Habitat use, growth, and mortality of post-settlement lane snapper (*Lutjanus synagris*) on natural banks in the northwestern Gulf of Mexico

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A B S T R A C T

Three low-relief banks in the northwestern Gulf of Mexico were evaluated as nursery habitat of lane snapper (*Lutjanus synagris*). Trawl surveys were conducted in three habitat types (inshore mud, shell ridge, offshore mud) to quantify lane snapper distribution and abundance. Heald Bank and Sabine Bank were trawled in 2003 while Freeport Rocks was trawled in 2000 (Freeport A) and 2004 (Freeport B). Density of lane snapper varied among banks and years sampled: Sabine Bank (20.8 ± 2.8 ind ha^{-1}), Heald Bank (1.1 ± 0.4 ind ha^{-1}), Freeport A (12.7 ± 2.3 ind ha^{-1}), and Freeport B (3.0 ± 1.0 ind ha^{-1}). Habitat-specific differences in density were observed, although patterns were not consistent among banks. Otolith microstructure analysis indicated that post-settlement lane snapper ranged in age from 21 to 66 d, with hatch dates from 1 May to 31 August. Growth rates varied from 0.90 mm d^{-1} at Heald Bank to 1.27 mm d^{-1} at Sabine Bank, and habitat-specific differences in growth were negligible. Mortality of post-settlement lane snapper ranged from 15.2% d^{-1} at Sabine Bank to 9.2% d^{-1} at Freeport A. Our findings indicate that Heald Bank, Sabine Bank, and Freeport Rocks all serve as settlement habitat of lane snapper, which appear to be capable of successful settlement across a variety of habitats.

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1. Introduction

Adult lane snapper (*Lutjanus synagris*) range from North Carolina to southeastern Brazil (Allen, 1985). They have been found in turbid, clear, and brackish waters, and occur over artificial and natural reefs as well as soft bottom habitats (Bortone and Williams, 1986). Lane snapper are an important component of the recreational and commercial fisheries in the Caribbean, often accounting for a significant fraction of the overall commercial catch in countries such as Puerto Rico (Matos-Caraballo, 2000) and Cuba (Bustamante et al., 2000). To a lesser extent, lane snapper are caught in the Gulf of Mexico (Bortone and Williams, 1986). Despite their commercial and recreational importance, the early life history of lane snapper is poorly understood and demographic data are needed to effectively characterize and protect nursery areas utilized by this species.

Information on post-settlement lane snapper is limited to basic distribution data from broad-scale surveys (Rooker and Dennis, 1991; Lindeman et al., 1998). These studies indicate that juvenile lane snapper use a variety of habitats (e.g. seagrass, mangrove prop roots, shell ridges, soft bottoms), including areas impacted by trawling activity (Gutherz and Pellegrin, 1988; Franks and VanderKooy, 2000), and thus survival and recruitment success of lane snapper may be reduced due to incidental bycatch from shrimp fisheries (Workman and Foster, 1994; Gillig et al., 2001). While several studies have attempted to characterize nursery habitat of other lutjanids in the Gulf of Mexico (e.g. Gallaway and Cole, 1999; Workman et al., 2002; Rooker et al., 2004), comparable studies have not been conducted for lane snapper.

In the northwestern Gulf, relic barrier islands form low-relief banks (i.e. sand-shell ridges) that are prominent features on the inner continental shelf, and along with associated non-structured (i.e. mud bottom) habitats, these areas serve as post-settlement habitat of lutjanids (Rooker et al., 2004; Wells, 2007). While habitat complexity (i.e. refuge) typically reduces predation-mediated mortality (Hixon and Beets, 1993), the relative importance of habitats on these natural banks is still undetermined for post-settlement lane snapper. Here, we evaluate the importance of banks and associated habitats in the northwestern Gulf of Mexico as nurseries of lane snapper. Estimates of density, growth, mortality, and recruitment potential were determined for post-settlement lane snapper collected from different banks and habitats (e.g. shell ridge, mud bottom).

2. Materials and methods

2.1. Field work

The study area included three natural banks in the Gulf of Mexico: Heald Bank, Sabine Bank, and Freeport Rocks (Fig. 1).

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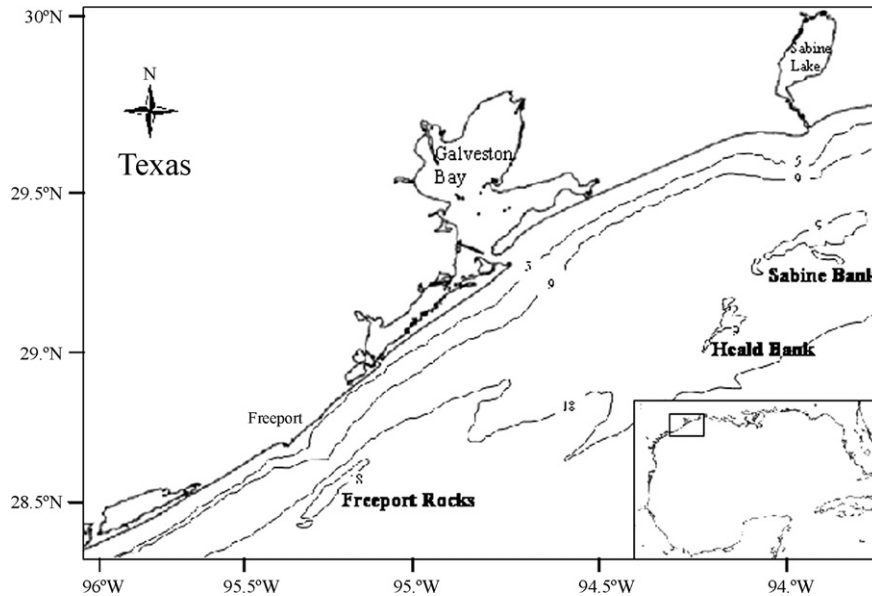*E-mail address:* rookerj@tamug.edu (J.R. Rooker).

Fig. 1. Study area in the northwestern Gulf of Mexico. Approximate depth contours are in meters.

