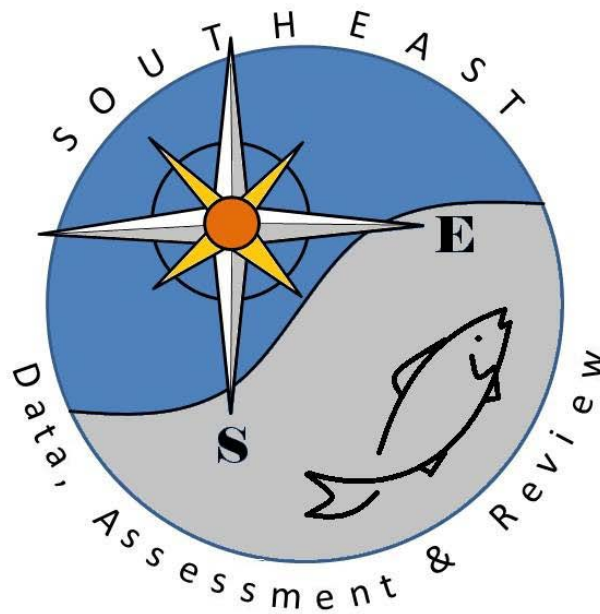# Effect of trawling on juvenile red snapper (*Lutjanus campechanus*) habitat selection and life history parameters

R.J. David Wells, James H. Cowan, Jr., William F. Patterson III, and Carl J. Walters

SEDAR31-RD31

14 August 2012

Effect of trawling on juvenile red snapper (*Lutjanus campechanus*) habitat selection and life history parameters

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Abstract: This study documents ontogenetic habitat shifts of red snapper (*Lutjanus campechanus*) and highlights possible impacts of shrimp trawling on age-0 fish life history parameters on the northern Gulf of Mexico (GOM) continental shelf. Red snapper were collected quarterly during 2004 and 2005 over sand, low-relief shell rubble, high-relief shell rubble, and natural high-relief reef habitats within a de facto nontrawl area and in similar habitats on the open shelf where commercial shrimp trawling occurred. Age-0 red snapper were most dense over sand and low-relief shell rubble habitats and moved to higher-relief shell rubble and natural reef habitats by age-1. Habitat-specific daily growth rates of age-0 fish were highest over sand (range 0.65–1.03 mm·day^{-1}). Densities of age-0 red snapper were highest over trawled sand, but higher over nontrawled shell rubble by 6 months of age (age-0.5+). Red snapper collected over sand and low-relief shell rubble areas exposed to trawling had truncated size distributions, higher mortality estimates, and lower production potential (the latter evaluated with *G–Z* and *P–B* ratios) compared with fish over nontrawled areas of similar habitat. Results suggest that juvenile red snapper residing over nontrawled areas may have a higher probability of survival than fish in areas exposed to commercial shrimp trawling.

Résumé : Notre étude renseigne sur les modifications ontogéniques de l'habitat chez le vivaneau rouge (*Lutjanus campechanus*) et met en évidence les impacts possibles de la pêche à la crevette au chalut sur les paramètres démographiques des poissons d'âge 0 sur la plate-forme continentale du nord du golfe du Mexique (GOM). Nous avons récolté des vivaneaux rouges à tous les trimestres en 2004 et 2005 sur des substrats de sable, de débris de coquillages à relief bas, de débris de coquillages à relief accentué et dans des habitats de récifs naturels à fort relief dans une zone en fait sans chalutage, ainsi que dans des habitats similaires sur la plate-forme découverte où il se fait de la pêche commerciale à la crevette. Les vivaneaux rouges d'âge 0 se retrouvent en plus forte densité sur les substrats de sable ou de débris de coquillages à bas relief et, à l'âge 1, ils se sont déplacés vers les habitats de débris de coquillages à relief accentué et vers les récifs naturels. Les taux de croissance spécifiques à l'habitat des poissons d'âge 0 les plus élevés s'observent sur les substrats de sable (étendue : 0,65–1,03 mm·jour^{-1}). Les densités les plus grandes de vivaneaux rouges d'âge 0 se retrouvent sur les substrats sablonneux soumis au chalutage, mais, à l'âge de six mois (âge 0,5+), elles sont plus élevées sur les débris de coquillages non affectés par le chalutage. Les vivaneaux rouges récoltés dans les zones de sable et de débris de coquillage à bas relief soumises au chalutage affichent des distributions tronquées des tailles, des estimations plus élevées de la mortalité et un potentiel de production plus faible (ce dernier évalué d'après les rapports *G–Z* et *P–B*) que les poissons vivant dans des habitats similaires dans des zones non exposées au chalutage. Nos résultats laissent croire que les jeunes vivaneaux rouges vivant dans des zones non soumises au chalutage ont une plus grande probabilité de survie que les poissons exposés à la pêche commerciale à la crevette par chalutage.

[Traduit par la Rédaction]

Introduction

Trawling may affect targeted and nontargeted species directly by fishing or bycatch mortality and indirectly by reducing habitat complexity and thus quality (Auster et al.

1996; National Research Council (NRC) 2002). Shrimp trawl bycatch of juveniles is the most significant source of mortality for red snapper (*Lutjanus campechanus*) in US waters of the Gulf of Mexico (GOM) (Goodyear 1995). An estimated 25–30 million individuals are caught annually in

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shrimp trawls (Ortiz et al. 2000), which may account for as much as 90% of juvenile red snapper mortality (Goodyear and Phares 1990; Goodyear 1995). The GOM trawl fishery, which currently produces the highest discard to landings ratio of any US marine fishery (Harrington et al. 2005), targets shrimp on soft-sediment habitats that are assumed to be of low structural complexity and species diversity. However, soft-sediment habitats support a high diversity of organisms that play key roles in the ecosystem and provide important prey resources for fishes such as red snapper (Bradley and Bryan 1975; Arreguin-Sanchez et al. 2004; McCawley et al. 2006). Furthermore, trawling in the northern GOM is not confined to soft sediments and often affects more complex habitats, such as sandbanks and shell rubble habitats. Auster (1998) identified habitats such as biogenic structures and shell aggregates as some of the more susceptible habitats to adverse impacts of trawling.

Reduction in juvenile bycatch by shrimp trawls appears to be necessary to increase the spawning stock biomass of adult red snapper. It has been surmised that a technological solution to bycatch reduction may not exist, and the addition of shrimp nontrawl areas or time closures may be necessary for fisheries management to provide additional protection for juvenile red snapper (Gallaway et al. 1999; Diamond 2004; Patterson et al. 2005). However, studies addressing the relative importance of different habitats (i.e., differential growth rates and production potential) for juvenile red snapper are necessary to evaluate that management option. The following four habitat-specific levels of information have been proposed to evaluate habitat quality and to assess whether a given habitat should be considered essential fish habitat (EFH) (Minello 1999): (*i*) fish presence–absence, (*ii*) fish density, (*iii*) fish growth, reproduction, or survival, and (*iv*) fish production. Furthermore, large-scale closure experiments are needed to test for possible compensatory changes in mortality rates of juveniles protected from bycatch mortality, as such effects could cancel the intended positive benefits of reduced mortality.

The purpose of this study was to characterize ontogenetic habitat use of red snapper among natural substrates on the GOM inner continental shelf in areas that have historically supported high concentrations of red snapper. Specifically, we investigated habitat use over sand, low-relief shell rubble, high-relief shell rubble, and natural reefs. We assessed habitat value with comparisons of red snapper density, size, age, growth, mortality, and production potential among habitat types. In addition, we assessed habitat-specific effects of shrimp trawling on red snapper demographics, vital rates, and production potential, with comparisons focused on sand and low-relief shell rubble habitats where juvenile red snapper were most abundant.

