

Abstract.—Patterns of growth and mortality were examined for post-settlement red drum, *Sciaenops ocellatus*, inhabiting seagrass meadows in the Aransas Estuary, Texas. Age and growth rates of larvae and early juveniles were estimated in 1994 and 1995 by using daily increments in otoliths. Otolith-derived estimates of age indicated that individuals spend approximately 20 d in the pelagic environment before entering demersal habitats (i.e. before settlement). Instantaneous growth coefficients (g) of red drum ranged from 0.049 (4.8%/d) in 1994 to 0.051 (5.0%/d) in 1995. Site-specific differences in growth were also examined and a significant site effect was detected in 1994; however, no site effect was observed in 1995. Interannual and cohort-specific (10-d cohorts) mortality rates were estimated from declines in \log_e abundance (abundance-at-age plots), and results indicated that mortality during the early postsettlement period was substantial. Instantaneous mortality coefficients (Z) were similar between years (0.134 [12.5%/d] in 1994; 0.139 [13.0%/d] in 1995), and no significant interannual effect was observed. Conversely, cohort-specific mortality rates ranged widely (0.106–0.265 [10.1–23.3%/d]) and losses were lowest for midseason cohorts. Recruitment potential ($G:Z$ ratio) was highest for mid-season cohorts (1.30–1.56) and lowest for early and late-season cohorts (<1). Although $G:Z$ ratios varied over spatial and temporal scales, ratios were >1 in 1994 and 1995, suggesting that both year classes experienced favorable nursery conditions.

Spatial and temporal variability in growth, mortality, and recruitment potential of postsettlement red drum, *Sciaenops ocellatus*, in a subtropical estuary*

Jay R. Rooker

Scott A. Holt

G. Joan Holt

Lee A. Fuiman

Marine Science Institute
The University of Texas at Austin
750 Channelview Drive
Port Aransas, Texas 78373

Present address (for J. R. Rooker): Department of Marine Biology
Texas A&M University
5007 Avenue U
Galveston, Texas 77551

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

Survival during the larval and juvenile stages of marine fishes is highly variable and plays a critical role in determining recruitment potential (Cushing, 1975; Houde, 1987). Early life survival is a function of both growth and mortality, and it is clear that these mechanisms act in concert to determine an individual's probability of survival (Houde, 1996). Individuals experiencing rapid growth will spend less time in vulnerable size ranges (reduced stage duration) and achieve a larger body size at a given age, thus enhancing their ability to detect and escape predators (Bailey and Houde, 1989; Fuiman and Magurran, 1994). Consequently, recruitment success or failure is closely linked to variation in growth and mortality during the early life stage.

Much of our current understanding of early life growth and mortality is based on information derived from the examination of otolith microstructures. The daily deposition of growth increments on otoliths has been demonstrated for many marine teleosts and provides a means

of estimating age, growth rate, and hatching date (see reviews by Campana and Neilson, 1985; Jones, 1986). Moreover, knowledge of a population's age structure can be combined with density data (abundance-at-age relationships) to estimate mortality rates. Thus, fundamental demographic parameters can be obtained through otolith analysis, and these data are essential for determining the causes and consequences of differential survival.

Red drum (*Sciaenops ocellatus*) inhabit subtropical and temperate waters in the Western Atlantic and support important commercial and recreational fisheries throughout the coastal waters of the Gulf of Mexico (Swingle, 1990; NOAA, 1991). Red drum spawn in the early fall in offshore waters and areas near tidal inlets, and tidal currents transport larvae through passes and into estuarine nursery habitats (Holt et al., 1989; Comyns et al., 1991). Individuals settle into sea-

grass and marsh-edge habitats following a fairly short pelagic interval and remain in these habitats during the juvenile stage (Baltz et al., 1993; Rooker and Holt, 1997; Rooker et al., 1998b).

Although much effort has been directed toward the management of red drum stocks, research on growth and survival during early life has received limited attention. As a result, the aim of this study was to examine spatial and temporal patterns of growth and mortality during the postsettlement period. Specific objectives of this research were to estimate annual variation in growth and mortality, to estimate cohort- and site-specific mortality rates, and to determine the recruitment potential of different cohorts.