Heald Bank is located southwest of the Texas/Louisiana border, approximately 71 km southwest of Sabine Pass, Texas, and is oriented from northeast to southwest. The study area of Heald Bank was approximately 20 km² and ranged in depth from 9 to 14 m. Sabine Bank is located south of the Texas/Louisiana border, approximately 39 km south of Sabine Pass, Texas, and is oriented northeast to southwest. The study area of Sabine Bank was approximately 27 km² and ranged in depth from 8 to 11 m. Freeport Rocks is approximately 22 km south of Freeport, Texas, and is oriented northeast to southwest. The area of Freeport Rocks covered in this study was approximately 80 km² and ranged in depth from 13 to 24 m.

Habitat maps were developed using an Edge Tech 272-TD dual frequency digital side-scan sonar, coupled with CODA data interpretation software. Habitats were delineated by reflectivity (density) of bottom sediments from side-scan sonar mosaics. Interpreted side-scan sonar images, along with bathymetric data of the banks, allowed us to choose trawl sites representative of different bottom types. The side-scan unit was towed at five knots, swath width was 200 m (100 m on either side). Ponar grab samples were also collected to ground truth bottom types. Sediment samples were oven dried in a tin and treated with HCl to determine the amount of carbonate in the sediment.

Trawl sites were chosen within each habitat type (inshore mud, shell ridge, offshore mud) based on imagery from side-scan sonar mosaics. Twelve trawl sites were chosen for Heald Bank, with 4 inshore, 4 ridge, and 4 offshore sites. Eighteen trawl sites were chosen for Sabine Bank, with 6 inshore, 6 ridge, and 6 offshore. Both Heald Bank and Sabine Bank were sampled in 2003. Freeport Rocks was sampled in two different years, 2000 and 2004. Hereafter, Freeport Rocks 2000 and Freeport Rocks 2004 will be referred to as Freeport A and Freeport B, respectively. Eighteen sites were chosen for Freeport A (6 inshore, 6 ridge, and 6 offshore), while 24 sites were chosen for Freeport B (6 inshore, 12 ridge, and 6 offshore). Post-settlement snapper were collected in bottom trawls from June through September to cover the anticipated recruitment period of lane snapper (Mikulas, 2007) in the Gulf of Mexico. We sampled each bank over a 2-d period every 2–4 weeks. Trawl locations were recorded with GPS and tow direction was against prevailing surface currents. Trawling speed was 2.5 knots and lasted for 5 min for surveys conducted in 2003 and 2004; 10 min trawls were taken during the earlier 2000 survey. A 6-m otter trawl, equipped with 2 cm mesh, a 1.25 cm mesh liner, and a 0.6 cm link tickler chain spread by 45 cm × 90 cm doors, was used to collect lane snapper. All lane snapper were immediately placed in a freezer for future processing. Temperature, salinity, and dissolved oxygen were recorded on the bottom of each bank with a Hydrolab Scout. All shells collected in each trawl were weighed to the nearest 0.1 kg.

2.2. Laboratory work

Prior to otolith extraction, standard length (SL) of each lane snapper was measured to the nearest 0.1 mm. Blotted weight was measured to the nearest 0.01 g. Sagittal otoliths were removed, cleaned, and processed based upon protocol described by Rooker et al. (2004). One sagitta was randomly selected, embedded, and sectioned along a transverse plane, adjacent to the core. Sections were polished and examined through transmitted light on an Olympus BX41 compound microscope. Image Pro Plus 4.5 image analysis software was employed to aid in counting growth increments. Daily growth increments were counted along the sulcus from the core to the otolith edge.

Ages were based upon the average of two counts for each otolith. In the event of a mean difference of counts greater than 10%, a third count was taken and used for age estimates. To complete hatch–date distributions and age–frequency plots, ages were also predicted for individuals with unreadable otoliths, and for individuals not included in age determination. Of the 420 otoliths prepared, 292 (70%) were included in analyses. Fish greater than 60 mm SL were considered beyond the scope of the post-settlement period, and therefore were not included in age-based results.

Daily increment formation was validated by marking otoliths of lane snapper with alizarin complexone following Thomas et al. (1995). Wild lane snapper were captured from Freeport Rocks in August of 2005, held in a circular tank for 6 d, dipped in 100 mg L⁻¹ alizarin complexone for 2 h, and sacrificed 5, 10, and 15 d later. Otoliths were removed, processed, and analyzed for the number of growth increments after the alizarin complexone mark, which confirmed that increments were deposited daily.

Daily growth rates were estimated by regressing standard length on predicted age. Samples were restricted to lane snapper ≤60 mm SL. Instantaneous mortality rates were calculated using a log-linear

regression equation of $\log_e$ abundance on age:

$$N_t = N_0 e^{-Zt}$$

where N_t represents the abundance at time t (age in days), N_0 represents abundance at time of hatching, and Z represents the instantaneous mortality coefficient. Our assessment of Z was based on the premise that lane snapper remained in settlement habitats during the time period mortality was estimated, and immigration and settlement from other habitats was negligible. To minimize the effect of dispersive behaviors (immigration, emigration) and size-based gear avoidance, mortality rates were only estimated over short (10 d) time intervals (Rooker and Holt, 1997).

2.3. Data analysis

All statistical analyses were performed using SPSS 13.0, and significance was accepted at $\alpha = 0.05$ level. Percent carbonate and shell weight were analyzed across habitats, with a one-way analysis of variance (ANOVA). Two-factor ANOVA was performed for all environmental parameters (temperature, salinity and DO), with date as a blocking factor. Two-factor ANOVA was also performed with density as a dependent variable, and habitat and date as independent variables. Many trawl sites and dates contained values of zero, so data were Ln + 1 transformed prior to analysis. Analysis of covariance (ANCOVA) was employed to determine the effects of date and habitat on length, age, growth, and mortality. Additionally, mortalities based on abundance decline over age were compared with ANCOVA for Sabine Bank only. The assumption of normality was tested with a Kilmogorov–Smirnov test, while the assumption of homogenous variances was examined with Levene's test and residual analysis. *Post hoc* differences among factor levels ($\alpha = 0.05$) were examined with Tukey's honestly significant difference (HSD) test when variances were equal, and with a Dunnett's T-3 test when variances were unequal (Zar, 1996). Since banks were sampled in different years, statistical testing of life history parameters was restricted to within bank (i.e. habitat, date) comparisons.