Materials and methods

Study sites

Our study region was located on the northern GOM continental shelf and had two main subregions (Fig. 1). The first subregion was an area of open shelf that was exposed to shrimp trawling. Based on the surface area of the seafloor and shrimp effort data, Wells et al. (2008a) conservatively estimated that shrimp trawling effort in this subregion was

Fig. 1. Map of habitat types on the north-central Gulf of Mexico (GOM). Inset map shows the location of the study region in relation to the Gulf coast of southern USA. The 20 and 40 m depth contours are shown; in the inset, the 200 m depth contour represents the shelf edge. Enclosed shaded regions indicate the de facto nontrawl areas inside the Alabama artificial reef permit areas.
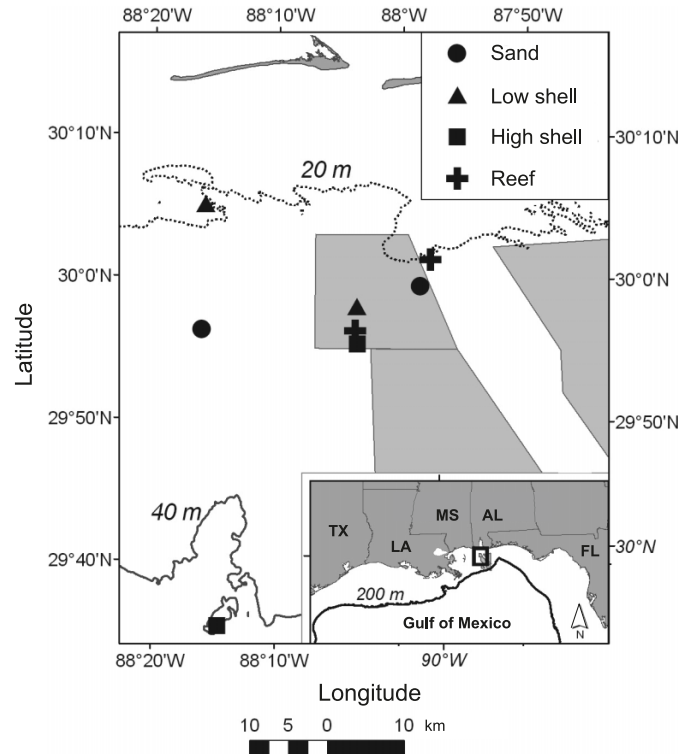
sufficient to sweep the area at least once per year during 2004 and 2005. Moreover, electronic logbook data indicate that some areas of the shelf are targeted with much greater frequency (Benny Gallaway, LGL Ltd., 1410 Cavitt Street, Bryan, TX 77801, USA, personal communication). The second subregion of our study was an extensive (>3000 km²) artificial reef permit area in the northern GOM that was directly adjacent to our open shelf areas (Fig. 1). This artificial reef permit area served as a de facto nontrawl area because shrimp vessels rarely enter it for fear of losing their nets (Link 1997; NRC 2002).

Seabed characterization of the region inside and outside the permit areas was recently performed with digital side-scan sonar and analysis of box core sediment samples during previous studies (Dufrene 2005; Patterson et al. 2005). Results indicate that similar habitat types inside and outside the permit areas have similar geotechnical properties (e.g., sand–mud ratio, percent $CaCO_3$, organic carbon content) (Dufrene 2005; Patterson et al. 2005). Habitat types identified include sand sites with interspersed mud (hereafter sand), low-relief shell-rubble sites (<1 m vertical relief; <40% $CaCO_3$) (hereafter low shell), high-relief shell-rubble sites (1–3 m vertical relief; >40% $CaCO_3$) (hereafter high shell), and natural high-relief (>2 m vertical relief) reef sites (hereafter reef) (Fig. 1). However, because no trawling occurs directly on reef sites and the proximity of the trawled high shell site was distant and at a greater depth

than other sites, our trawling comparisons were limited to sand and low shell habitats.

Shell rubble ridges in the study area are relict oyster reefs formed prior to the Holocene transgression (Schroeder et al. 1988; Dufrene 2005). Ridges are oriented in a northwest to southeast direction, extend for several kilometres in length with distances between ridges varying from 100s of metres to over a kilometre, and are thought to be part of the Perdido shoals on the eastern Alabama–Florida continental shelf (Dufrene 2005). McBride et al. (1999) described the Perdido shoals over the midshelf as two long (30–120 km) and relatively narrow (<6 km) parallel shore features.

Field sampling

Trawl sampling was conducted quarterly in 2004 and 2005 from the R/V *Caretta*, an 18 m research vessel operated by NOAA Fisheries Pascagoula Laboratory (hereafter NMFS). Three sampling stations were selected for trawl sampling over each habitat type both exposed and not exposed to trawling; stations were fixed for the duration of the study, although care was taken to avoid repeatedly sampling the same transects. A total of 171 trawl samples was obtained for the duration of the study: trawl sand ($n = 21$), nontrawl sand ($n = 24$), trawl low shell ($n = 21$), nontrawl low shell ($n = 24$), trawl high shell ($n = 12$), nontrawl high shell ($n = 24$), trawl reef ($n = 21$), and nontrawl reef ($n = 24$). All stations were trawled in a northwest to southeast direction and remained on the habitat of interest. Vessel position was overlain onto bathymetric side-scan mosaics in ArcPad 6.0 (ESRI, Redlands, California) for continuous global positioning system (GPS) tracking of trawl position and to aid in navigation. This enabled trawls to be towed along the edges of the reefs to minimize damage to immobile fauna (i.e., sponges, corals).

Standard NMFS Fall Groundfish Survey trawl gear was used, which included a single, 12.8 m wide otter trawl with 4 cm mesh size, towed at approximately 4.6 km·h^{-1} for 10 min·sample^{-1}. A 0.7 cm cod-end lining was added to increase capture efficiencies for smaller individuals. Trawl sampling occurred only during daylight hours (30 min after sunrise and 30 min before sunset). All red snapper were immediately frozen and taken back to the laboratory following each cruise. Fish were measured to the nearest millimetre total length (TL) and weighed to the nearest gram. Water mass characteristics (salinity, temperature, depth, and dissolved oxygen) were measured at each site with a conductivity–temperature–depth (CTD) instrument (model SBE-25; Sea-Bird Electronics, Inc., Bellevue, Washington).

Density and size

Differences in densities of red snapper from the trawl surveys (number·ha^{-1}) were assessed with a block-designed four-way factorial analysis of variance (ANOVA) with habitat, the presence or absence of trawling, season, and age group as the factors and year (2004 and 2005) as the block. In addition, an analysis of covariance (ANCOVA), with depth as the covariate, was performed with all factors to assess red snapper density with respect to depth differences among study sites. Prior to ANCOVA testing, the homogeneity of slopes was examined using an interaction regression, and main effects (*y* intercepts) were then tested when

the homogeneity of slopes assumption was met (Ott 1993). Red snapper densities were $\log_e(x + 1)$-transformed to normalize data and reduce heteroscedasticity. A posteriori differences among means were detected with Tukey's honestly significant difference (HSD) test with an α level of 0.05. Length differences among habitats and between trawled and nontrawled areas of similar habitats were analyzed with a two-factor ANCOVA (factors: habitat, presence of trawling), with season as the covariate. A linear regression was used to examine the relationship between red snapper TL and depth.

Age and growth

Sagittal otoliths of red snapper collected at each habitat were used for age estimates. A subsample ($n = 25$ if available) of juvenile red snapper from each habitat during each quarter was selected so that the entire juvenile size range was included in daily age estimates. Subsamples were obtained by randomly selecting five to 10 fish from three 50 mm size bins (0–50, 51–100, 101–150 mm TL) for each habitat by quarter. Because of the large size range of red snapper collected, either daily or annual increment analysis was performed depending on fish size and time of year. Left or right sagittal otoliths were selected and measured to the nearest 0.001 mm and weighed to the nearest 0.0001 g. Otoliths for daily age estimates were prepared using standard techniques (Secor et al. 1992). Because of the compression of daily rings with increasing age, it was difficult to discern daily ages of red snapper larger than 150 mm TL; thus only red snapper less than this size were used for daily increment analysis. Two readers independently counted increments of a random subsample of red snapper otoliths. Subsamples represented 27% and 20% of 2004 and 2005 daily otoliths, respectively.

