area closures). Studies characterizing habitat use of red snapper have suggested that juveniles are not randomly distributed, but attracted to complex habitats

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such as low-profile reefs or coarse shell hash (Workman and Foster, 1994; Bailey, 1995; Szedlmayer and Howe, 1997). Apart from production platforms and pipelines, shell material found on many banks represents the only structured benthic habitat on the inner shelf in the northern Gulf and appears to serve as critical habitat for newly settled red snapper. To date, attempts to assess the value of structured benthic habitat have been conducted in areas northeast of the Mississippi River (Workman and Foster, 1994; Szedlmayer and Conti, 1999). Similar studies in the northwestern Gulf do not exist, despite indications that this region may serve as an important source of juveniles (Gutherz and Pellegrin, 1988). In addition, bathymetric highs consisting of shell substrate are prominent features on the inner continental shelf in this region, and the increased abundance of these topographic features may be closely linked to red snapper productivity throughout the Gulf.

Here, we evaluate the importance of a prominent shell bank in the northwestern Gulf as nursery habitat of red snapper. Our primary aim was to assess patterns of distribution and abundance of red snapper and evaluate the quality of different habitats (shell bank or bathymetric high, inshore mud, offshore mud) associated with

the system. In addition, otolith-based methods were used to determine the age structure and hatch-date distribution of new recruits, and age information was used in conjunction with length and abundance data to estimate habitat-specific rates of growth and mortality.

2. Materials and methods

2.1. Study site

Postsettlement red snapper were collected from the Freeport Rocks Bathymetric High (FRBH) and adjacent mud bottom habitat off Freeport, Texas (W $95^{\circ}18'$, N $28^{\circ}44'$). The shell bank occurs at a depth of approximately 15–20 m and runs northeast southwest for approximately 20 km (Fig. 1). The bank is dominated by coarse shell hash, relic oysters beds and sand patches, while silt and mud-sized sediments are present off the shell bank. Paleoenvironmental analysis of the FRBH indicates original deposition in a barrier island or deltaic setting (Rodriguez et al., 2000). Boundaries of the FRBH and associated areas were surveyed and mapped using a depth sounder and global positioning

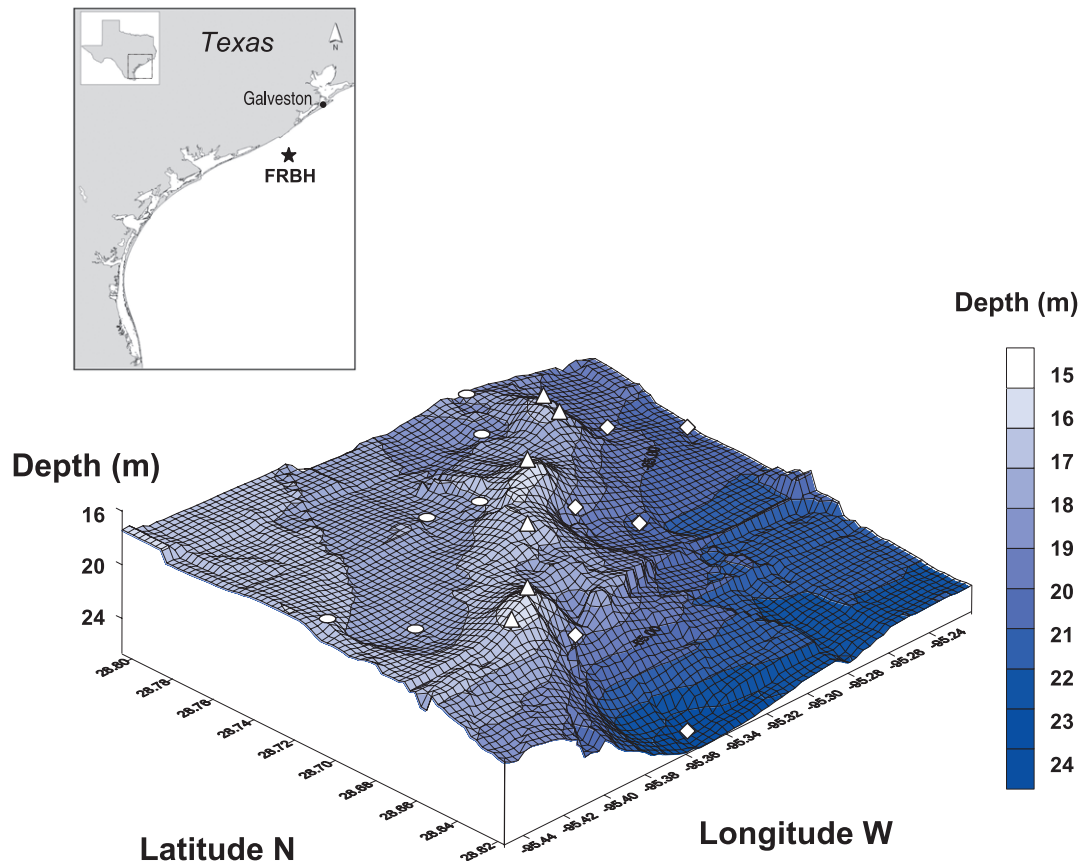


Fig. 1. Grid-based geostatistical map of Freeport Rocks Bathymetric High and associated habitats (Surfer, Golden Software, Inc.). Sampling sites within each habitat are designated with different symbols: inshore mud (circles), shell bank or bathymetric high (triangles), and offshore mud (diamonds).

system (GPS). Surface-sediment grab samples and a side scan sonar were used to ground truth mapping efforts and characterize bottom types.