Materials and methods

Field collections

Red drum were collected from two shoal grass (*Halodule wrightii*) meadows in the Aransas Estuary, Texas (Aransas Bay 1 and 2 [AB1, AB2]; Fig. 1), during the annual settlement period (August–December). Collections were taken over a two-year period (1994–95) with an epibenthic sled measuring 0.75 (w) × 0.5 (h) m, equipped with a 505- μ m mesh conical plankton net. Triplicate 20-m sled tows were taken every week at each site in 1994. A more comprehensive sampling strategy was employed in 1995 in order to evaluate cohort-specific variation in natural mortality. Ten 20-m sled tows were taken every 3–4 d at each site during the entire 1995 settlement season. Red drum larvae and juveniles were preserved in 70% ethanol immediately after capture. Environmental data collected at each site included depth, salinity, and water temperature.

Laboratory procedures

Removal and processing of otoliths (lapilli) followed the procedures described by Rooker and Holt (1997). Otolith radius, increment count, and increment widths were measured on a straight line from the core to the posterior edge using an image analysis system (Optimas, Bioscan). Because otolith growth is allometric (Campana and Neilson, 1985), all measurements were taken in the same field. Daily deposition of increments was validated in our laboratory by chemically marking the otoliths of known-age red drum with alizarin complexone (S.A. Holt, unpubl. data).

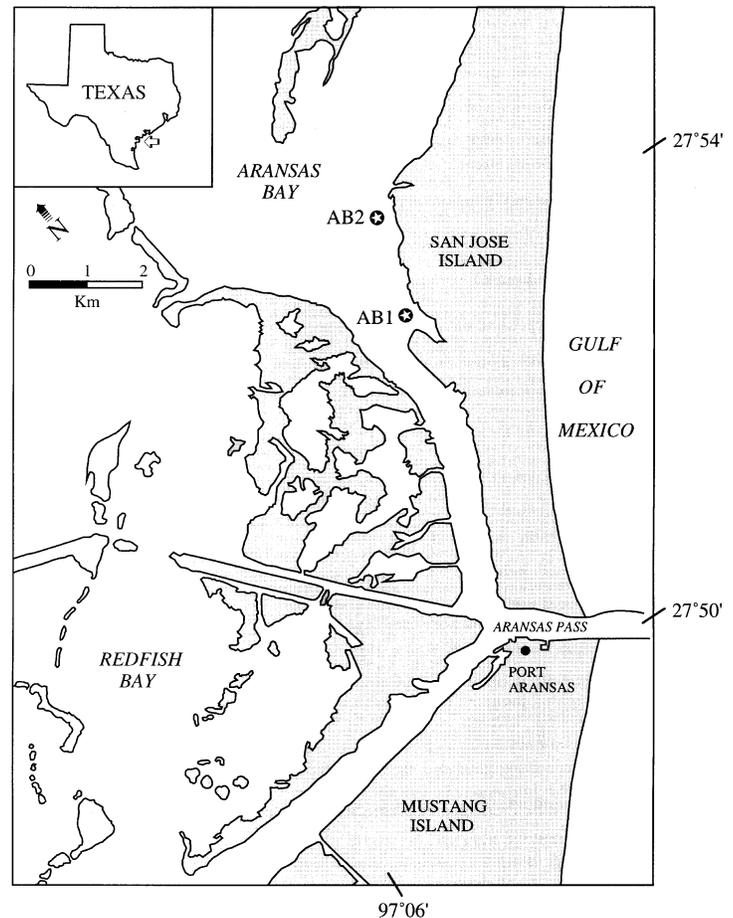


Figure 1

Location of shoal grass (*Halodule wrightii*) sampling stations (AB1 and AB2) in the Aransas Estuary, Texas.

Age was determined by enumerating growth increments from the core to the margin of the otolith. Inner increments (proximal to the core) on lapilli were often difficult to enumerate. Thus, in order to accurately determine the age of wild red drum, a relationship between age and otolith radius from laboratory-reared red drum was developed and used to predict the number of growth increments at various distances from the core (Rooker and Holt, 1997). Age was determined by adding the predicted age from the unreadable section (correction factor from age-radius relationship) to the increment count (number of increments from first identifiable increment to edge of the lapillus). Correction factors generally accounted for less than 25% of the actual age estimate, and the relative size of the correction did not differ between years. Both the left and right lapilli were examined and estimates of age and growth were derived by averaging readings from both otoliths. On average, age differences between otoliths were small (CV=3.6%; range 0–14%). For some individuals

(18%), only one of the lapilli was available owing to loss, breakage, or staining.

Growth rates were determined by using otolith-derived estimates of age (size-at-age plots) in 1994 ($n=249$) and 1995 ($n=140$). Daily instantaneous growth coefficients were calculated from an exponential model described as

$$L_t = L_0 e^{gt},$$

where L_t = length (mm SL) at time t ;
 L_0 = the estimated length at hatching;
 g = the instantaneous growth coefficient (/d);
 and
 t = the otolith-derived age (days after hatching).