Annual age estimates for fish larger than 150 mm TL were determined by counting the number of opaque rings from the core to the outer margin. Otoliths were processed and read following the methods of Cowan et al. (1995). Age was determined based on counts of opaque zones, assuming a mean birth date of 1 July and that opaque zone formation occurs between January and March in the northern GOM (Patterson et al. 2001). A large number of red snapper ages were classified as 0.5+. These fish were too old to discern daily ages but were not yet 365 days old because no opaque annual ring was present; thus, 0.5+ represents an age between 180 days and 1 year. Two readers independently counted annuli of all adult red snapper otoliths. Differences in the annulus counts were evaluated by the coefficient of variation (CV), index of precision (*D*), and average percent error (APE).

Growth rates of age-0 red snapper were estimated from slopes of linear regressions of TL versus otolith-derived daily age. Habitat-specific growth comparisons were performed only from winter and fall samples when sufficient sample sizes of age-0 red snapper were collected over most habitats. Analysis of covariance models were used to test for differences in growth rates (slope effect) of age-0 red snapper, with age as the covariate. Student's *t* tests and ANOVA models were also used to compare average growth rates for individual fish; however, results were similar to ANCOVA models and are therefore not reported.

Daily growth was modeled for all aged red snapper with a

von Bertalanffy growth equation using Proc NLIN (SAS Institute Inc. 2006). This equation was used to estimate ages of red snapper that were not aged with otolith-based techniques. Length-at-age data were also fit with other models (i.e., linear, logistic), but the percent variation in length explained by age was maximized with the von Bertalanffy.

Mortality and production potential

Mortality estimates of red snapper were derived using a maximum likelihood approach for monthly birth cohorts, where catch per effort for each cohort was assumed to be distributed as a Poisson random variate with mean dependent on three parameters: initial cohort size, catchability, and monthly survival rate. This is a dynamic catch curve method in which decline in abundance of monthly cohorts from each annual spawning is estimated. In addition, mortality estimates were also derived from regressions of $\log_e$-transformed abundance on age, in a static catch curve. Instantaneous daily mortality rates of age-0 red snapper were estimated using an exponential model of decline in numbers at age (Ricker 1975). Mortality estimates were based on 10-day groupings of the 2004 cohort collected over consecutive seasons over the age range in which a descending catch curve was observed. An ascending catch curve was observed for young red snapper (<120 days), and only a small number of older red snapper (>200 days) were collected because of both gear avoidance and emigration. Thus, all red snapper collected from the 2004 cohort between 120 and 199 days of age from sand and low shell sites were used to obtain mortality estimates. Analysis of covariance models were used to test for differences in mortality rates (slope effect) of age-0 red snapper, with age as the covariate.

Mortality estimates were based on the assumptions that equal immigration and emigration took place on the habitats of interest and that the only difference between sites was the presence of trawling. The age range used for mortality estimates was most frequently observed over the sand and low shell habitat types, suggesting that these were the preferred habitats at this life stage. In addition, our comparisons were limited to similar habitat types (sand and low shell) that were and were not likely exposed to trawling and did not compare among habitat types owing to possible ontogenetic habitat shifts. Red snapper mortality rates over high shell trawled and nontrawled areas were not estimated because of the small number of red snapper collected, remote distance, and depth of the trawled site relative to other sites.

The ratio of the weight-specific growth coefficient (G) to the instantaneous mortality coefficient (Z) was used to index habitat-specific and life-stage-specific production potential. The incorporation of both G (g·day^{-1}) and Z (day^{-1}) allows these to be used to assess stage-specific productivity. Estimates of G were calculated from slopes of linear regressions relating changes in weight with respect to age. Cohorts of red snapper with G–Z ratios less than one lose biomass, whereas those with G–Z ratios greater than one gain biomass and have higher survivorship and production potential (Cowan and Houde 1990; Houde 1996; Rooker et al. 1999). In addition, habitat-specific G and Z estimates were incorporated into the Ricker (1975) production model to calculate production to biomass ratios (P–B ratios).

Production and biomass relationships were calculated using the following equations:

$$\overline{B} = \frac{B_0 \left(e^{(G-Z)} - 1 \right)}{G - Z}$$

$$P = G\overline{B}$$

where $\overline{B}$ is the mean biomass over the time interval, B_0 is the initial biomass, and P is the production estimate in grams wet weight per hectare. Initial habitat-specific biomass estimates were derived from mean weight multiplied by total number per hectare over the 120–129 day age group. The G–Z and P–B ratios were calculated for red snapper collected over trawled and nontrawled sand and low shell habitats to assess differences in the production potential that may be attributable to trawling.

Results

Water mass characteristics were similar among all habitats within each quarter (Table 1). Low dissolved oxygen (1.76 mg·L^{-1}, which is characterized as hypoxic (<2 mg·L^{-1})) was observed during the summer cruise in 2004. A total of 1454 red snapper was collected in trawl samples over the two-year study period. Red snapper between 23 and 435 mm TL were captured in trawls, with ages ranging from 28 days to 5 years.

Density and size

Red snapper densities increased with age over higher relief habitats (e.g., high shell and reef) and were higher over nontrawled areas; however, differences were age-specific (Fig. 2). Red snapper densities were significantly affected by habitat type (ANOVA: $F_{[3,711]} = 6.56$, $p < 0.001$), exposure to trawling (ANOVA: $F_{[1,710]} = 6.53$, $p = 0.011$), and age group (ANOVA: $F_{[4,710]} = 30.25$, $p < 0.001$). Seasonal differences were not significant (ANOVA: $F_{[3,708]} = 2.20$, $p = 0.087$), thus age-specific, post-hoc density comparisons were analyzed with both habitat and the exposure to trawling as factors. In addition, parallelism of slopes assumptions were met and significant main effects for habitat, trawling, and age group were found when depth was included as a covariate. A significant habitat effect was observed for age-1 red snapper (ANOVA: $F_{[3,166]} = 3.71$, $p = 0.013$), with significantly higher densities associated with reef (2.65 fish·ha^{-1}) compared with sand (0.16 fish·ha^{-1}) habitat ($p = 0.014$). In addition, a significant trawling effect was observed for age-0.5+ red snapper (ANOVA: $F_{[1,165]} = 6.63$, $p = 0.011$), with higher densities over nontrawled areas (5.41 fish·ha^{-1}) relative to areas exposed to trawling (2.69 fish·ha^{-1}). However, pairwise density differences of red snapper collected from trawled versus nontrawled areas of similar habitats were not significant. Habitat × trawl interactions were not significant for both age-0.5+ and age-1 fish ($p > 0.05$).

Red snapper size-frequency distributions correlated well with age-specific density estimates, indicative of an ontogenetic habitat shift from lower-relief to higher-relief habitats with size and age. Habitat-specific size-frequency distributions varied among seasons. A significant habitat effect was detected (ANCOVA: $p < 0.001$), with the smallest

Table 1. Bottom water mass characteristics at each site on quarterly surveys during 2004 and 2005.