2.2. Trawl surveys

Trawl surveys were conducted semi-monthly in 2000 during the annual settlement period of red snapper (May–September). In addition, monthly trawl surveys were conducted in 2001 during the peak recruitment of juveniles (July–August) to further examine effects of region and habitat on red snapper density at the FRBH. In both years, eighteen trawl tows were taken during each survey from three different habitats: shell bank or bathymetric high, inshore mud, and offshore mud (six per habitat). Sites were evenly distributed among three regions: northern, central, and southern portions of the FRBH. Red snapper were collected by towing a 6-m otter trawl (2-cm mesh with 1.25-cm mesh liner) equipped with a chain (0.6 cm link) attached to the bottom of trawl doors to dislodge substrate. Each trawl haul was 10 min in duration at a speed of approximately 2.5 knots. Trawls were always towed against prevailing surface currents to standardize tow speed, and GPS coordinates were recorded at the beginning and end of each trawl to calculate area sampled. Environmental data collected at each site on all cruises included water depth, salinity, water temperature, and dissolved oxygen content. Trawl samples were immediately frozen after capture, and red snapper were identified and measured to the near 0.1 mm (standard length) in the laboratory.

2.3. Otolith-microstructure analysis

Sagittal otoliths were removed from a sub-sample of red snapper collected in 2000 that included representatives from each habitat, region, and trawl survey. One otolith from each pair was randomly selected and set in epoxy resin. A transverse section containing the core was cut from each otolith using an ISOMET low-speed saw. Thin sections were mounted on slides with thermoplastic cement, and sections were polished to the core on each side using 320–600 grit wet-dry sand paper and a polishing cloth with 0.3 μm alumina polishing compound. Age was estimated by enumerating growth increments on sagittal otoliths, and counts were made on an image analysis system (Olympus BX41 and Image Pro v. 4.5 software). A sub-sample of red snapper otoliths ($n = 60$) was aged independently by two readers, and a high level of agreement (1:1 relationship) was observed between readers (Reader A age = $1.01 \times$ Reader B age + 1.05, $r^2 = 0.96$). In response, a single reader was used to age remaining otoliths, and multiple counts by the same individual were averaged to estimate age of individual red snapper.

Daily increment deposition has been validated for juvenile red snapper (Szedlmayer, 1998), and this observation was confirmed using a small sample of known-age red snapper from the University of Mississippi, Gulf Coast Research Laboratory (GCRL). Increments proximal to the core were clear in some individuals and thus readers could effectively delineate all growth increments. Still, inner increments were difficult to count on many otoliths and, as a result, an age–radius relationship was developed (age = $0.20 \times$ otolith radius + 0.381; $r^2 = 0.98$). This relationship was developed using otoliths from GCRL as well as wild caught red snapper with clear inner increments. Age estimates for individuals with unclear increments near the core were determined by adding the predicted age from the unreadable section of the otolith to counts from the first identifiable increment. On average, correction factors accounted for only 4% of the total increment count (range 0–12%) and thus age estimates were based on nearly complete otolith increment counts. Of the 461 otoliths processed, 97 otoliths were scored as unreadable and not used for age and growth assessments.

Linear regression analysis was used to determine growth rates of postsettlement red snapper. Growth was estimated from the slope of the regression of standard length on otolith-derived estimate of age (size-at-age plots). Mortality rates were estimated using a log-linear regression equation of \log_e abundances on age (i.e. catch–curve analysis). Due to incomplete capture (ascending limb of catch curve) of small red snapper (ca. <47 d, <33 mm), these individuals were not included in mortality regressions. Regression coefficient (slope) was used to predict the instantaneous mortality rate. Catch–curve analysis is based upon the premise that juvenile red snapper show site fidelity and dispersive behaviors (emigration, immigration) are assumed negligible; nevertheless, movements from settlement sites are possible and thus mortality was estimated only during a restricted postsettlement period to minimize the effect of movement. Moreover, restricting mortality rates to short time intervals minimizes the effect of size-based gear avoidance (Rooker and Holt, 1997).

2.4. Data analysis

A three-way factorial analysis of variance (ANOVA) with a single blocking factor (date) was applied to abundance data (factors: habitat, region, date). Seasonal patterns of red snapper abundance were pronounced and several samples contained zero values. Consequently, the assumption of multivariate normality (normality of error terms) was not met when all dates were processed; however, departures from normality are unlikely to compromise results (Underwood, 1997). Nonetheless, to minimize deviations from normality, statistical testing was restricted to samples collected during the primary

recruitment episode in 2000. This period included four trawl surveys (July 5–6, July 17–18, August 17–18, August 31–September 1). In addition, red snapper from both surveys conducted in 2001 (July 9–10, August 13–14) were used for statistical comparisons. Prior to all parametric testing, the assumption of homogeneity of variances was inspected via residual examination, and log transformations were performed to minimize heteroscedasticity as required. Effects of habitat and location on length of red snapper were evaluated using a two-factor analysis of covariance ANCOVA (main effects: habitat, region). Date of collection (expressed as number of days since June 1) was the designated covariate in the model and accounted for seasonal variation in length of red snapper. ANCOVA was also used to assess spatial and temporal variation in growth and mortality of red snapper collected in 2000. The covariate (age) was used to compensate for size-related differences among groups. Power analysis was performed on density data when the null hypothesis was not rejected (based on $\alpha = 0.05$).