Ages of red drum not assessed with otolith-based techniques (1994 [$n=1,057$], 1995 [$n=8004$]) were estimated by using age-length relationships.

Weight-specific instantaneous growth coefficients (G) were calculated by using the equation

$$W_t = W_0 e^{Gt},$$

where W_t = the wet weight (mg) at time t ;
 W_0 = the estimated weight at hatching;
 G = the weight-specific instantaneous growth coefficient (/d); and
 t = the otolith-derived age.

Red drum lengths (mm) were converted to wet weight (mg) by using a polynomial equation (third order) based on measurements from laboratory-reared red drum (range: 6–30 mm): $W = -7.745 + 2.122L - 0.205L^2 + 0.024L^3$ ($n=200$, $r^2=0.97$), where W and L represent wet weight and standard length, respectively.

Mortality rates were estimated from regressions of the decline in \log_e -transformed abundance on age. Although interannual variation in mortality was examined by pooling individuals from each year (all cohorts combined), cohort-specific rates were based on regression plots of \log_e -transformed abundance of individuals from 10-d cohorts determined from hatching-date analysis. Hatch dates of individual red drum were determined by subtracting the otolith-derived age from the date of collection. Hatching dates were then used to separate individuals into specific cohorts, defined as individuals hatched within a 10-d period. Each cohort was designated by a letter (A to F): 1–10 Sep (A); 11–20 Sep (B); 21–30 Sep (C); 1–10 Oct (D); 11–20 Oct (E); and 21–30 Oct (F). Densities for the first and last cohort (A, F) were low and thus mortality regressions were not fitted to these data. Daily instantaneous mortality rates were calculated from the exponential model of decline:

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

where N_t = abundance at time t ;
 N_0 = the estimated abundance at hatching;
 Z = the instantaneous mortality coefficient (/d); and
 t = the otolith-derived age.

Owing to incomplete capture (i.e. ascending limb of catch curve) of small red drum (<25 d, ≤ 8 mm), these individuals were not included in mortality regressions. Also, size-based gear avoidance was suspected, which placed constraints on the upper age (or size) of individuals used in regression analysis. In preliminary trials, the capture efficiency of the epibenthic sled was compared with a bag seine (seine dimensions: 7 m length \times 1 m height; mesh size: 3 mm) and size-specific differences in capture efficiency (individuals/m² of habitat sampled) between the two gears were not detected for sciaenids <25 mm (Rooker, 1997). However, density estimates of sciaenids >25 mm were higher with the seine. This suggested that individuals >25 mm are capable of avoiding the sled and that densities calculated for these individuals would be underestimated. Consequently, only red drum between 8 and 20 mm (25–40 d) were used to estimate mortality rates.

Our assessment of early life mortality was based on two assumptions: 1) individuals entering seagrass sites remained in these habitats (i.e. settle and stay) during the time period when mortality rates were estimated, and 2) immigration and settlement (i.e. late settlers) to the designated study sites from other locations or habitats, or both, was negligible. Although postsettlement movement (emigration or immigration, or both) can be important for certain species and failure to account for such movements can severely bias mortality estimates (Frederick, 1997), our assumptions are reasonable because red drum appear to settle and stay in seagrass meadows at least through the early juvenile stage (Rooker et al., 1998b). Furthermore, no salient increases or decreases in density were observed in length-frequency profiles which would be expected in the presence of postsettlement emigration or immigration activity.

Since total mortality (Z) is the sum of both natural (M) and fishing mortality (F), it is important to account for the fishing mortality (F) caused by our sampling (Ricker, 1975). Most studies evaluating early life mortality do not estimate F (=sampling mortality) and assume F to be inconsequential. In this study, seagrass meadows of limited size (ca. 25,000 m²) were sampled repeatedly and, as a result, the effect of F was considered potentially significant. Therefore, mortality regressions were run on abundance data

adjusted to compensate for sampling losses (F). Abundance at each sampling time was adjusted by subtracting the number of individuals collected (removed from population) with the epibenthic sled from the overall abundance at the site (site abundance = area of site/area sampled \times number of red drum collected). Regressions of \log_e -adjusted abundance on age were then run and mortality coefficients derived in this manner were basically estimates of M since the effect of F was removed. Consequently, F was determined by subtracting adjusted mortality rate (M) from Z . Because F values were relatively small, 2.3 to 6.9% of Z , only estimates of Z are presented.