Water parameter	Habitat	Winter, March 2004	Spring, May 2004	Summer, August 2004	Fall, October 2004	Winter, January 2005	Spring, April 2005	Summer, July 2005	Fall, October 2005
Temperature (°C)	NT Sand	18.62	21.08	22.34	25.78	19.25	20.38	25.81	24.21
	T Sand	NA	19.91	22.85	23.11	20.10	20.20	26.28	25.47
	NT Low shell	17.92	20.55	22.56	27.04	20.76	20.47	26.13	25.23
	T Low shell	NA	22.21	23.46	25.98	20.10	20.20	25.92	24.18
	NT High shell	18.05	20.74	22.90	26.74	20.76	20.20	25.83	24.74
	T High shell	NA	19.52	20.72	28.13	NA	NA	26.06	NA
	NT Reef	17.98	20.56	22.51	26.48	19.80	20.55	25.92	25.02
	T Reef	18.72	24.38	24.01	25.95	18.10	20.31	25.99	NA
Salinity (ppt)	NT Sand	35.73	35.01	36.18	35.80	35.21	35.91	35.50	34.65
	T Sand	NA	35.18	36.34	36.27	35.61	36.28	35.76	35.43
	NT Low shell	35.51	35.17	36.11	36.33	35.68	35.94	35.45	35.33
	T Low shell	NA	34.20	35.98	35.52	35.61	36.28	35.44	34.70
	NT High shell	35.49	35.13	36.06	36.29	35.68	36.28	35.47	35.01
	T High shell	NA	35.73	36.39	36.24	NA	NA	35.77	NA
	NT Reef	35.50	35.15	36.13	36.27	35.47	35.98	35.46	35.25
	T Reef	35.56	34.63	35.95	35.32	34.45	35.47	35.47	NA
Dissolved oxygen (mg·L^{-1})	NT Sand	7.78	7.45	1.76	4.65	6.37	3.57	4.53	6.15
	T Sand	NA	6.54	4.18	4.92	5.93	3.67	5.30	5.91
	NT Low shell	7.82	7.25	3.35	5.73	5.94	3.97	4.92	6.01
	T Low shell	NA	7.02	3.30	3.85	5.93	3.67	4.82	6.15
	NT High shell	7.79	7.13	3.61	5.20	5.94	3.67	4.41	6.09
	T High shell	NA	6.33	5.01	5.82	NA	NA	5.44	NA
	NT Reef	7.94	7.29	2.93	5.16	6.30	4.10	4.65	6.09
	T Reef	7.85	6.92	4.56	5.35	6.72	3.90	4.87	NA
Depth (m)	NT Sand	24.4	24.0	23.0	27.5	23.5	24.0	25.3	28.1
	T Sand	NA	30.3	30.6	30.7	30.8	31.0	30.3	31.2
	NT Low shell	29.7	29.0	28.8	28.8	29.0	29.5	29.0	29.0
	T Low shell	NA	17.3	18.0	17.7	18.0	18.0	17.8	17.5
	NT High shell	28.0	27.3	28.0	26.5	26.5	27.0	30.1	28.6
	T High shell	NA	39.6	37.2	37.4	NA	NA	37.2	NA
	NT Reef	30.6	28.0	30.7	29.0	31.5	31.0	30.1	30.7
	T Reef	20.0	19.0	19.8	18.3	19.0	18.6	17.5	NA

Note: NT, nontrawl; T, trawl; NA, not applicable because no samples were taken at the site because of inclement weather.

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Fig. 2. Age-specific density estimates (±1 standard error, SE) of red snapper (*Lutjanus campechanus*) collected using trawls: (*a*) age-0; (*b*) age-0.5+; (*c*) age-1; (*d*) age-2; and (*e*) age-3+. Solid bars represent habitats exposed to trawling; open bars represent habitats not exposed to trawling. Note the magnitude of the ordinate differs with age because of the low number of older individuals collected using trawls.
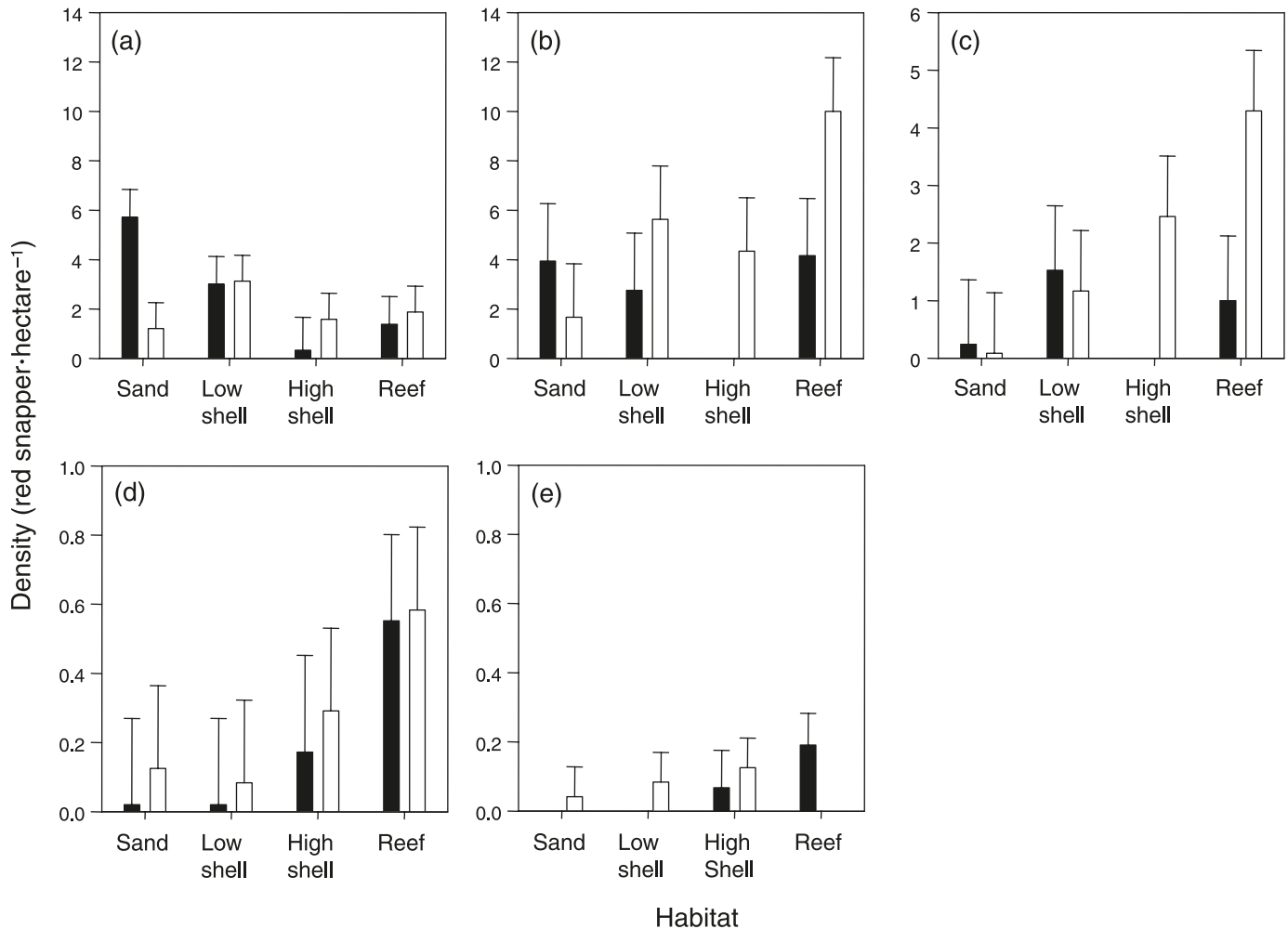
red snapper observed over sand habitat (LS mean = 111.9 ± 3.5 mm TL standard error), particularly during summer and fall. Post-hoc differences among habitats indicated that red snapper were significantly smaller over trawled sand (LS mean = 96.1 ± 3.3 mm TL) than over trawled low shell ($p < 0.001$; LS mean = 127.0 ± 4.3 mm TL) and reef habitats ($p < 0.001$; LS mean = 172.3 ± 7.9 mm TL). Red snapper collected over nontrawled sand habitats (LS mean = 127.8 ± 6.1 mm TL) were significantly smaller than those collected over nontrawled high shell ($p < 0.001$; LS mean = 166.0 ± 3.2 mm TL) and reef ($p < 0.001$; LS mean = 158.1 ± 2.3 mm TL) habitats. Red snapper between 50 and 200 mm TL (LS mean = 133.5 ± 2.6 mm TL) were consistently collected over the low shell habitats in all seasons, whereas the 100–250 mm TL (LS mean = 143.4 ± 11.8 mm TL) size range was collected over high shell habitats. The largest red snapper were found over reef habitat, where red snapper larger than 300 mm TL (LS mean = 165.2 ± 4.1 mm TL) were frequently captured. Pairwise comparisons among habitats indicated that red snapper were significantly larger on reefs than over both sand and low shell habitats in

the trawled and nontrawled areas ($p < 0.001$). Lastly, results of the linear regression showed no significant relationship with increasing red snapper TL and depth ($r^2 = 0.003$, $p = 0.270$).

Red snapper were significantly larger on nontrawled habitats than over similar trawled habitats (ANCOVA: $p = 0.012$) (Fig. 3). Specifically, sand and low shell habitats were the two habitats investigated for post-hoc trawl effects, which was significant for both (sand $p < 0.001$; low shell $p = 0.012$). Average TL (± standard error, SE) of red snapper collected over nontrawled and trawled sand habitats were 127.8 ± 6.1 and 96.1 ± 3.3, respectively, and those over nontrawled and trawled low shell habitats were 140.1 ± 2.9 and 127.0 ± 4.3, respectively.