3. Results

3.1. Environmental conditions

Salinity, temperature, dissolved oxygen were measured during the study, and differences among habitats or among regions were not statistically significant for any parameter ($p > 0.05$). Salinity ranged from 33.9 to 37.4‰, and differences among habitats and regions during respective trawl surveys were negligible (0.2–0.3‰). Water temperatures increased across the sampling season with maximum values observed in August (29.9°C), and differences among habitats or regions within trawl surveys were typically less than 1°C. Dissolved oxygen ranged from 5.1 to 6.4 mg L⁻¹ and, although differences were not significant, levels were typically lower inshore of the FRBH. Also, shell material was frequently collected during trawl surveys but limited to the shell bank habitat (range: 0–179 kg tow⁻¹). The amount of shell material collected in trawls varied among regions of the shell bank, and mean values were statistically lower in the northern (20.6 kg tow⁻¹) or southern (33.8 kg tow⁻¹) regions than near the center of the bank (43.2 kg tow⁻¹).

3.2. Distribution and abundance

Densities of postsettlement red snapper ($n = 2432$) peaked during four sampling trips in 2000 (5–6 July, 17–18 July, 17–18 August, 31 August–1 September). During peak recruitment, densities ranged from 19 to 89 ind hectare⁻¹. Catch numbers from 2001 were low ($n = 383$) relative to 2000, and mean densities during the July and August surveys ranged from 15 to 34 ind

hectare⁻¹. Estimated values for aforementioned dates in 2000 and 2001 accounted for over 99% of the total catch of red snapper and were used for statistical and graphical comparisons.

Date and region were identified as significant factors ($p < 0.001$ and $p = 0.011$, respectively) affecting red snapper density in 2000. Mean density was significantly higher during July 17–18 survey (187 ind hectare⁻¹) than the three other sampling trips (range: 34–67 ind hectare⁻¹) (Fig. 2). Differences in mean density by region were also pronounced, with significantly higher numbers observed near the center of the FRBH (121 ind hectare⁻¹) as opposed to the northern (72 ind hectare⁻¹) and southern (50 ind hectare⁻¹) ends of the system ($p < 0.001$); no effect of region ($p = 0.539$; power = 0.144) was detected for limited sampling conducted in 2001. Mean density of red snapper among habitats was similar in 2000 (range: 50–52 ind hectare⁻¹), and no effect of habitat was detected ($p = 0.833$; power = 0.144).

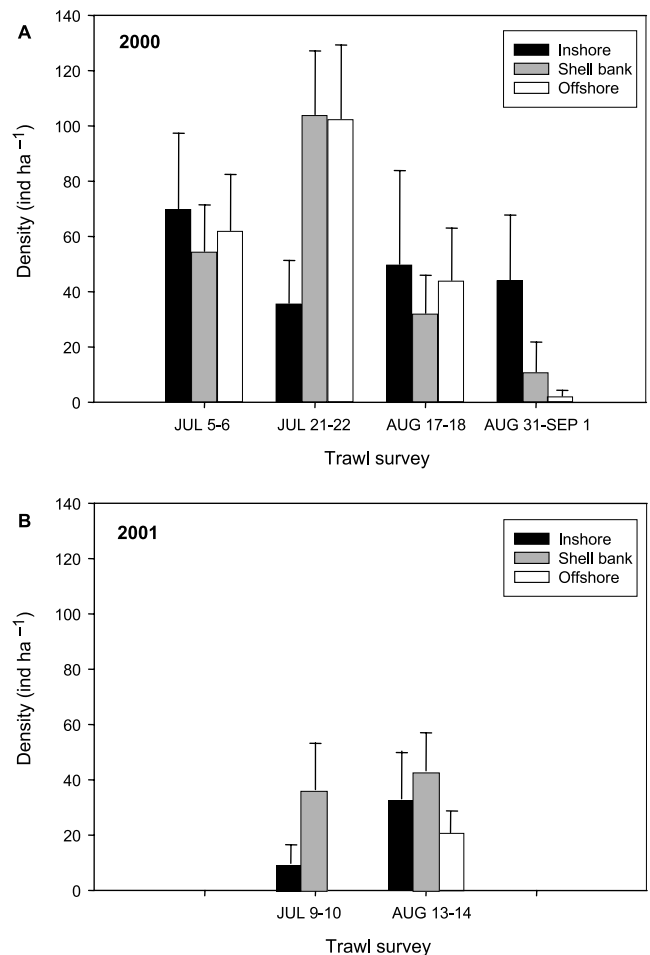


Fig. 2. Mean density (± 1 SE) of postsettlement red snapper (*Lutjanus campechanus*) by habitat (inshore mud, shell bank or bathymetric high, offshore mud) on the Freeport Rocks Bathymetric High and associated habitats. Data are limited to (A) four trawl surveys conducted in 2000 (July 5–6, July 17–18, August 17–18, August 31–September 1) and (B) two trawl surveys conducted in 2001 (July 9–10, August 13–14).

Conversely, a habitat effect was detected in 2001 ($p = 0.041$), and densities were higher on the shell bank (41 ind hectare⁻¹) than either the inshore (21 ind hectare⁻¹) or offshore (11 ind hectare⁻¹) habitat. The first order interactions (region \times habitat) were not significant in 2000 ($p = 0.255$; power = 0.392) or 2001 ($p = 0.210$; power = 0.418). Since catch rates were variable on the shell bank, the relationship between shell material (per trawl) and red snapper density was examined. No correlation between shell material and density (adjusted for temporal differences) was detected (Pearson's $r = -0.297$, $p = 0.405$).