The relative recruitment potential of individual cohorts was assessed by examining the ratio of weight-specific growth (G) to mortality (Z). The ratio is commonly used as an index of stage-specific survival because it incorporates both growth and mortality (Werner and Gilliam, 1984; Houde, 1996). Because cohorts with $G:Z$ ratios >1 gain biomass, the probability of survival (recruitment potential) for these individuals is assumed to be high.

Data analysis

Analysis of covariance (ANCOVA) was used to test for intra- and interannual differences in growth and mortality (covariate: age). Prior to each ANCOVA test, a preliminary model (interaction regression) was tested to determine if the slopes of the regression lines differed (homogeneity of slopes assumption; Sokal and Rohlf, 1981). The main significance test of the ANCOVA (homogeneity of y -intercepts) was performed when the parallelism of slopes assumption was met. Since differences in abundance affect the elevation of regression plots used to estimate mortality, spatial and temporal trends in mortality were evaluated by comparing slopes (y -intercept test not performed). Analysis of variance (ANOVA) was used to examine variability in density. Estimates of density were \log_e -transformed to minimize heteroscedasticity.

Results

Environmental conditions

Water temperature and salinity were recorded daily from August to December in 1994 and 1995. Temporal variation in both parameters was pronounced and trends were similar between years (Fig. 2). Temperature during the primary settlement period was variable (September–October) and ranged from 23.3° to 30.2°C in 1994 and from 22.7° to 31.6°C in 1995, respectively. Mean temperature during this period was

similar between years 1995 (27.5°C) and 1994 (27.2°C). Salinity ranged from 25.3‰ to 37.0‰ and from 25.3‰ to 30.8‰ in 1994 and 1995, respectively. Similar to temperature, mean salinity was relatively similar between years: 30.0‰ (1994) and 28.6‰ (1995). Peak values for both parameters occurred during the initial spawning period and declined for later spawning and settlement dates. Cohorts arriving early in the season experienced high temperature and salinity, whereas late-season cohorts were exposed to lower temperature and salinity (Fig. 2). No conspicuous differences in temperature or salinity were observed between sampling sites (AB1, AB2).