Age and growth

A total of 942 (65%) red snapper collected in this study was aged; daily ages were obtained for 377 fish (40% of aged fish) and annual age estimates were obtained for 565 (60% of aged fish). Agreement between readers of red snapper daily otolith counts was high (2004, reader 1 age =

Fig. 3. Size-frequency distributions of red snapper (*Lutjanus campechanus*) collected relative to the exposure to trawling over sand and low shell habitats: (*a*) sand trawl; (*b*) sand nontrawl; (*c*) low shell trawl; (*d*) low shell nontrawl.
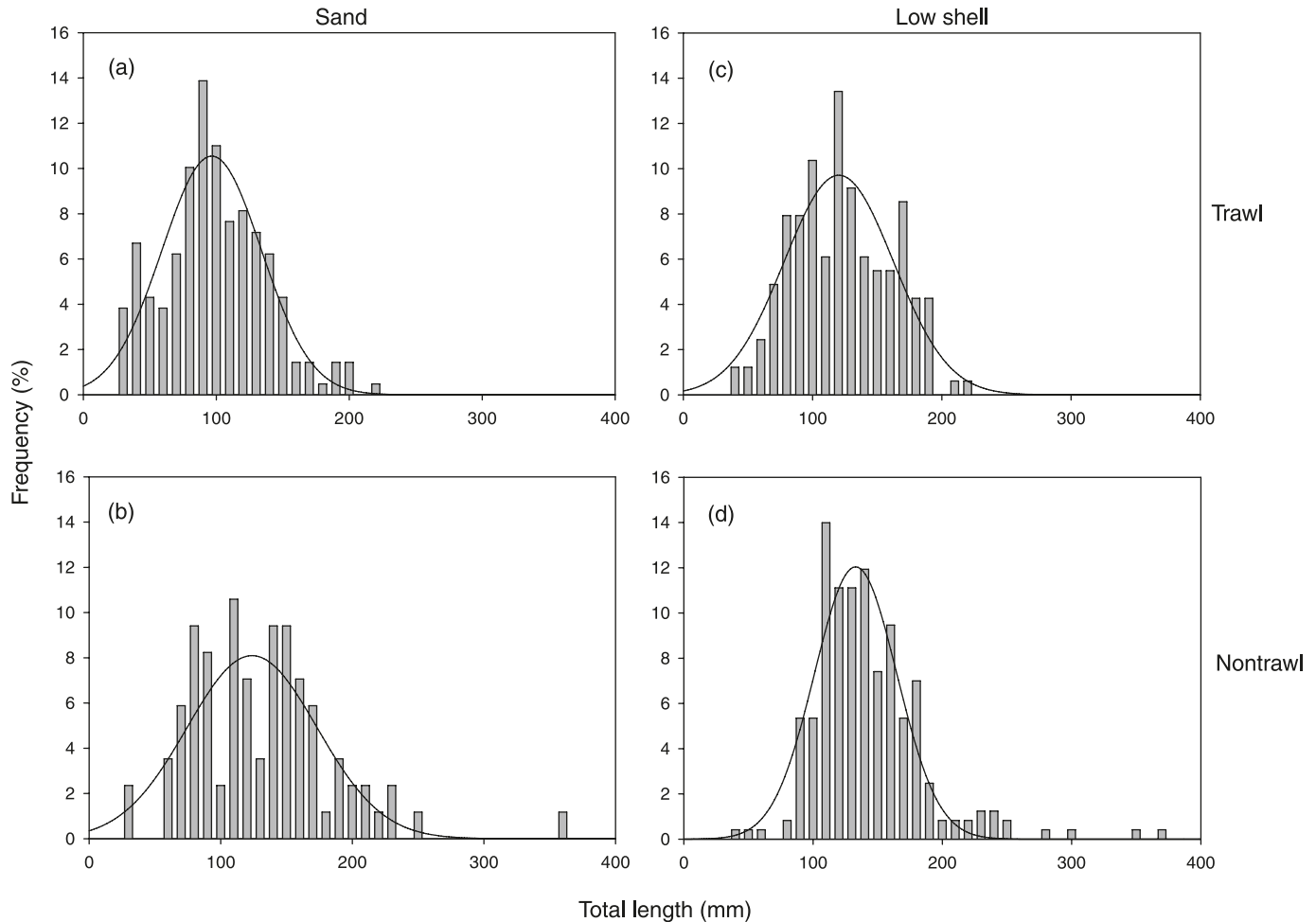
0.95 × reader 2 age + 12.72, r^2 = 0.91; 2005, reader 1 age = 0.93 × reader 2 age + 5.16, r^2 = 0.93). In addition, annual age estimates differed for only 4.4% of the readings. Because of the low variability between reader counts (CV = 0.011, D = 0.008, APE = 0.500%), annulus counts by reader 1 were used.

Habitat-specific growth rates of age-0 red snapper showed differences among habitats during winter and fall, with highest growth rates over sand habitat (Fig. 4). A significant growth rate difference was detected for red snapper collected among habitats exposed to trawling during winter, with the highest growth rates of 1.03 mm·day^{-1} over the sand habitat (ANCOVA test for equal slopes: p = 0.047) (Fig. 4*a*). No significant winter growth differences were detected for red snapper in habitats that were not exposed to trawling (ANCOVA slopes: p = 0.116) (Fig. 4*b*). However, trends in habitat-specific growth rates were similar, as red snapper collected over sand habitat had average growth rates of 1.01 mm·day^{-1}, followed by reef (0.74 mm·day^{-1}), and low shell (0.72 mm·day^{-1}) habitats. Growth rates were similar for red snapper collected among habitats exposed (ANCOVA slopes: p = 0.575) (Fig. 4*c*) and not exposed (ANCOVA slopes: p = 0.207) (Fig. 4*d*) to trawling in fall. Fall habitat-specific growth rates averaged 0.65 and
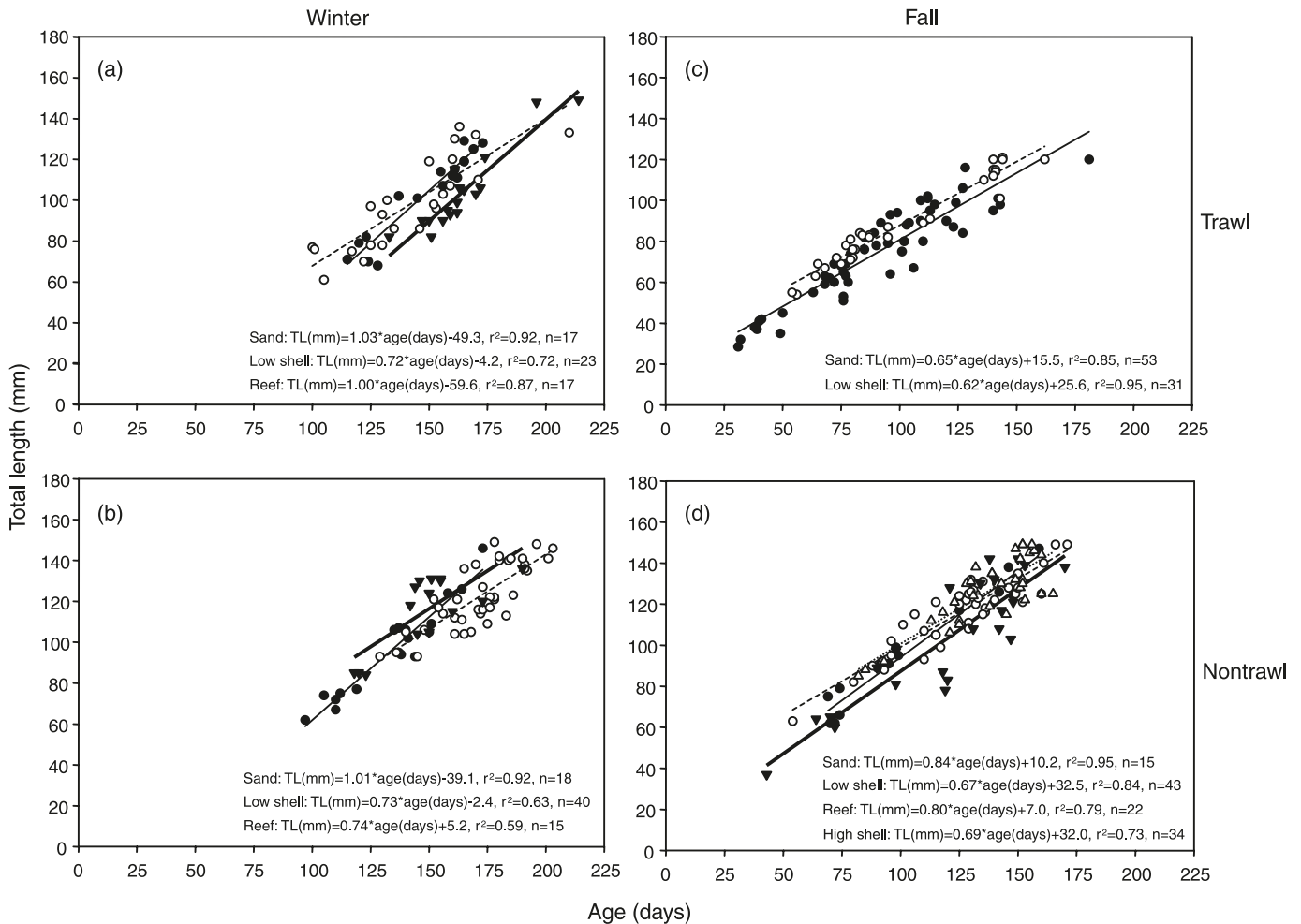
0.84 mm·day^{-1} over trawled and nontrawled sand habitats, respectively.