3.3. Size distribution

Postsettlement red snapper were first detected at approximately 16 mm standard length. Several individ-

uals less than 20 mm were detected in all habitats in both years, suggesting settlement events occurred on the shell bank as well as adjacent mud bottom habitats. Red snapper were present in all three habitats throughout the entire early juvenile stage and densities were highest for individuals 20–40 mm (Fig. 3). Median length of red snapper was similar ($p = 0.558$) among habitats (inshore 33.8 mm, shell bank 35.9 mm, offshore 34.4 mm).

3.4. Age, growth, and mortality

Predicted age of postsettlement red snapper from otolith-microstructure analysis ($n = 364$) ranged from 26 to 121 d in 2000. New settlers (≤ 20 mm) were less than 28 d, while the dominant size-class of red snapper (20–40 mm) ranged between 31 and 54 d. An overall age-length relationship was developed, and the model

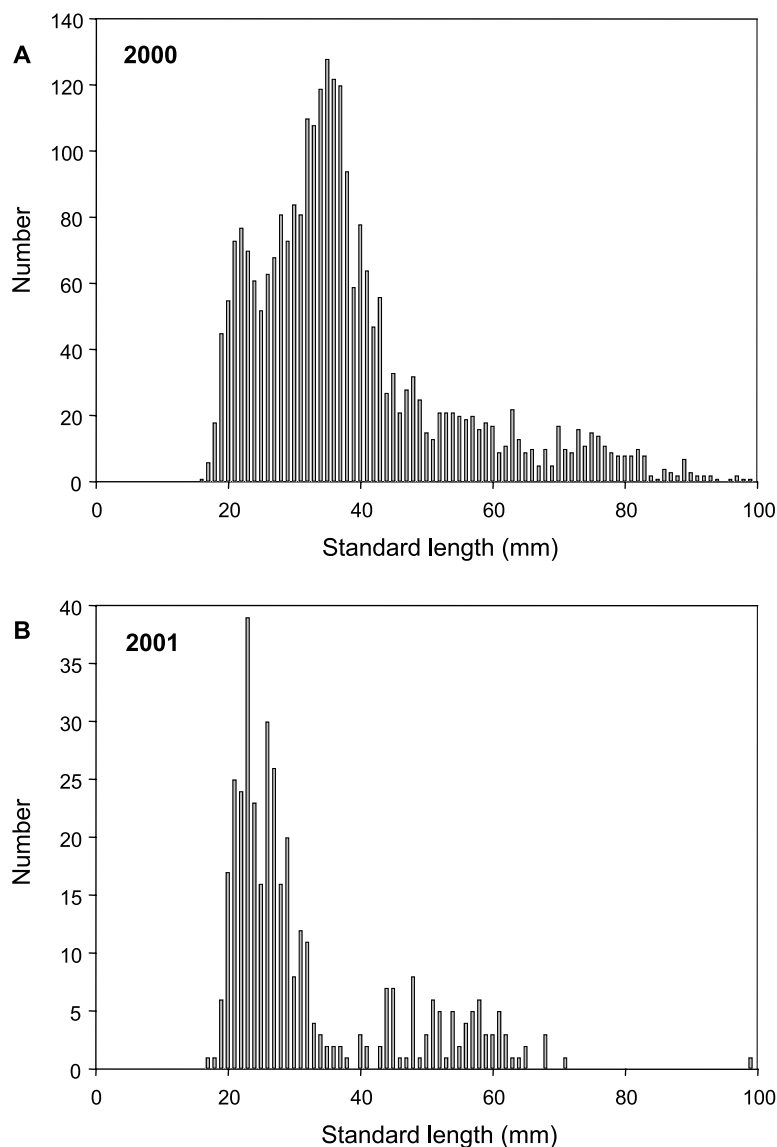


Fig. 3. Length–frequency distribution of postsettlement red snapper (*Lutjanus campechanus*) collected in (A) 2000 ($n = 2432$) and (B) 2001 ($n = 383$) from the Freeport Rocks Bathymetric High and associated habitats.

predicted that $\text{Age} = 8.793 + 1.130 \times \text{standard length}$ ($r^2 = 0.93$). Using this model, age was estimated for all remaining red snapper collected ($n = 2068$). Predicted mean and median ages of red snapper were 53 and 48 d, respectively.

Age estimates were used in conjunction with data on collection date and size to determine hatch dates and growth rates of red snapper collected in 2000. Predicted hatch dates ranged from early April to mid August with a single peak occurring from late May to early June (Fig. 4). The majority of individuals (78%) hatched over a 30-day period from 15 May to 15 June. Hatch-date estimates were used to separate red snapper into two cohorts: early season (April–May, $n = 138$) and late season (June–July, $n = 226$). Cohort-specific growth rates were estimated using linear length-at-age models, and rates for the April–May cohort (0.817 mm d^{-1}) were statistically similar to the June–July cohort (0.830 mm d^{-1}) (ANCOVA slope test: $p = 0.919$). As a result, cohorts were pooled to examine the effect of habitat on growth. Habitat-specific differences in growth were observed (ANCOVA slope test: $p = 0.001$), with the highest rate occurring for red snapper from the inshore habitat (0.881 mm d^{-1}) (Fig. 5). Growth rates of individuals from offshore and shell bank habitats were 0.829 mm d^{-1} and 0.774 mm d^{-1} , respectively.