3. Results

3.1. Environmental conditions

During the primary settlement period (July–August), water temperatures increased at all banks (Fig. 2). Mean water temperature was lowest for offshore mud habitat at all banks except Sabine. Temperature differences among habitats were relatively small (i.e. within +1 °C); however, a significant effect was detected at one bank, Freeport B, where temperatures were lower in the offshore mud habitat (Fig. 2). Similarly, salinity varied little among habitats at each bank but a significant effect was observed for Freeport B with salinity being higher in the offshore mud habitat (Fig. 2). Dissolved oxygen values were significantly higher in the offshore mud habitats at Sabine Bank and Freeport A.

Shell material collected and carbonate sedimentary facies (expressed as kg ha^{-1} trawled and % CO$_3$, respectively) were also assessed on all banks. Shell material in trawls varied significantly among habitats at each location, with the majority of the shell collected in trawls over shell ridge habitat: Heald Bank (33.3 ± 7.8 kg ha^{-1}), Sabine Bank (18.5 ± 3.5 kg ha^{-1}), Freeport A (86.4 ± 23.7 kg ha^{-1}), and Freeport B (16.2 ± 3.1 kg ha^{-1}) ($P < 0.001$ for all banks). In some cases, the inshore and offshore mud habitats had shell material, which were orders of magnitude less than that of the shell ridge habitat. Similarly, percent carbonate values in sediment samples were also highest on the shell ridge habitat at the two banks examined.
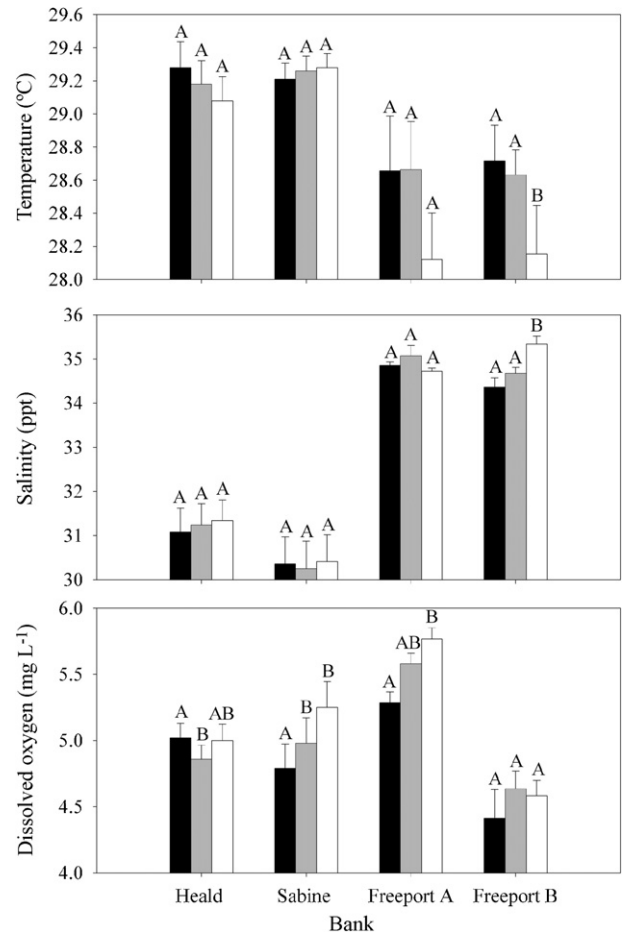

Fig. 2. Environmental conditions (±1 S.E.) on natural banks in the northwestern Gulf of Mexico: Heald Bank and Sabine Bank (2003), Freeport A (2000), and Freeport B (2004). Habitats are designated as inshore mud (■), shell ridge (▨), and offshore mud (□). Factor levels with the same letters are not significantly different, based upon *a posteriori* comparisons, $\alpha = 0.05$.

3.2. Abundance and distribution

Overall, 813 post-settlement lane snapper were collected, with mean densities from 20.8 ± 2.8 ind ha^{-1} at Sabine Bank to 1.1 ± 0. ind ha^{-1} at Heald Bank (Fig. 3). Densities varied as a function of both date and habitat at Sabine Bank (date $P = 0.018$, habitat $P = 0.020$) and Freeport A (date $P = 0.002$, habitat $P = 0.031$). Densities peaked during the 4 August sampling trip on Sabine Bank (37.9 ± 10.5 ind ha^{-1}), and numbers were significantly higher on the shell ridge (26.5 ± 6.9 ind ha^{-1}) and offshore mud habitats (25.5 ± 3.4 ind ha^{-1}), relative to inshore mud habitat (10.3 ± 2.8 ind ha^{-1}). On Freeport A, peak densities were significantly higher during the 5 July (17.8 ± 6.2 ind ha^{-1}) and 17 July (18.6 ± 5.6 ind ha^{-1}) sampling trips, and numbers were significantly higher inshore (17.6 ± 4.9 ind ha^{-1}) than offshore (5.2 ± 1.7 ind ha^{-1}). Densities peaked during the 1 August (4.0 ± 1.1 ind ha^{-1}) and 1 September (6.2 ± 4.4 ind ha^{-1}) sampling trips on Freeport B, but no significant difference in date ($P = 0.148$, power = 0.515) or habitat (habitat $P = 0.528$, power = 0.155) was detected.