In general, red snapper collected on habitats not exposed to trawling grew faster than their counterparts on trawled habitats. Red snapper collected over nontrawled sand habitats in fall grew significantly faster than conspecifics collected over similar sand habitats exposed to trawling (ANCOVA slopes: p = 0.022) (Fig. 5*c*). Average fall daily growth rate of red snapper over nontrawled sand was 0.84 mm·day^{-1}, in contrast to red snapper collected on trawled sand with an average growth rate of 0.65 mm·day^{-1}. A similar difference in fall was observed over low shell habitat; however, differences were not significant (ANCOVA slopes: p = 0.425) (Fig. 5*d*). Growth rates of red snapper in fall over nontrawled and trawled low shell habitat averaged 0.67 and 0.62 mm·day^{-1}, respectively. Winter growth rates were similar, regardless of the exposure to trawling (Figs. 5*a*, 5*b*).

Mortality and production potential

Mortality rate estimates over the size ranges examined show that red snapper in trawled areas suffered higher mortality rates than those in similar nontrawled areas, regardless of the approach used. Using the maximum likelihood

Fig. 4. Size-at-age relationships of age-0 red snapper (*Lutjanus campechanus*) collected during winter and fall trawl cruises determined with linear growth curves for habitat-specific comparisons: (*a*) winter trawl; (*b*) winter nontrawl; (*c*) fall trawl; (*d*) fall nontrawl. Habitats consist of sand (solid circles, solid line), low shell (open circles, broken line), high shell (open triangles, dotted line), and reefs (solid triangles, solid bold line).

method, total mortality estimates (Z) were 0.042 and 0.007·day^{-1} over trawled and nontrawled low shell habitats, respectively. Similarly, mortality estimates were 0.043 and 0.025·day^{-1} over trawled and nontrawled sand habitats, respectively. Mortality estimates were similar using the catch-curve method (Fig. 6). Red snapper collected over trawled low shell habitats had mortality rates of 3.54%·day^{-1} ($Z = 0.036$·day^{-1}) compared with red snapper collected over nontrawled low shell of 1.69%·day^{-1} ($Z = 0.017$·day^{-1}) (ANCOVA slopes: $p = 0.005$) (Fig. 6*b*). Similar trends were observed for red snapper collected over sand habitats, with red snapper mortality rates of 3.63%·day^{-1} ($Z = 0.037$·day^{-1}) on trawled areas and 2.37%·day^{-1} ($Z = 0.024$·day^{-1}) on similar nontrawled areas (Fig. 6*a*), but results were not significant (ANCOVA slopes: $p = 0.176$). Differences in mortality rates between similar habitat types exposed or not exposed to trawling provided a trawl-related fishing mortality (F) of 1.88%·day^{-1} ($F = 0.019$·day^{-1}) over low shell and 1.29%·day^{-1} ($F = 0.013$·day^{-1}) over sand.

Juvenile red snapper collected from habitats exposed to trawling had lower G–Z ratios than those collected from similar nontrawled habitats. The highest G–Z ratio of 0.93 was observed for red snapper over nontrawled sand, whereas similar trawled sand areas had a ratio of 0.40, indicating over a twofold difference in production potential between habitats. The G–Z ratio of red snapper collected on nontrawled low shell habitats was 0.89, in contrast to 0.59 for red snapper residing on similar trawled habitat. Similar trends of higher P–B ratios of red snapper collected from nontrawled relative to similar trawled habitats were observed with production estimates of 0.022 and 0.014 from red snapper collected over nontrawled and trawled sand habitats, respectively. Similarly, the P–B ratios of red snapper collected from nontrawled and trawled low shell habitats were 0.022 and 0.021, respectively.

Discussion

Our results suggest that postsettlement processes acting on age-0 red snapper are affected by trawling. Truncated size distributions observed in this study are consistent with previous studies that reported decreases in the biomass of demersal fish and invertebrate fauna due to trawling and

Fig. 5. Size-at-age relationships of age-0 red snapper (*Lutjanus campechanus*) collected during winter and fall surveys over sand and low shell habitats in trawled (solid circles, solid line) and nontrawled (open circles, broken line) areas: (*a*) winter sand; (*b*) winter low shell; (*c*) fall sand; (*d*) fall low shell.
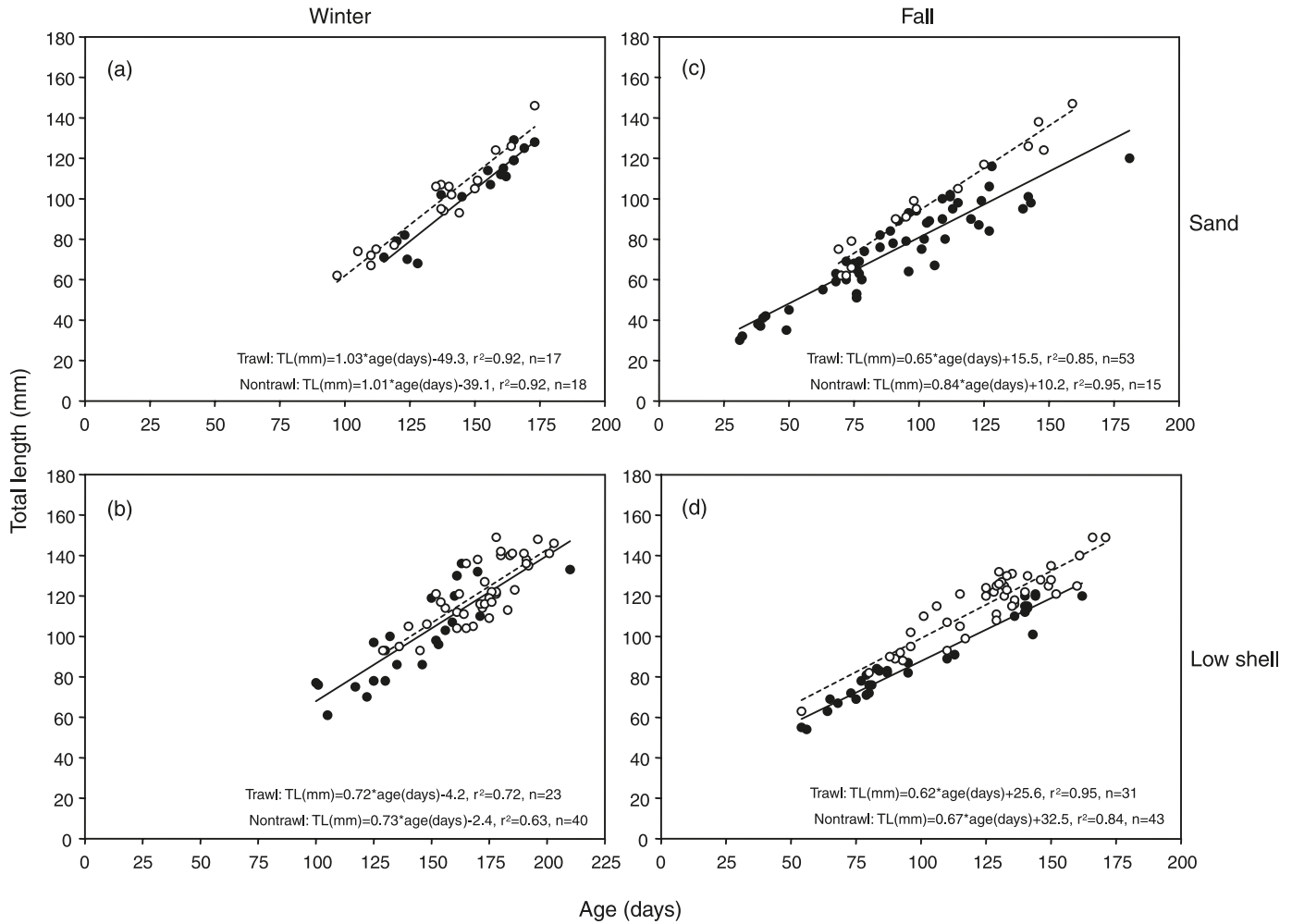