Mortality rates (Z) during the early postsettlement period (age: 47–57 d) were approximated using catch curves, and overall mortality for the 2000 year class of red snapper was $12.1\% \text{ d}^{-1}$ ($Z = 0.129$). Cohort-specific mortality was estimated by comparing April–May and

June–July catch curves, but no effect was observed (ANCOVA, slopes, $p = 0.276$). Habitat-specific differences in mortality were also examined, and a significant difference was detected among habitats (ANCOVA, slopes, $p = 0.007$) (Fig. 6). Specifically, the predicted mortality rate of red snapper from the inshore habitat ($Z = 0.045$, $4.4\% \text{ d}^{-1}$) was lower than that of conspecifics from the shell bank ($Z = 0.120$, $11.9\% \text{ d}^{-1}$) or offshore ($Z = 0.099$, $9.3\% \text{ d}^{-1}$) habitat. Cumulative mortality (habitats pooled) during the early postsettlement interval (47–57 d) was relatively high ($Z = 1.317$, 73.2%).

4. Discussion

Findings from previous studies examining patterns of distribution and abundance of red snapper suggest that structured, low-profile banks or complex substrate represent essential nursery habitat. Szedlmayer and Howe (1997) examined substrate preference of juvenile red snapper ($\sim 80 \text{ mm}$) in the laboratory and reported that individuals selected shell over sand substrate. Similarly, field studies conducted by Workman and Foster (1994) reported that age-0 red snapper in the northeastern Gulf of Mexico are more abundant in low topographical relief habitat than uniform sand flats. In the present study, we observed that red snapper density was significantly higher on the shell bank than adjacent habitats sampled in 2001. Conversely, red snapper settled throughout the FRBH and adjacent substrates in 2000, suggesting that the shell

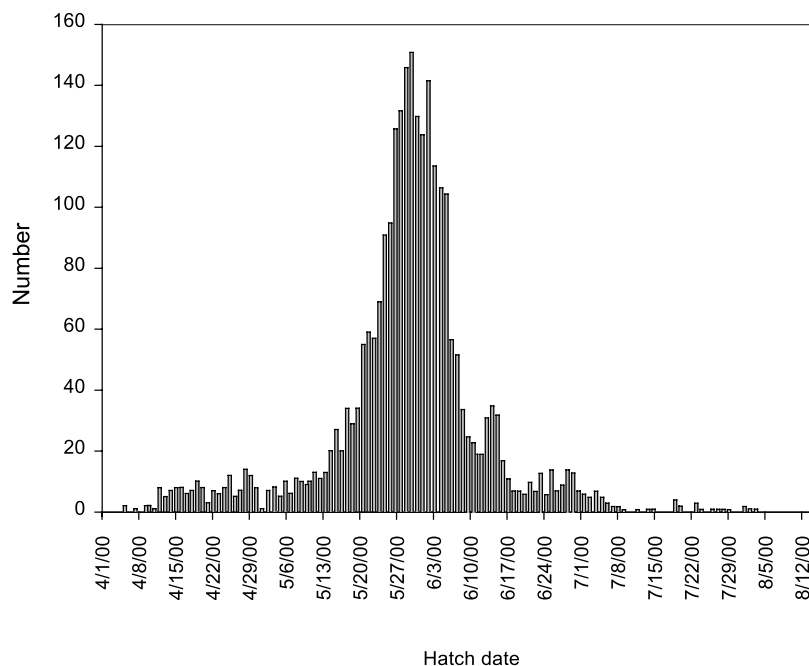


Fig. 4. Hatch-date distribution of postsettlement red snapper (*Lutjanus campechanus*) estimated from otolith-based estimates of age of postsettlors collected in 2000 from the Freeport Rocks Bathymetric High and associated habitats.