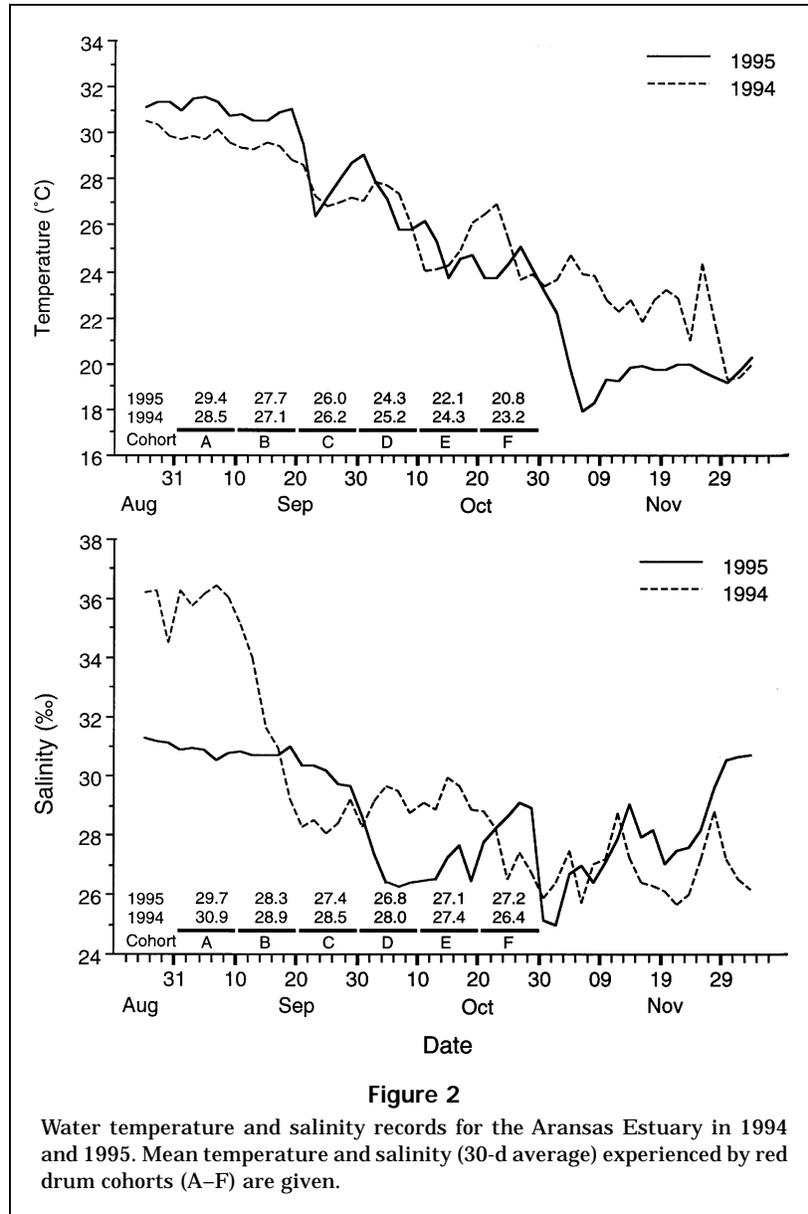
Catch characteristics

Overall, 1306 and 8144 red drum larvae and early juveniles (3–40 mm) were collected from the two sampling sites in the Aransas Estuary in 1994 and 1995. In both years, settlers were first detected in early September and peak densities of recently settled red drum (≤ 10 mm) were present in early October (Fig. 3). Larger postsettlers (>10 mm) were most abundant from mid-October to early November. Mean densities of recently settled red drum (<10 mm) ranged from 0.0 to 1.7/m² in 1994 and from 0.0 to 4.1/m² in 1995; densities of all postsettlement red drum (≤ 40 mm) ranged from 0.0 to 3.0/m² in 1994 and from 0.0 to 4.2/m² in 1995 (Fig. 3). Maximum densities (per sled tow) observed in 1994 and 1995 in the Aransas Estuary were 3.4/m² and 11.5/m², respectively. Interannual variation in postsettlement density during the two seasons (October–November) was small: 1.53/m² (1994), 1.63/m² (1995). No significant differences in density were detected between years or sites (ANOVA, $P>0.05$).

Although collection effort varied between years, length-frequency distributions of red drum from the Aransas Estuary were similar (Fig. 4). In both years, the smallest individuals collected were 3 mm and large recruits (>30 mm) were collected infrequently. Catch rates showed a steeply ascending left limb which peaked at approximately 8–9 mm, suggesting that recruitment to seagrass meadows was complete for these individuals. A long descending right limb characterized catches for individuals >10 mm.

Age and growth

Age-length relationships (age-length keys) were developed for each year class and described by the following equations: $Age = -17.05 + 42.25 \text{ Log}SL$ (1994, $n=249$, $r^2=0.90$, $CV=8.9$); $Age = -11.43 + 40.11 \text{ Log}SL$ (1995, $n=140$, $r^2=0.90$, $CV=7.5$). Predicted ages of red drum (3–30 mm) ranged from 6 to 45 d in 1994 and from 10



to 48 d in 1995. Individuals from the most abundant size class (8–10 mm) were approximately 20–28 d. Age data were used to determine hatch dates and these data were used to partition individuals into 10-d cohorts.

Instantaneous growth coefficients (*g*) ranged from 0.049 (4.8%/d) in 1994 to 0.051 (5.0%/d) in 1995 (Fig. 5) and differed significantly between years (ANCOVA, *y*-intercepts, *P*<0.001). Instantaneous growth coefficients were also estimated on a site-specific basis within the Aransas Estuary (Table 1). In 1994, growth rates at AB1 were significantly higher than AB2 (ANCOVA, *y*-intercepts, *P*=0.015); however, no site effect was observed in 1995 (ANCOVA, *y*-intercepts, *P*=0.440). The weight-specific growth coefficients (*G*) ranged from 0.159 to 0.162 (14.7–15.0%/d) and from 0.163

to 0.165 (15.0–15.2%/d) in 1994 and 1995, respectively (Table 1).

Mortality

Instantaneous mortality coefficients (*Z*) ranged from 0.134 (12.5%/d) in 1994 to 0.139 (13.0%/d) in 1995 and no significant interannual effect was observed (ANCOVA, slopes, *P*=0.737) (Fig. 6). Stage-specific mortality rates (cumulative mortality during the early postsettlement period: 12-d period, ca. 10–20 mm) ranged from 1.668 (81.1%) to 1.608 (79.9%) in 1994 and 1995, respectively. Spatial variation in mortality was also examined within each year by estimating mortality rates at the two sites within

the Aransas Estuary. Site-specific mortality rates in 1994 ranged from 0.129 to 0.141 and no significant difference was detected between sites (ANCOVA, slopes, $P=0.741$); however, in 1995 mortality rates were significantly lower in AB1 (0.129) than in AB2 (0.193) (ANCOVA, slopes, $P<0.001$).