dredging (Bianchi et al. 2000; Zwanenburg 2000; Duplisea et al. 2002). In addition, large declines of small coastal elasmobranchs in the northern GOM have been documented where shrimp effort was highest (Shepherd and Myers 2005). In contrast, we found higher densities of age-0 red snapper over trawled sand habitat, but by age-0.5+, densities were higher over nontrawled low shell habitat. A possible explanation for this pattern is the size selectivity of the shrimp trawls targeting red snapper at the age-0.5+ range, which is the age at which juvenile red snapper are more vulnerable to the trawl gear. Results herein also are consistent with those of Diamond et al. (2000), who showed that bycatch mortality has an impact on population growth rates of GOM Atlantic croaker, *Micropogonias undulatus*, a fish species commonly collected as shrimp trawl bycatch in the GOM. However, Diamond et al. (1999) also reported that life history parameters such as size distribution, number of large fish, and size at maturity of GOM Atlantic croaker have not changed since the 1930s, despite major declines in abundance.

The greater habitat complexity and absence of commercial shrimp trawling over nontrawled habitats in this study may contribute to faster growth and decreased mortality

rates of age-0 red snapper. Habitat complexity has been shown to enhance the survivorship of age-0 Atlantic cod, *Gadus morhua*, at both the microhabitat (Lindholm et al. 1999) and landscape (Lindholm et al. 2001) levels by reducing the vulnerability of fish to predation. Likewise, the epibenthic community (i.e., tubeworms, bryozoans, anemones, corals, and algae) and vertical relief estimates in our study area were greater over nontrawled habitats (Wells et al. 2008*a*) and may therefore provide additional protection from predators. The concept of habitat-mediated survivorship has been well documented in tropical and temperate reef systems (Carr 1991; Connell and Jones 1991; Sale 1991) but has not been well studied for red snapper. However, more than 20 000 artificial reefs are estimated to exist within the permit areas off Alabama (Patterson et al. 2001), and these reefs may have an effect on the distribution and abundance of red snapper and co-occurrence of predators and prey. Differences in the predation pressure between sites exposed and not exposed to trawling may have existed. Large piscivorous fishes and sharks are frequently found over highly structured habitats such as artificial reefs that aggregate large quantities of potential prey (Simpfendorfer and Milward 1993; Rademacher and Render 2003), which

Fig. 6. Mortality estimates of red snapper (*Lutjanus campechanus*) collected from (*a*) sand and (*b*) low shell habitats exposed (solid circles) and not exposed (open circles) to trawling. Mortality estimates are based on age-specific catch curves using regression plots of log$_e$ abundance on age for 10-day cohorts.
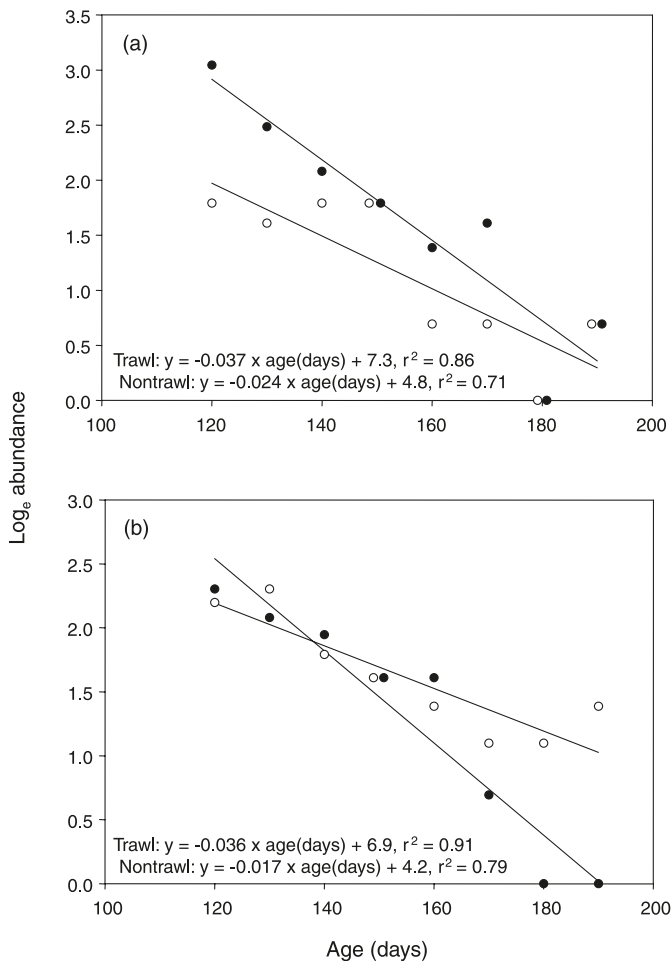
would increase the predation potential within the nontrawled area. Additionally, fishing pressure for adult red snapper may have been higher over the nontrawled habitats owing to the presence of the artificial reefs that attract recreational anglers. If true, these factors likely would have increased mortality rates of age-0 and adult red snapper over non-trawled areas, resulting in reported differences between trawled and nontrawled habitats being conservative.

Movement between trawled and nontrawled areas or to different habitats such as artificial reefs within the reef permit area may have occurred during this study. An assumption in our approach was that the presence or absence of commercial shrimp trawling was the primary factor responsible for the observed differences between similar habitat types within and outside of the de facto nontrawl permit area. Workman et al. (2002) concluded that juvenile red snapper display site fidelity and may have homing capabilities based on ultrasonic tagging data. In addition, Bailey et al. (2001) found that age-0 red snapper were excluded from reefs by older (age-1 and above) conspecifics. Our results are consistent with the finding of Patterson et al. (2005) that although red snapper habitat use was age-specific, simi-

lar ages overlapped among different habitat types and dispersion between areas is therefore possible.