3.3. Size

Mean length of post-settlement lane snapper increased over the sampling season at all banks, and size varied by habitat. Lane
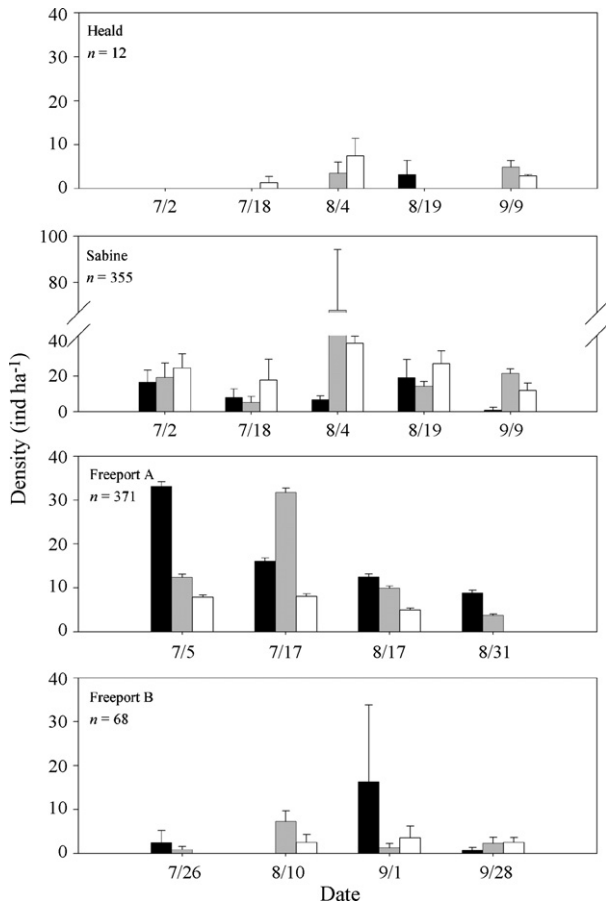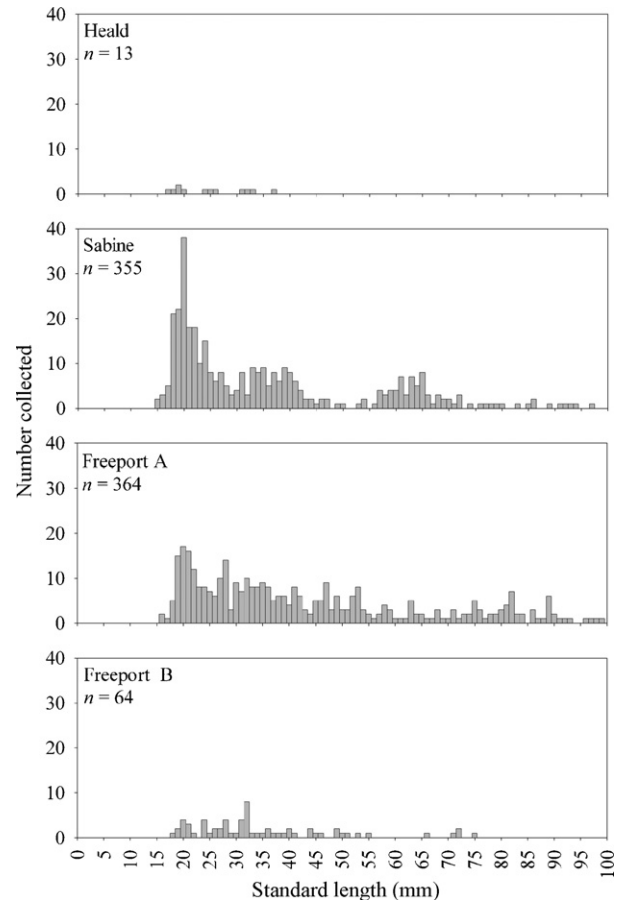
Fig. 3. Mean densities (±1 S.E.) of post-settlement lane snapper collected in trawls on Heald Bank (2003), Sabine Bank (2003), Freeport A (2000) and Freeport B (2004). Habitats are designated as inshore mud (■), shell ridge (▨), and offshore mud (□).
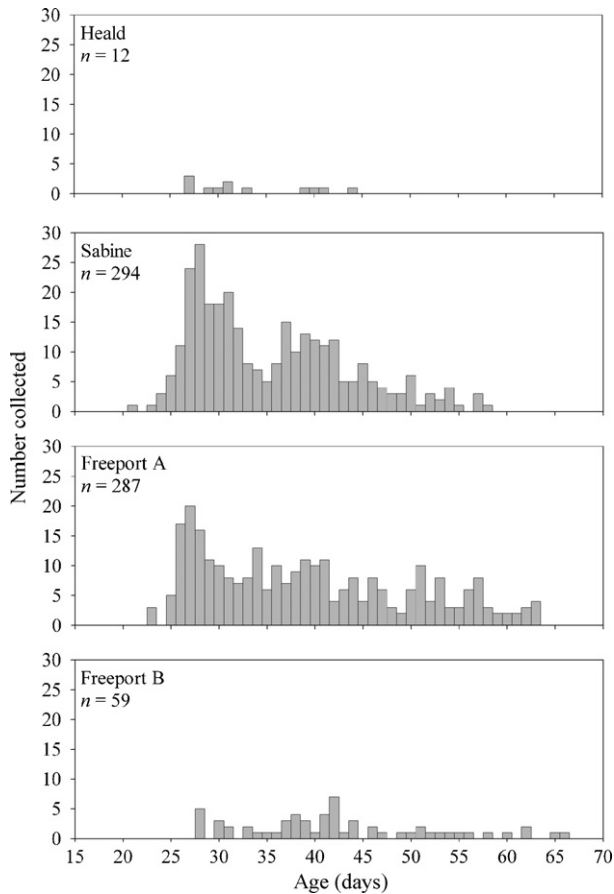

Fig. 4. Length–frequency distributions of post-settlement lane snapper from Heald Bank and Sabine Bank (2003), Freeport A (2000), and Freeport B (2004). Twelve out of the 813 individuals collected (1.5%) were ≥100 mm SL and not included.

snapper at Freeport A and Freeport B (44.2 ± 1.2 and 43.1 ± 4.3 mm, respectively) were larger than lane snapper from either Heald Bank (28.0 ± 3.6 mm) or Sabine Bank (36.2 ± 1.0 mm). Still, the minimum length of new settlers present on each bank was relatively similar with individuals <19 mm collected on all banks: Heald Bank (16.9 mm), Sabine Bank (15.1 mm), Freeport A (15.9 mm), and Freeport B (18.1 mm) (Fig. 4). Date was identified as a factor significantly affecting mean length of lane snapper on Freeport A and Freeport B (ANCOVA, intercepts test, $P < 0.001$ and $P = 0.034$, respectively), with length doubling from July to August at Freeport A (28.2–74.7) and Freeport B (25.8–62.9). In addition to date, mean length of post-settlement lane snapper varied as a function of habitat. Individuals found on the shell ridge habitat were significantly larger than those on the inshore or offshore mud habitats of Freeport A and Freeport B (ANCOVA, intercepts test, $P < 0.001$ and ANCOVA, intercepts test, $P = 0.018$, respectively). Similarly, the mean length of lane snapper at Sabine Bank was higher on the shell ridge habitat (37.3 ± 1.8 mm) than either the inshore (33.0 ± 1.8 mm) or offshore (36.4 ± 1.5 mm) mud habitats.