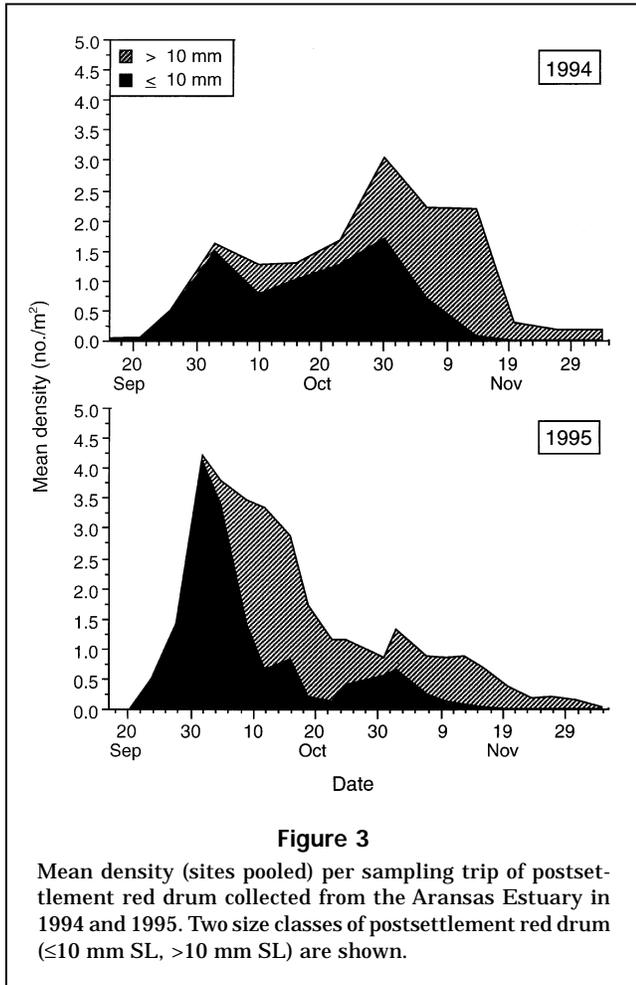


Figure 3

Mean density (sites pooled) per sampling trip of postsettlement red drum collected from the Aransas Estuary in 1994 and 1995. Two size classes of postsettlement red drum (≤ 10 mm SL, >10 mm SL) are shown.

Table 1

Growth and mortality coefficients of postsettlement red drum collected from the Aransas Estuary in 1994 and 1995. The $G:Z$ recruitment index is also shown.

Year	Site	g	G	Z	$G:Z$
1994	AB1	0.051	0.159	0.141	1.128
	AB2	0.048	0.161	0.129	1.248
	All sites	0.049	0.162	0.134	1.209
1995	AB1	0.052	0.165	0.129	1.279
	AB2	0.049	0.163	0.193	0.845
	All sites	0.051	0.165	0.139	1.187

Cohort-specific mortality rates were estimated for the 1995 year class (Fig. 7). Instantaneous mortality coefficients for 10-d cohorts ranged from 0.106 (10.1%/d) to 0.265 (23.3%/d) and a significant temporal trend was detected (ANCOVA, slopes, $P=0.004$). Mortality rates were lowest for midseason cohorts (C, D) and highest for early and late cohorts (B, E), and individuals from the last cohort (E) experienced the greatest mortality. Stage-specific mortality rates (10–20 mm, 12 d) ranged from 1.272 to 1.524 (71.9–78.2%) for midseason cohorts and 2.316 and 3.180 (90.1–95.8%) for early and late-season cohorts.