Production estimates indicate that age-0 red snapper were losing biomass, therefore suffered decreasing production potential within all habitats. However, production estimates were lower in habitats exposed to trawling. One explanation may be that trawl selection for fastest-growing individuals of a given age is higher in trawled relative to nontrawled areas, which would have biased down our estimates of growth and production for red snapper collected from trawled habitats. Mortality estimates for juvenile red snapper in this study were high and should be interpreted with caution given the inherent assumptions. Movement and gear avoidance of red snapper likely affected the mortality estimates and consequently overestimated total mortality and therefore underestimated production potential in this study. Our estimates of bycatch mortality rates (1.29%–1.88%·day^{-1}) imply annual loss rates (4.7–6.9·year^{-1}) that are two to four times higher than those reported from stock assessment modeling and analysis of survey data by recent stock assessment teams (Southeast Data Assessment and Review 2005). However, our results are consistent with the mortality rates estimated by Rooker et al. (2004), where habitat-specific mortality rates of juvenile red snapper ranged from 4% to 12%·day^{-1} for fish 47–57 days of age. Growth, mortality, and production results also were age-specific in that we focused on juvenile red snapper between the ages of 120 and 199 days. Wang and Houde (1995) found that annual *P–B* ratios of bay anchovy (*Anchoa mitchilli*) in Chesapeake Bay decreased from 8.07 to 0.97, after excluding the larval and youngest juvenile stages (3 months posthatch), and to 0.19 for age-1 anchovy. To date, most studies have used *G–Z* ratios to evaluate production potential of larvae (Cowan and Houde 1990; Houde 1996) and recently settled individuals (<50 days) (Rooker et al. 1999). Thus, caution should be used when interpreting production calculations for annual estimates because we used an 80-day period during the late juvenile stage. Additional studies clearly are needed to estimate life-stage-specific mortality rates and production potential of red snapper.

Several other factors may have led to the observed differences in this study. Distance and depth differences among study sites may have affected density and size, particularly over the high relief shell site located on the 40 m depth contour. However, this site was not used to test for the effects of trawling, nor did we see any increasing size with depth relationships. Gallaway et al. (1999) found that juvenile red snapper habitat preference lies between 18 and 64 m, similar to the depth range of our study area. Additionally, mortality estimates in this study may have been affected by differences in location or depth, and these differences may account for the faster rate of emigration in trawled habitats. Given that red snapper display ontogenetic habitat shifts, as observed in this study, a significant component of our mortality estimates may have been attributed to movement. Studies also found decreased numbers of juvenile red snapper when dissolved oxygen levels become hypoxic (<2 mg·L^{-1}) (Szedlmayer and Shipp 1994; Gallaway et al. 1999). Consequently, the low dissolved oxygen level (1.76 mg·L^{-1}) observed in the summer of 2004 at the nontrawled sand

habitat may have had the effect of depressing age-0 red snapper numbers, resulting in a shallower slope and lower mortality estimate. It should also be noted that our study was limited to one artificial reef permit area, which may affect overall conclusions regarding the exposure to trawling activities. Future studies should aim at greater replication over a larger area of the shelf to test for the presence of fishing activities on vital rates of commercial and recreationally important species. Unfortunately, as was the case in this study, limited spatial closures exist on the northern GOM shelf, which limited our ability to cover a large spatial area.

Changes in juvenile red snapper vital rates may have repercussions at the subadult and adult stages. Results of this study demonstrate the effects that trawling has on life history parameters of juvenile red snapper, while others have observed demographic differences in adult populations of red snapper. Fischer et al. (2004) found that adult red snapper off Texas reached smaller maximum sizes at a faster rate and had smaller weight-at-age than red snapper collected off Louisiana and Alabama. In addition, Woods et al. (2003) reported that female red snapper off Alabama reached sexual maturity at smaller sizes and at earlier ages than conspecifics off Louisiana. It has been suggested that fishing pressure may select for phenotypic traits of fishes, such as reduced size-at-maturity and size-at-age, in addition to changes in growth rates (Law 2000). For example, the North Sea plaice (*Pleuronectes platessa*) has decreased in both length- and age-at-maturity since 1900 as the result of fishing pressure (Rijnsdorp 1993). In addition, Kamukuru et al. (2005) reported that blackspot snapper (*Lutjanus fulviflamma*) collected in intensively fished areas off Tanzania had higher total and fishing mortality rates, lower maximum and average ages, and smaller sizes than conspecifics in an adjacent marine reserve. Diamond et al. (1999) found severe declines in the abundances of both Atlantic Ocean and GOM Atlantic croaker, but only the Atlantic fish demonstrated changes in vital rates and demographics. These changes were attributed to the fishing pressure on both juveniles (as bycatch in shrimp trawls) and adults (recreational and commercial catch). Similar selective pressures appear to be occurring on GOM red snapper. Therefore, demographic differences in GOM red snapper may be driven by fishing practices during early life when fishing mortality rates are highest.

Our findings of age-specific habitat use of red snapper, specifically an ontogenetic shift from low-relief to higher-relief habitats with increasing size and age, were similar to results from other studies. Studies characterizing juvenile red snapper habitat use have found juveniles in association with a variety of habitats, including mud, sand, relict shell rubble, low-relief microhabitats (sponges, rubble patches, debris) (Szedlmayer and Conti 1999; Rooker et al. 2004; Patterson et al. 2005), and artificial structures with vertical relief (Bradley and Bryan 1975). In contrast to juveniles, both subadult (age-1) and adult (age-2+) red snapper have been shown to occupy habitats such as gravel bottoms, coral reefs, and rock outcrops, as well as artificial reefs, petroleum platforms, and submerged wreckage (Bradley and Bryan 1975; Moran 1988; Szedlmayer and Shipp 1994). Differences in age-specific habitat use may

be attributed to the agonistic behavior by adults toward younger conspecifics (Bailey et al. 2001), but later occupation of offshore reef structures occurs as these younger fish reach a size refuge and recruit into the adult population, generally at or around age-2 (Nieland and Wilson 2003). Results herein suggest that juvenile red snapper begin recruiting to the reef structure as early as age-0 but are primarily found over these natural reefs at age-1 and older.

To date, studies have been equivocal with respect to the habitat-specific enhancement of early life survival of red snapper. Rooker et al. (2004) found higher growth rates and lower mortality rates of age-0 red snapper over an inshore mud habitat than at a shell bank in the northwestern GOM. They found no density differences in the first year of the study but found juvenile red snapper densities to be higher over shell substrates during a limited survey in the following year. Patterson et al. (2005) found no differences in red snapper densities between sand and shell substrates but inferred that sponges found on sand habitat provided similar structural complexity as shell rubble among sites within the trawled area of our study region. Other studies investigating density differences have found that age-0 red snapper have an affinity for shell-rubble habitat over sand habitat (Szedlmayer and Howe 1997; Szedlmayer and Conti 1999). Our results highlight the benefits of occupying both sand and low shell habitats because of faster daily growth rates over sand habitat, lower mortality over nontrawled shell habitat, and corresponding changes in production potential. The consistently higher growth rates of age-0 red snapper found over sand habitat may be due to prey availability. Age-0 red snapper have been shown to feed on prey associated with open sand and mud habitats (Bradley and Bryan 1975; Szedlmayer and Lee 2004), and diet analyses from fish in this study suggest the same (Wells et al. 2008*b*). Nagelkerken and van der Velde (2004) found that the majority of fishes utilizing both seagrass beds and mangrove habitats obtained most of their food sources from seagrass beds and attributed these habitat-specific feeding differences to the greater food availability in seagrass beds. Wells et al. (2008*b*) showed that red snapper rely on sand- and mud-associated prey, regardless of the habitat from which the red snapper were collected, suggesting that shell rubble may be more important for providing refuge than additional prey resources.

This study was unique in that all four levels of information needed to identify and evaluate EFH for red snapper were analyzed and the apparent effects of shrimp trawls on red snapper life history parameters were quantified. Based on the four habitat-specific levels by Minello (1999), it appears that all habitats (sand, shell, reefs) may be essential at some life history stage. Other studies that have attempted to delineate EFH for federally managed fish species have found similar results, identifying almost all waters and habitats encountered over the life history of a species as EFH (Packer and Hoff 1999; Roni et al. 1999). In addition, higher densities of age-0.5+ combined with larger sizes, faster growth rates in the fall, lower mortality estimates, and higher estimates of production potential suggest that juvenile red snapper residing over nontrawled areas may have a higher probability of survival than juvenile red snapper in areas exposed to commercial shrimp trawling. Thus, if man-

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agement strategies such as shrimp closures are implemented in the GOM to enhance survival of age-0 and age-1 red snapper, then all habitat types in this study will need to be protected, which is consistent with an ecosystem-based management approach.

Acknowledgments

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