3.4. Age and growth

Age of post-settlement lane snapper ranged from 21 to 66 d, and individuals <29 d old were collected from all banks (Fig. 5). The majority of lane snapper were 25–40 d (peak at 27–28 d) for Heald Bank, Sabine Bank, and Freeport A. At Freeport B, most individuals were greater than 40 d (peak at 42 d). The oldest individuals were collected during trawl surveys at the end of the season at Heald Bank, Sabine Bank, and Freeport A; however, no temporal effect on age was detected at Freeport B (ANCOVA, intercepts test, $P = 0.069$, power = 0.446). A significant interaction between date and habitat on age was observed for Sabine Bank (ANCOVA, slopes test, $P = 0.021$) and Freeport A (ANCOVA, slopes test, $P = 0.008$). The mean age of lane snapper on the shell ridge habitat at both Freeport A and Freeport B was approximately 5–10 d older than observed for the inshore and offshore mud habitats.

Hatch dates of lane snapper ranged from early May to late August across all banks, and both bimodal and unimodal hatch–date distributions were observed (Fig. 6). While catch numbers were too low on Heald Bank to show any clear pattern, the majority of hatch dates were from July. The hatch–date distribution at Sabine Bank was bimodal, with peaks in early June and mid July. In contrast, Freeport A had a unimodal hatch–date distribution, with a single peak in early June. The majority of lane snapper from Freeport B (78%) were from June and July spawning events.

Growth rates were similar among Heald Bank (0.9 mm d^{-1}), Sabine Bank (1.3 mm d^{-1}), Freeport A (1.1 mm d^{-1}), and Freeport B (0.9 mm d^{-1}) (Fig. 7). Using hatch–date distributions, two distinct cohorts (1 May to 21 June and 23 June to 31 July) were identified for Sabine Bank. Cohort-specific variation in growth was detected, with the early season rate (1.0 mm d^{-1}) being significantly lower than the later season rate (1.4 mm d^{-1}) at Sabine Bank (ANCOVA, slopes, $P = 0.048$). Habitat-specific growth was also investigated at

Fig. 5. Age-frequency distributions of post-settlement lane snapper (≤60 mm SL) from Heald Bank and Sabine Bank (2003), Freeport A (2000), and Freeport B (2004).
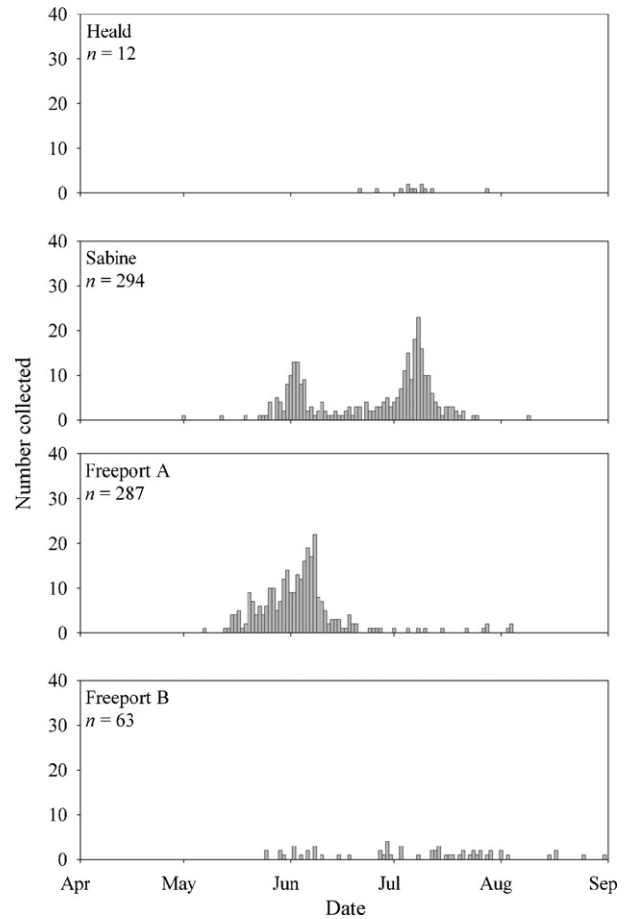
Fig. 6. Hatch–date distributions of post-settlement lane snapper (≤60 mm SL) from Heald Bank and Sabine Bank (2003), Freeport A (2000), and Freeport B (2004).

Sabine Bank and no effect was detected (ANCOVA, slopes $P = 0.126$, power = 0.427).

3.5. Mortality

Daily instantaneous mortality coefficients ($Z\,d^{-1}$) were estimated for lane snapper over 10-d intervals at Sabine Bank and Freeport A (Fig. 8). Overall, Z estimates were higher on Sabine Bank ($Z = 0.165$) than Freeport A ($Z = 0.097$) over similar age intervals (27–36 d and 26–35 d, respectively). Mortality rates of early season ($Z = 0.162$) and late season (0.155) cohorts were similar (ANCOVA, slopes test, $P = 0.894$, power = 0.018), thus cohorts were pooled for estimates of habitat-specific mortality at Sabine Bank. Significant differences in instantaneous mortality were detected between the ridge ($Z = 0.275$) and offshore mud ($Z = 0.111$) habitats (ANCOVA, slopes test, $P = 0.021$) at Sabine Bank.

4. Discussion

Post-settlement lane snapper were observed on banks from June through September, with peak densities occurring from July to August. Similar to other marine teleosts, spawning seasons of lane snapper (Luckhurst et al., 2000) and other lutjanids (Allman and Grimes, 2002; Denit and Sponagule, 2004) are often restricted to specific seasons. Thus, intra-annual variability in settlement density observed in the present study is not surprising. Inter-annual variation in settlement of lane snapper was also observed at Freeport Rocks and this is relatively common among lutjanids (Rooker et al., 2004). Observed differences in settlement time

between years may be attributed to variation in abiotic or biotic conditions such as temperature (Lankford and Targett, 2001), prey availability (Cowan and Shaw, 2002), and predation mortality (Webster, 2002).