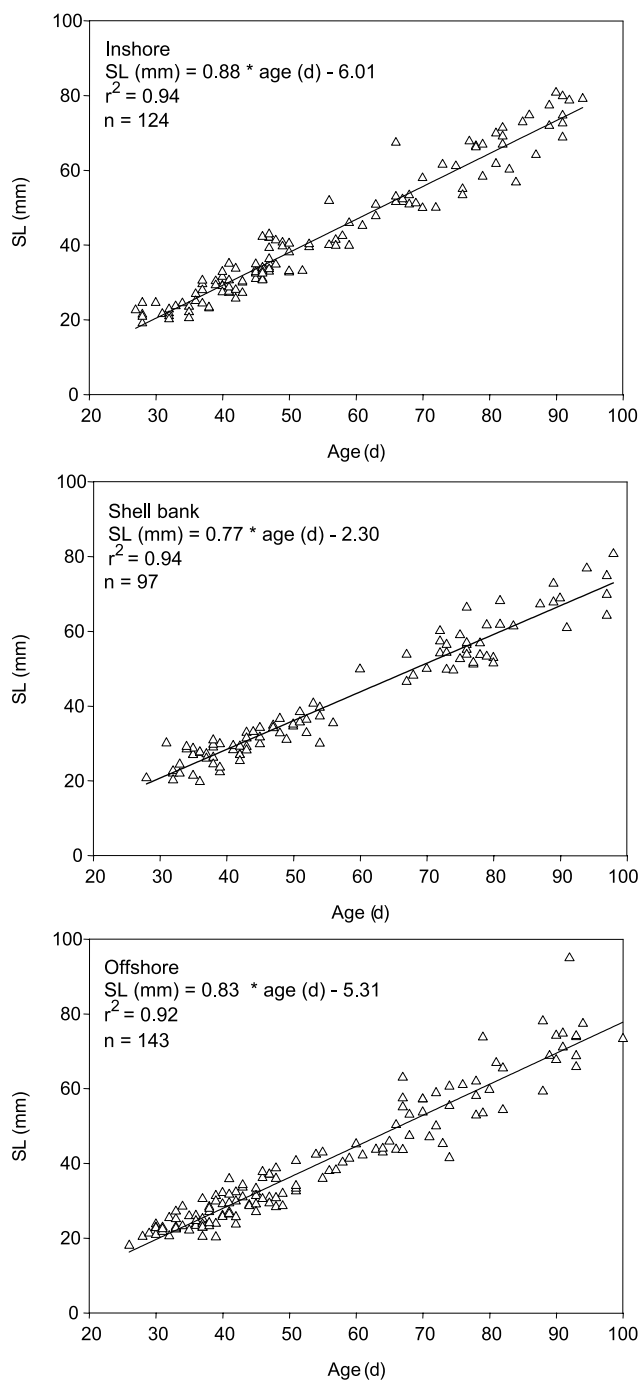


Fig. 5. Size-at-age relationships of postsettlement red snapper (*Lutjanus campechanus*) collected in 2000 from the Freeport Rocks Bathymetric High and associated habitats. Linear growth estimates are shown for inshore mud, shell bank or bathymetric high, and offshore mud habitats.

bank and adjacent mud bottom habitats were equally important as nurseries of newly settled red snapper. However, observed power for the habitat effect was low for the 2000 model (power = 0.144) relative to the 2001 model (power = 0.616), and thus it is possible that the null hypothesis (no habitat effect) was falsely accepted in 2000.

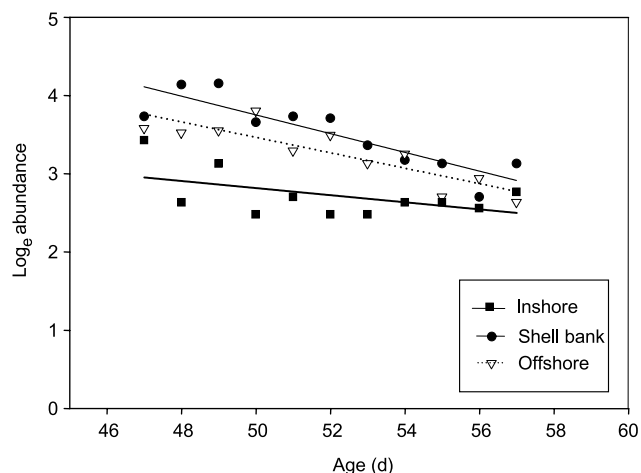


Fig. 6. Regression plots of \log_e abundance on age of postsettlement red snapper (*Lutjanus campechanus*) collected in 2000 from the Freeport Rocks Bathymetric High and associated habitats.

Overall, results on habitat use are equivocal but suggest that large numbers of new recruits use shell bank habitat during early life.

Temporal variation in settlement of red snapper to the shell bank and adjacent habitats was present, and new recruits were first observed in June with collection numbers peaking in July and August. Similar patterns of red snapper recruitment in the northwestern Gulf of Mexico have been reported previously. Holt and Arnold (1982) observed peak recruitment of red snapper less than 40 mm standard length on the outer continental shelf from June to October. More recently, Szedlmayer and Conti (1999) sampled age-0 red snapper in the northeastern Gulf of Mexico and reported that catch per unit effort (CPUE) was highest from July to mid September. Incidentally, initial recruitment of red snapper to the FRBH and adjacent areas coincides with the annual reopening of the shrimp season in waters off the Texas coast (e.g. early to mid July), indicating the timing of current closure strategies may affect postsettlement survival of red snapper.

Otolith-microstructure analysis provided critical information on settlement age of red snapper on the FRBH. Red snapper were first detected at 16 mm or 27 d, and significant numbers of 16–19 mm or 27–30 d red snapper were collected, indicative of a planktonic larval duration (PLD) of approximately 4 weeks. In addition, new settlers (<20 mm) were present in each habitat sampled, indicating settlement is not restricted to a specific habitat. The range of sizes and ages collected at the shell bank and adjacent habitats is consistent with reports of newly settled red snapper and other lutjanids in the Western Atlantic. Using the smallest individuals in their collections, Szedlmayer and Conti (1999) hypothesized that larval red snapper metamorphose at approximately 18 mm or 26 d. Similar estimates of PLD have been

reported for other congeners using settlement marks. Specifically, PLD of the gray snapper (*Lutjanus griseus*) in the Western Atlantic is approximately 25 d (Allman and Grimes, 2002), while PLDs of congeners from the tropical eastern Pacific (*Lutjanus argentiventris*, *Lutjanus guttatus*, *Lutjanus novemfasciatus*) range from 22 to 24 d (Zapata and Herron, 2002). As a consequence, the PLD of red snapper in the northwestern Gulf is similar to other lutjanids as well as the majority of reef fishes that typically settle 3–4 weeks post-hatch (Victor, 1991).

Hatch-date analysis indicated that spawning (approximately 25 h prior to hatch; Rabalais et al., 1980) occurred from April to August, supporting the premise that red snapper are protracted spawners (Collins et al., 1996). Nevertheless, the majority of successful recruits collected in 2000 were derived from May and June spawning events. The general trend of the hatch-date distribution was unimodal, with approximately 80% of red snapper produced over a one-month period (15 May–15 June). In contrast, Szedlmayer and Conti (1999) observed a bimodal hatch-date distribution of red snapper in the northeastern Gulf, and a similar trend has been reported for other marine teleosts in the Gulf (Rooker et al., 1998). Regardless of the hatch-date profile (unimodal versus bimodal), it appears that red snapper in the Gulf spawn over several months, and this is probably a bet hedging strategy to counter unpredictable hydrodynamic conditions and variable mortality during early life (Begg and Marteinsdottir, 2002; Houde, 2002).