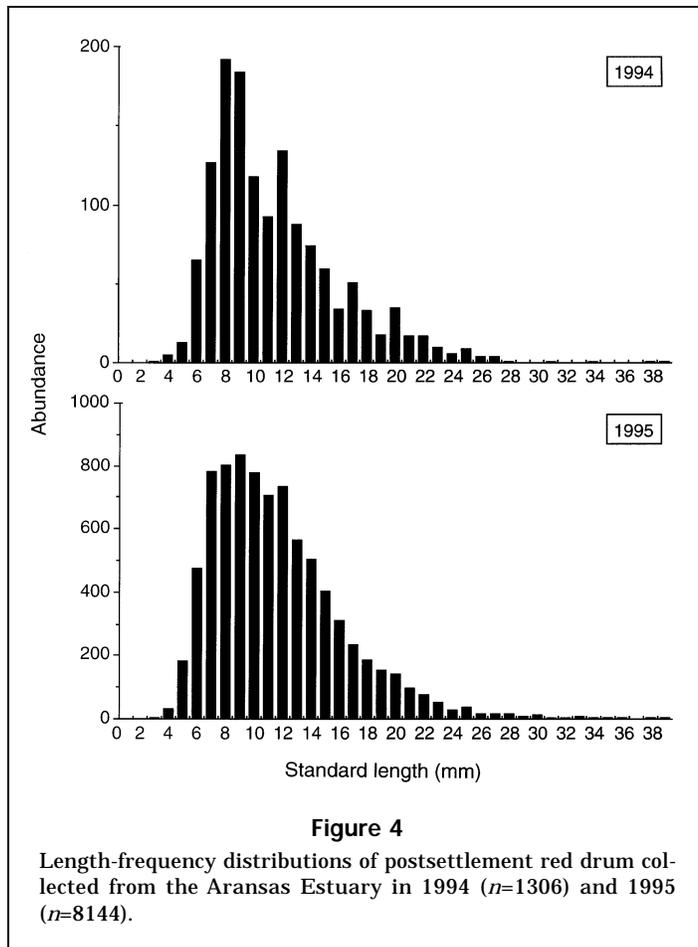
G:Z Index

Recruitment potential of different cohorts was evaluated by comparing $G:Z$ ratios and temporal variation was observed (Fig. 8). The ratio of $G:Z$ was highest for mid-season cohorts; 1.305 (cohort C) and 1.565 (cohort D). In contrast, $G:Z$ ratios of early and late-season cohorts (B, E) were <1 , suggesting that these cohorts were losing biomass. Moreover, annual estimates of $G:Z$ were calculated and ratios were >1 in both 1994 and 1995. Site-specific variation was also observed and, apart from site AB2 in 1995, $G:Z$ ratios were always >1 (Table 1).

Discussion

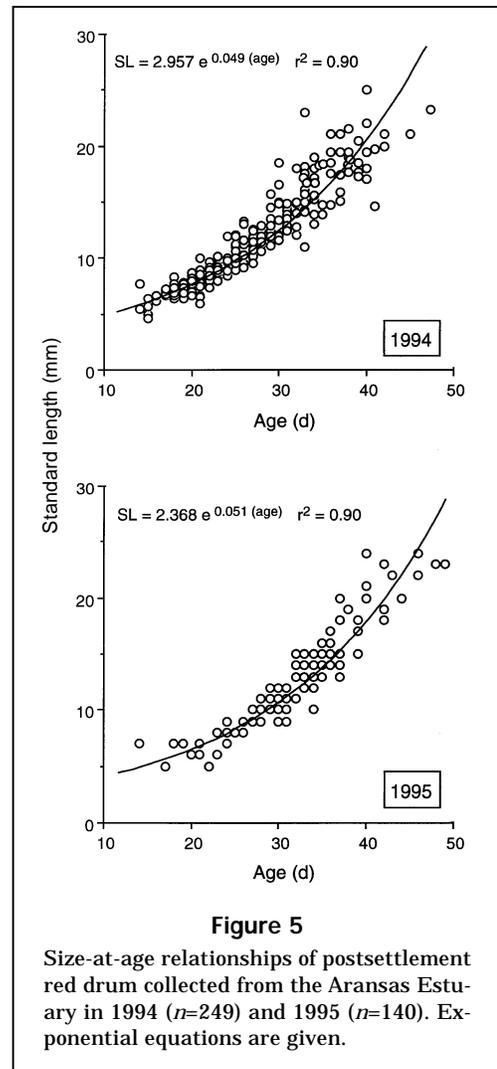
Otolith-derived estimates of age indicate that red drum enter estuarine seagrass meadows after a short pelagic interval. Peak densities were observed for individuals 8–9 mm (20–24 d), suggesting that recruitment to seagrass meadows follows a planktonic period of approximately 20 d. In support of this finding, studies examining red drum during the planktonic phase have shown that the upper size range of red drum larvae in pelagic environments is 6–8 mm (Peters and McMichael, 1987; Comyns et al., 1989; Holt et al., 1989). In addition, Peters and McMichael (1987) sampled demersal habitats in Tampa Bay, Florida, and reported that red drum were first detected at 8 mm. Consequently, red drum appear to move from pelagic to demersal habitats (i.e. settlement) at approximately 8 mm.

Once in seagrass meadows, length- and weight-specific growth of red drum increases rapidly with increasing size (exponential relationships). Length-specific growth rates of new settlers (20–40 d) in the Aransas Estuary averaged 0.58 and 0.62 mm/d in 1994 and 1995, respectively. Growth estimates in the Aransas Estuary are similar to rates reported by Peters and McMichael (1987) for red drum in Tampa Bay, Florida (0.58 mm/d). With size-at-age equations



derived for red drum, we predicted that the length of a 40-d individual ranged from 20.2 mm (1994) to 18.2 mm (1995), which was similar to the predicted length of a 40-d individual collected in Tampa Bay (20.5 mm). Although seasonal trends in growth variation were not examined in this study, Rooker and Holt (1997) observed considerable variability among cohorts of newly settled red drum (0.5–0.8 mm/d), and growth was generally highest for midseason cohorts.