Densities of post-settlement lane snapper were variable across habitats, and patterns were not consistent across banks surveyed. Still, catch numbers of lane snapper in this region of the Gulf were high relative to estimates of post-settlement densities reported by Thayer et al. (1999) in Florida Bay (FL), suggesting natural banks in the NW Gulf may serve as important nursery habitat. In our study, significantly higher densities of post-settlement lane snapper were found on Sabine Bank's ridge and offshore habitats. Conversely, lane snapper densities at Freeport A were significantly higher on the inshore habitat than the offshore habitat. This inconsistency of lutjanid density by habitat was also observed by Rooker et al. (2004) where post-settlement red snapper were found across all habitats and peak densities occurred on different habitats in different years. Although this congener has been shown to settle to structured habitat (Szedlmayer and Conti, 1999), it appears that young red snapper settle on both structured (shell ridge), and unstructured (inshore and offshore mud) habitats, and tend to move to structured habitats with increasing size (Szedlmayer and Lee, 2004; Wells and Cowan, 2007). Mean sizes of lane snapper within banks were greater on the ridge habitat in three of four surveys (Sabine Bank, Freeport A and Freeport B), suggesting larger individuals select for, or move to structured habitat. However, lane snapper do not appear to favor shell ridge habitats over mud bottoms during the early post-settlement period, and this finding has been reported for other
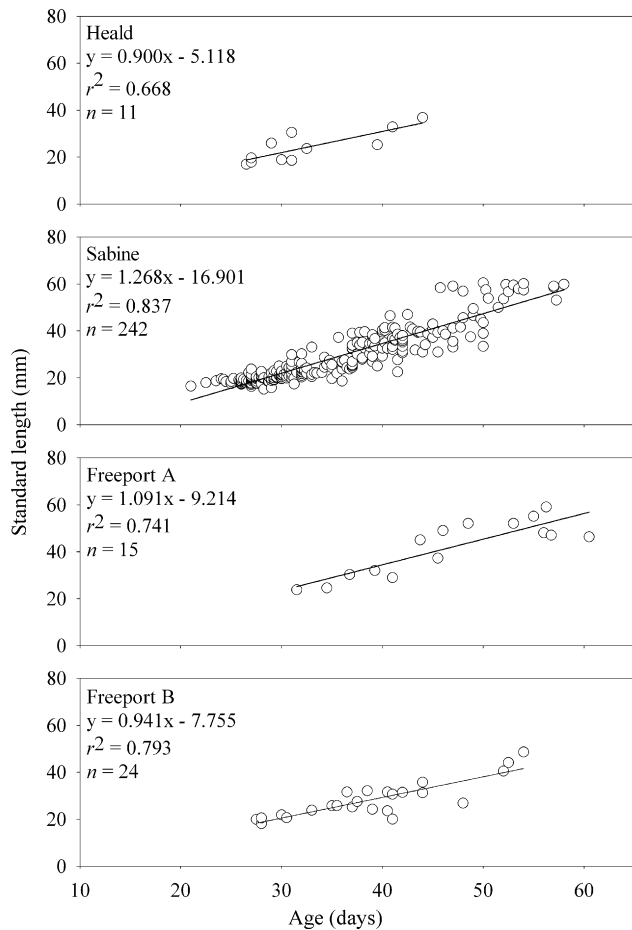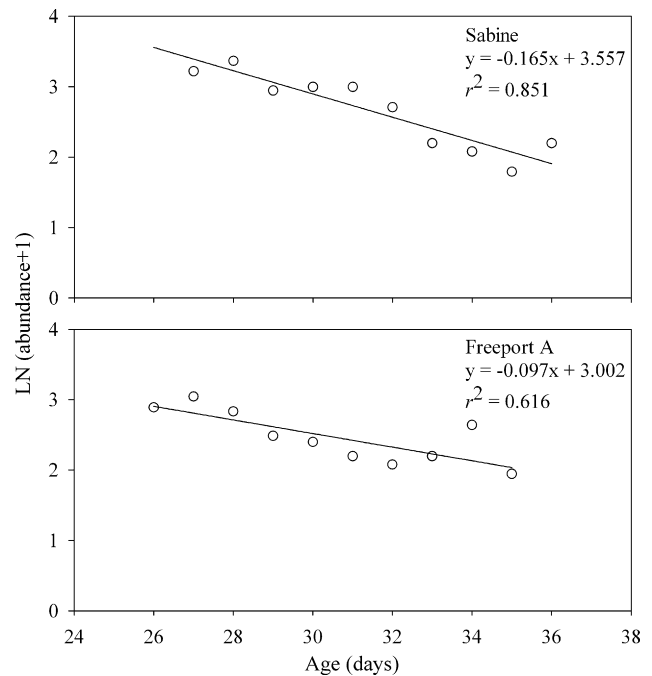
Fig. 7. Size-at-age relationships by bank for post-settlement lane snapper (≤60 mm SL) from Heald Bank and Sabine Bank (2003), Freeport A (2000), and Freeport B (2004). Linear regression plots and equations included. Growth rate based on slope of regression equation.

Fig. 8. Linear regression of Ln (abundance +1) on age of post-settlement lane snapper from Sabine Bank (2003) and Freeport Rocks A (2000). Age range is from 27 to 36 d for Sabine and from 26 to 35 d for Freeport A. Linear regression plots and equations included.

lutjanids (Rooker et al., 2004; Szedlmayer and Lee, 2004). Ontogenetic shifts to more structured habitats by red snapper have been attributed to increased size (Patterson et al., 2005) and possibly occur for lane snapper as well.

Estimated hatch dates (May–August) observed here were similar to reported spawning times (approximately 20–24 h prior to hatch, Borrero et al., 1978) of lane snapper in Bermuda, which range from May through early September, with peaks in June–August (Luckhurst et al., 2000). In warmer waters of the Caribbean, lane snapper are perennial (Acosta and Appeldoorn, 1992), and prolonged spawners (Manickchand-Dass, 1987; Aiken, 2001). Still, times of peak spawning in many of these regions fall within the range observed for lane snapper reported in this study. Peak spawning in Puerto Rico and Jamaica occurred in May (Acosta and Appeldoorn, 1992), and July–August (Aiken, 2001), respectively. In contrast, peak spawning in Trinidad occurs earlier (March) than reported in other studies (Manickchand-Dass, 1987). Although perennial spawning is not expected in the northwestern Gulf of Mexico, protracted spawning is possible.

Growth rates observed for lane snapper in this study were comparable to studies on congeners from the Gulf of Mexico. To date, previous assessments of growth for lane snapper have focused on larger (>150 mm FL) individuals (Acosta and Appeldoorn, 1992; Johnson et al., 1995; Luckhurst et al., 2000; Aiken, 2001). Thus, otolith-based estimates of growth determined here for post-settlers serve as the baseline for future studies. In

general, growth rates of post-settlement lane snapper ranged from 0.9 to 1.3 mm d^{-1}, and these values are in the upper range of rates reported for post-settlement red snapper (Szedlmayer and Conti, 1999; Rooker et al., 2004; Geary et al., 2007) and gray snapper (Allman and Grimes, 2002; Denit and Sponagule, 2004) in the Gulf of Mexico.