Daily growth rates observed in this study (0.78–0.88 mm d⁻¹) were comparable to previous estimates of age-0 red snapper in the Gulf of Mexico (0.54–0.86 mm d⁻¹, Szedlmayer and Conti, 1999), as well as gray snapper along the West Florida Shelf (0.60–1.02 mm d⁻¹, Allman and Grimes, 2002). While seasonal variation in growth of reef fishes is often reported (e.g. Dahlgren and Eggleston, 2000; Searcy and Sponaugle, 2000), growth of red snapper in the present study did not differ between early and late cohorts. Since growth is a function of both physical (e.g. temperature) and biological (e.g. food availability) factors, it appears that conditions experienced by April–May and June–July cohorts were similar, and this assumption was supported by our environmental monitoring. Conversely, habitat-specific differences in growth were detected and may indicate that environmental conditions varied among habitats. Since physiochemical conditions were similar among habitats, it is likely that biological factors were responsible for observed patterns of higher growth on the inshore substrate than either the shell bank or offshore substrate. Sediment characteristics have been shown to influence the colonization of soft-bottom benthos, and the availability and abundance of benthic prey typically consumed by lutjanids (e.g. amphipods, crabs, polychaetes; Rooker, 1995) will vary as a function of sediment characteristics such as particle size and organic content

(Wu and Shin, 1997). An inverse relationship between sediment size and abundance of soft-bottom benthos has been reported (Brown and McLachlan, 1990; McLachlan, 1996), suggesting that prey availability may be greater in offshore and inshore mud habitats than the shell bank habitat. However, this observation fails to explain the differences in red snapper growth between the offshore and inshore mud habitats. Due to its proximity to the coastline, the inshore habitat will likely receive greater runoff or nutrient loading, increasing the organic content of the sediment and increasing productivity of benthic microflora or phytoplankton. As a consequence, differences in particle size and potentially organic content found in the inshore zone may enhance the foraging success and growth of postsettlement red snapper.

Estimated mortality was relatively high for newly settled red snapper, and habitat-specific mortality rates ranged from 4 to 12% d⁻¹ during the early postsettlement period. Our results are in accordance with several studies that suggest postsettlement mortality is substantial (Rooker et al., 1999; Forrester and Steele, 2000; Shima, 2001). For example, Watson et al. (2002) predicted the mortality of juvenile yellowtail snapper (*Ocyurus chrysurus*) was 4–24% d⁻¹, with approximately 90% of the settlers being lost during the first 30 days after settlement. Also, Dahlgren and Eggleston (2001) observed high losses (90%) of early juvenile Nassau grouper (*Epinephelus striatus*) during the first few months of life. Similar to estimates of growth, mortality in the inshore habitat was different than other habitats, and estimates were approximately twofold greater for red snapper collected from shell bank and offshore habitats. Habitat-specific variation in predator densities may be partly responsible for observed patterns of mortality since relative abundances of certain piscivores vary across habitats in this region (J. Rooker, unpublished data). Finally, postsettlement movement may influence mortality estimates (e.g. immigration to inshore habitat after settlement in other areas); however, juvenile red snapper show site fidelity (Workman and Foster, 1994), and age-at-length profiles show no apparent sign of emigration or immigration.

Based on findings from this study, newly settled red snapper occupying the inshore habitat grew more rapidly than in other habitats. Since rapid growth shortens the length of time new settlers are vulnerable to predators, mortality rates may be lower for these individuals (Houde, 2002). This extension of the “Stage Duration Hypothesis” (see Cowan and Shaw, 2002) to the settlement period has been suggested previously (Sogard, 1992; Rooker and Holt, 1997; Dahlgren, and Eggleston, 2000); however, field observations often fail to link increased growth with reduced mortality. Here, we show that individuals residing in the inshore mud habitat had significantly higher growth rates and significantly lower mortality rates. Consequently, recruitment potential of red snapper residing in the inshore habitat appears to be

greater than for individuals using shell bank or offshore mud habitat.