Spatial and temporal variation in growth is not uncommon during early life for lutjanids (Allman and Grimes, 2002) as well as other fishes in the Gulf of Mexico (e.g. DeVries and Grimes, 1997; Rooker et al., 1999). Cohort-specific variation in growth was observed in the present study, with early season settlers growing at a slower rate (1.0 mm d^{-1}) than individuals arriving later in the season (1.4 mm d^{-1}). Cohort-specific differences in growth have been attributed to a variety of factors, including temperature (Taylor and Able, 2006), salinity (Secor et al., 2000), food availability (Cowan and Shaw, 2002; Katersky et al., 2006) and predation mortality (Rilling and Houde, 1999; Taylor and Able, 2006). Slower growth observed for the early season cohort of lane snapper is possibly linked to temperature, since the early cohort experienced water temperatures 1–2 °C lower. No significant differences in growth were detected among habitats, and the lack of significant habitat-specific differences in growth of lane snapper suggests that environmental conditions were relatively consistent across the three habitats. Temperature, typically the primary physical factor affecting growth (Jones, 2002), did not vary significantly among habitats, and salinity and dissolved oxygen levels were higher than the minimum thresholds for other lutjanids (Gallaway and Cole, 1999), lending support to this premise.

Mortality of post-settlement lane snapper on Sabine Bank (15.2% d^{-1}) was almost double that of Freeport A (9.2% d^{-1}). Although no previous mortality estimates of post-settlement lane snapper exist, rates observed in this study were comparable to mortality rates for other species. Rooker et al. (2004) reported a mortality rate of 0.129 (12.1%) for post-settlement red snapper

(47–57 d) from the same site. In addition, mortality coefficients, both higher and lower than those observed in this study, have been estimated from other lutjanids: 0.19–0.29 for larval vermillion snapper (*Rhomboplites aurorubens*) (Comyns et al., 2003), 0.04–0.28 for juvenile yellowtail snapper (*Ocyurus chrysurus*) (Watson et al., 2002) and 0.14–0.43 for juvenile gray snapper (Allman and Grimes, 2002). Early life mortality is often linked to water quality (Sponagule and Grorud-Colvert, 2006), and density-dependent processes, such as predation mortality (Holbrook and Schmitt, 2002), starvation (Leggett and DeBlois, 1994; Sogard, 1997), and disease (Houde, 2002). Although it is difficult to determine the exact cause of observed differences in mortality between the two banks examined, both density and mortality of lane snapper were lower on Freeport A, possibly indicating that density-dependent factors could be involved.

Acknowledgements

References

Acosta, A., Appeldoorn, R.S., 1992. Estimation of growth, mortality and yield per recruit for *Lutjanus synagris* (Linnaeus) in Puerto Rico. Bull. Mar. Sci. 50, 282–291.

Aiken, K.A., 2001. Aspects of reproduction, age and growth of the lane snapper, *Lutjanus synagris* (Linnaeus, 1758) in Jamaican coastal waters. Proc. Gulf Carib. Fish. Inst. 52, 116–134.

Allen, G.R., 1985. FAO species catalogue. Snappers of the world. Annotated and illustrated catalogue of lutjanid species known to date. FAO Fish. Synop. 6 (125), 2008.

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. Fish. Bull. 100, 391–403.

Borrero, M., Gonzales, E., Millares, N., Damas, T., 1978. Embryological and prelarval development of the lane snapper (*Lutjanus synagris* Linne, 1758). Rev. Cub. Invest. Pesq. 3, 1–28.

Bortone, S.A., Williams, J.L., 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (south Florida)—gray, lane, mutton, and yellowtail snappers. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.52). U.S. Army Corps of Engineers, TR EL-82-4.

Bustamante, G., Chiappone, M., Kelly, J., Lowe, A., Sealy, K.S., 2000. Fish and fisheries in Guantanamo Bay, Cuba: recommendations for their protection. Proc. Gulf Carib. Fish. Inst. 51, 242–257.

Comyns, B.H., Shaw, R.F., Lyczkowski-Shultz, J., 2003. Small-scale spatial and temporal variability in growth and mortality of fish larvae in the subtropical northcentral Gulf of Mexico: implications for assessing recruitment success. Fish. Bull. 101, 10–21.

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, pp. 88–111.

Denit, K., Sponagule, S., 2004. Growth variation, settlement, and spawning of gray snapper across a latitudinal gradient. Trans. Am. Fish. Soc. 133, 1339–1355.

DeVries, D.A., Grimes, C.B., 1997. Spatial and temporal variation in age and growth of king mackerel, *Scomberomorus cavalla*, 1977–1992. Fish. Bull. 95, 694–708.

Franks, J.S., VanderKooy, K.E., 2000. Feeding habitats of juvenile lane snapper *Lutjanus synagris* from Mississippi coastal waters, with comments on the diet of gray snapper *Lutjanus griseus*. Gulf Carib. Res. 12, 11–17.

Gallaway, B.J., Cole, J.G., 1999. Delineation of essential habitat for juvenile red snapper in the northwestern Gulf of Mexico. Trans. Am. Fish. Soc. 128, 713–726.

Geary, B.W, Mikulas Jr., J.J., Rooker, J.R., Landry, A.M., Dellapenna, T.M., 2007. Patterns of habitat use by newly settled red snapper in the northwestern Gulf of Mexico. In: Patterson III, W.F., Cowan Jr., J.H., Fitzhugh, G.R., Nieland, D.L. (Eds.), Red Snapper Ecology and Fisheries in the U.S. Gulf of Mexico, Am. Fish. Soc. Symp. 60. Bethesda, Maryland.

Gillig, D., Griffin, W.L., Ozuna Jr., T., 2001. A bioeconomic assessment of Gulf of Mexico red snapper management policies. Trans. Am. Fish. Soc. 130, 117–129.

Gutherz, 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. Mar. Fish. Rev. 50, 17–25.

Holbrook, S.J., Schmitt, R.J., 2002. Competition for shelter space causes density-dependent predation mortality in damselfishes. Ecology 3, 2855–2868.

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, pp. 64–87.

Hixon, M.A., Beets, J.P., 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. Ecol. Monogr. 63, 77–101.

Johnson, A.G., Collins, L.A., Dahl, J., Baker, M.S., 1995. Age, growth, and mortality of lane snapper from the northern Gulf of Mexico. In: Proc. Annu. Conf. SEAFWA. 49, pp. 178–186.

Jones, C.M., 2002. Age and growth. In: Fuiman, L.A., Werner, R.G. (Eds.), Fishery Science: The Unique Contributions of Early Life Stages. Blackwell Science Ltd., Oxford, pp. 33–63.

Katersky, R.S., Peck, M.A., Bengtson, D.A., 2006. Oxygen consumption of newly settled summer flounder, *Paralichthys dentatus* (Linnaeus, 1766). Aquaculture 257, 249–256.

Lankford, T.E., Targett, T.E., 2001. Low-temperature tolerance of age-0 Atlantic croakers: recruitment implications for US Mid-Atlantic estuaries. Trans. Am. Fish. Soc. 130, 236–249.

Leggett, W.C., DeBlois, E., 1994. Recruitment in marine fishes—is it regulated by starvation and predation in the egg and larval stages. Neth. J. Sea Res. 32, 119–134.

Lindeman, K.C., Diaz, G.A., Serafy, J.E., Ault, J.S., 1998. A spatial framework for assessing cross-shelf habitat use among post-settlement grunts and snappers. Proc. Gulf Carib. Fish. Inst. 50, 385–416.

Luckhurst, B.E., Dean, J.M., Reichert, M., 2000. Age, growth and reproduction of the lane snapper *Lutjanus synagris* (Pisces: Lutjanidae) at Bermuda. Mar. Ecol. Prog. Ser. 203, 255–261.

Manickchand-Dass, S., 1987. Reproduction and growth of the lane snapper, *Lutjanus synagris* (Linnaeus), in Trinidad, West Indies. 1987. Bull. Mar. Sci. 40, 22–28.

Matos-Caraballo, D., 2000. Overview of Puerto Rico's small scale fisheries statistics: 1994–1997. Proc. Gulf Carib. Fish. Inst. 51, 215–231.

Mikulas, J.J. Jr., 2007. Habitat use, growth, and mortality of post-settlement lane snapper (*Lutjanus synagris*) on natural banks in the northwestern Gulf of Mexico. M.S. Thesis, Texas A&M University, College Station, Texas.

Patterson, W.F., Wilson, C.A., Bentley, S.J., Cowan, J.H., 2005. Delineating juvenile red snapper habitat on the northern Gulf of Mexico continental shelf. Am. Fish. Soc. Symp. 41, 277–288.

Rilling, G.C., Houde, E.D., 1999. Regional and temporal variability in distribution and abundance of bay anchovy (*Anchoa mitchilli*) eggs, larvae, and adult biomass in the Chesapeake Bay. Estuaries 22, 1096–1109.

Rooker, J.R., Dennis, G.D., 1991. Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. Bull. Mar. Sci. 49, 684–698.

Rooker, J.R., Holt, S.A., 1997. Utilization of subtropical seagrass meadows by newly settled red drum *Sciaenops ocellatus*: patterns of distribution and growth. Mar. Ecol. Prog. Ser. 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. Fish. Bull. 97, 581–590.

Rooker, J.R., Landry Jr., A.M., Geary, B.W., Harper, J.A., 2004. Assessment of a shell bank and associated substrates as nursery habitat of postsettlement red snapper. Est. Coast. Shelf Sci. 59, 653–661.

Secor, D.H., Gunderson, T.E., Karlsson, K., 2000. Effect of temperature and salinity on growth performance in anadromous (Chesapeake Bay) and nonanadromous (Santee-Cooper) strains of striped bass Morone saxatilis. Copeia 2000, 291–296.

Sogard, S.M., 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull. Mar. Sci. 60, 1129–1157.

Sponagule, S., Grorud-Colvert, K., 2006. Environmental variability, early life-history traits, and survival of new coral reef fish recruits. Integr. Comp. Biol. 46, 623–633.

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. Fish. Bull. 97, 626–635.

Szedlmayer, S.T., Lee, J.D., 2004. Diet shifts of juvenile red snapper (*Lutjanus campechanus*) with changes in habitat and fish size. Fish. Bull. 102, 366–375.

Taylor, D.L., Able, K.W., 2006. Cohort dynamics of summer-spawned bluefish as determined by length-frequency and otolith microstructure analyses. Trans. Am. Fish. Soc. 135, 955–969.

Thayer, G.W., Powell, A.B., Hoss, D.E., 1999. Compostion of larval, juvenile, and small adult fishes relative to changes in environmental conditions in Florida Bay. Estuaries 22, 518–533.

Thomas, L.M., Holt, S.A., Arnold, C.R., 1995. Chemical marking techniques for larval and juvenile red drum (*Scianops ocellatus*) otoliths using different fluorescent markers. In: Secor, D.H., Dean, J.M., Campana, S.E. (Eds.), Recent Developments in Fish Otolith Research. University of South Carolina Press, Columbia, pp. 703–717.

Watson, M., Munro, J.L., Gell, F.R., 2002. Settlement, movement and early juvenile mortality of the yellowtail snapper *Ocyurus chrysurus*. Mar. Ecol. Prog. Ser. 237, 247–256.

Webster, M.S., 2002. Role of predators in the early post-settlement demography of coral-reef fishes. Oecologia 131, 52–60.

Wells, R.J.D., 2007. The effects of trawling and habitat use on red snapper and the associated community. Ph.D. Dissertation, Louisiana State University, Baton Rouge, Louisiana.

Wells, R.J.D., Cowan Jr., J.H., 2007. Video estimates of red snapper and associated fish assemblages on sand, shell, and natural reef habitats in the northcentral Gulf of Mexico. In: Patterson III, W.F., Cowan Jr., J.H., Fitzhugh, G.R., Nieland, D.L.

(Eds.), Red Snapper Ecology and Fisheries in the U.S. Gulf of Mexico, Am. Fish. Soc. Symp. 60. Bethesda, Maryland, pp. 37–53.

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. Mar. Fish. Rev. 56, 9–11.

Workman, I.K., Shah, A., Foster, D., Hataway, B., 2002. Habitat preferences and site fidelity of juvenile red snapper (*Lutjanus campechanus*). ICES J. Mar. Sci. 59, S43–S50.

Zar, J.H., 1996. Biostatistical Analysis, 3rd ed. Prentice Hall, New Jersey.