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References

- Allman, R.J., 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. *Fishery Bulletin* 100, 391–403.
- Bailey, H.K., 1995. Potential interactive effects of habitat complexity and sub-adults on young-of-the-year red snapper (*Lutjanus campechanus*) behavior. M.S. thesis, University of South Alabama, Mobile, 73 pp.
- Begg, G.A., Marteinsdottir, G., 2002. Environmental and stock effects on spawning origins and recruitment of cod *Gadus morhua*. *Marine Ecology Progress Series* 229, 263–277.
- Brown, A.C., McLachlan, A., 1990. *Ecology of Sandy Shores*. Elsevier, New York.
- Collins, L.A., Johnson, A.G., Keim, C.P., 1996. Spawning and annual fecundity of the red snapper (*Lutjanus campechanus*) from the northeastern Gulf of Mexico. *Biology, fisheries and culture of tropical groupers and snappers*, ICLARM Conf. Proc. no. 48, International Cent. for Living Aquatic Resources Management, Manila, Philippines, pp. 174–188.
- Cowan Jr., J.H., Shaw, R.F., 2002. Recruitment. In: Fuiman, L.A., Werner, R.G. (Eds.), *Fishery Science: The Unique Contributions of Early Life Stages*. Blackwell Science Ltd., Oxford, UK, pp. 88–111.
- Dahlgren, C.P., Eggleston, D.B., 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* 81, 2227–2240.
- Dahlgren, C.P., Eggleston, D.B., 2001. Spatio-temporal variability in abundance, size and microhabitat associations of early juvenile Nassau grouper *Epinephelus striatus* in an off-reef nursery system. *Marine Ecology Progress Series* 217, 145–156.
- Forrester, G.E., Steele, M.A., 2000. Variation in the presence and cause of density-dependent mortality in three species of reef fishes. *Ecology* 81, 2416–2427.
- Gallaway, B.J., Cole, J.G., Meyer, R., Roscigno, P., 1999. Delineation of essential habitat for juvenile red snapper in the northwestern Gulf of Mexico. *Transactions on the American Fisheries Society* 128, 713–726.
- GMFMC, 2000. Regulatory amendment to the reef fish fishery management plan to set total allowable catch and management measures for red snapper for the 2000 and 2001 seasons, 56 pp.
- Goodyear, C.P., 1995. Red snapper in U.S. waters of the Gulf of Mexico. Stock assessment report MIA-95/96-05 Miami Laboratory, Southeast Fisheries Science Center, Miami, FL.
- Guthertz, E.J., Pellegrin, G.J., 1988. Estimate of the catch of red snapper, *Lutjanus campechanus*, by shrimp trawlers in the U.S. Gulf of Mexico. *Marine Fisheries Review* 50, 15–25.
- Holt, S.A., Arnold, C.R., 1982. Growth of juvenile red snapper *Lutjanus campechanus*, in the Northwestern Gulf of Mexico. *Fishery Bulletin* 80, 644–648.
- Houde, E.D., 2002. Mortality. In: Fuiman, L.A., Werner, R.G. (Eds.), *Fishery Science: The Unique Contributions of Early Life Stages*. Blackwell Science Ltd., Oxford, UK, pp. 64–87.
- McLachlan, A., 1996. Physical factors in benthic ecology: effects of changing sand particle size on beach fauna. *Marine Ecology Progress Series* 131, 205–217.
- Rabalais, N.N., Rabalais, S.C., Arnold, C.R., 1980. Description of eggs and larvae of laboratory reared red snapper (*Lutjanus campechanus*). *Copeia* 4, 704–708.
- Rodriguez, A.B., Anderson, J.B., Banfield, L.A., Taviani, M., Abdulah, K., Snow, J., 2000. Identification of a –15 m middle Wisconsin shoreline on the Texas inner continental shelf. *Palaeogeography Palaeoclimatology Palaeoecology* 158, 25–43.
- Rooker, J.R., 1995. Feeding ecology of the schoolmaster snapper, *Lutjanus apodus* (Walbaum), from southwestern Puerto Rico. *Bulletin of Marine Science* 56, 881–894.
- Rooker, J.R., Holt, S.A., 1997. Utilization of subtropical seagrass meadows by newly settled red drum (*Sciaenops ocellatus*): patterns of distribution and growth. *Marine Ecology Progress Series* 158, 139–149.
- Rooker, J.R., Holt, S.A., Holt, G.J., Fuiman, L.A., 1999. Spatial and temporal variability in growth, mortality, and recruitment potential of postsettlement red drum, *Sciaenops ocellatus*, in a subtropical estuary. *Fishery Bulletin* 97, 581–590.
- Rooker, J.R., Holt, S.A., Soto, A.M., Holt, G.J., 1998. Postsettlement patterns of habitat use by sciaenid fishes in subtropical seagrass meadows. *Estuaries* 21, 318–327.
- Searcy, S.P., Sponaugle, S., 2000. Variable larval growth in a coral reef fish. *Marine Ecology Progress Series* 206, 213–226.
- Shima, J.S., 2001. Recruitment of a coral reef fish: roles of settlement, habitat, and postsettlement losses. *Ecology* 82, 2190–2199.
- Sogard, S.M., 1992. Variability in growth rates of juvenile fishes in different estuarine habitats. *Marine Ecology Progress Series* 85, 35–53.
- Szedlmayer, S.T., 1998. Comparison of growth rate and formation of otolith increments in age-0 red snapper. *Journal of Fish Biology* 53, 58–65.
- Szedlmayer, S.T., Conti, J., 1999. Nursery habitats, growth rates, and seasonality of age-0 red snapper, *Lutjanus campechanus*, in the northeast Gulf of Mexico. *Fishery Bulletin* 97, 626–635.
- Szedlmayer, S.T., Howe, J.C., 1997. Substrate preferences in age-0 red snapper, *Lutjanus campechanus*. *Environmental Biology of Fishes* 50, 203–207.
- Underwood, A.J., 1997. *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge, pp. 140–197.
- Victor, B.C., 1991. Settlement strategies and biogeography of reef fishes. In: Sale, P.F. (Ed.), *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego, pp. 231–260.
- Watson, M., Munro, J.L., Gell, F.R., 2002. Settlement, movement and early juvenile mortality of the yellowtail snapper *Ocyurus chrysurus*. *Marine Ecology Progress Series* 237, 247–256.
- Workman, I.K., Foster, D.G., 1994. Occurrence and behavior of juvenile red snapper, *Lutjanus campechanus*, on commercial shrimp fishing grounds in the northeastern Gulf of Mexico. *Marine Fisheries Review* 56, 9–11.
- Wu, R.S.S., Shin, P.K.S., 1997. Sediment characteristics and colonization of soft-bottom benthos: a field manipulation experiment. *Marine Biology* 128, 475–487.
- Zapata, F.A., Herron, P.A., 2002. Pelagic larval duration and geographic distribution of tropical eastern Pacific snappers (Pisces: Lutjanidae). *Marine Ecology Progress Series* 230, 295–300.