Mortality rates of red drum were substantial and varied over spatial and temporal scales. Interannual estimates of mortality were similar and losses ranged from 12.5 to 13.0%/d ($Z=0.13$ – 0.14). Consequently, cumulative mortality during the settlement and early postsettlement period (12-d period) was relatively high; only about 20% of the initial settlers survived to 40 d. Although no estimates of mortality exist for red drum larvae and early juveniles, these mortality rates are comparable to values reported for other marine fishes during the early life stage. Houde (1987) reported instantaneous daily mortality coefficients for five species of marine fishes during the larval stage (first feeding to late-stage larvae) and



predicted values ranging from 0.04 to 0.18 (4–16%/d). In addition, Houde and Zastrow (1993) summarized natural mortality data for teleost larvae from a variety of sources and reported that the mean instantaneous daily mortality rate of larvae in estuarine habitats was 0.266 (23%/d). Also, McGurk (1986) developed a general mortality equation for marine fish larvae (based on dry weight), and using his equation we predicted the mortality rate of individual red drum 8–10 mm (ca. 750–1500 μg dry wt) would be approximately 0.05–0.11 (4.9–10.4%/d).

Although interannual patterns of mortality were insignificant, variability within a year was relatively high and a seasonal trend was evident. Cohort-specific estimates indicated that mortality rates were lowest for red drum produced in the middle of the spawning season (10%/d), when densities within the seagrass meadows reached maximum levels. Conversely, mortality rates for early and late-season co-

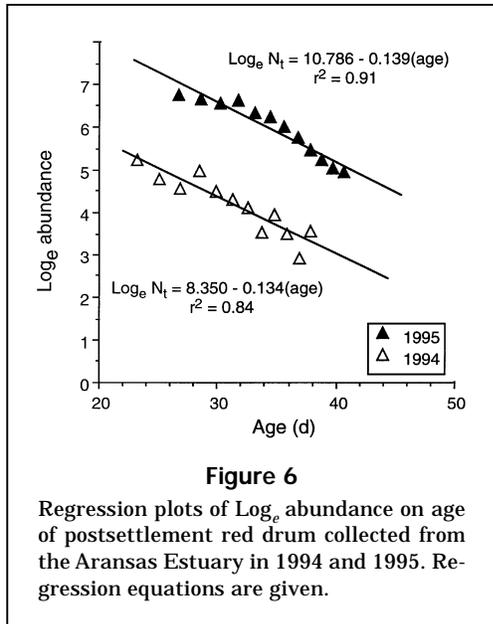


Figure 6

Regression plots of Log_e abundance on age of postsettlement red drum collected from the Aransas Estuary in 1994 and 1995. Regression equations and plots are given.

horts were approximately twofold higher, approaching 25%/d for the late-season cohort. Seasonal fluctuations of this magnitude have been reported in several studies on marine fish larvae and attributed to changes in environmental conditions (e.g. temperature, prey availability) which can directly or indirectly influence mortality (Rutherford and Houde, 1995; Secor and Houde, 1995).

Temperature is often implicated as a critical factor in recruitment because it has the potential of influencing growth rates and causing episodic mortality during early life (Houde and Zastrow, 1993; Houde, 1996). Temperature has been shown to be a primary determinant of growth variation in laboratory and wild populations of red drum (Holt et al., 1981; Lee et al., 1984; Rooker et al., 1997). Moreover, Rooker and Holt (1997) determined that seasonal trends in growth variation for red drum were related to temperature. Mean temperatures experienced by successive cohorts declined throughout the season; however, growth rates were highest for mid-

season cohorts (20 September–10 October) and lowest for early and late cohorts. Conversely, mortality rates were lowest for mid-season cohorts and highest for early and late cohorts. Growth and mortality data appear to be best described by curvilinear relationships (quadratic function), suggesting that there may be an optimal temperature range at which growth and survival of red drum are enhanced and that the midpoint of this range occurs at approximately 26°C.

Variability in other biotic and abiotic factors may also be responsible for observed trends in mortality. Similar to other marine fishes, growth and survival rates of red drum larvae are associated with prey availability (G.J. Holt, unpubl. data). Since spatial and temporal variation in prey density (i.e. meiofauna) are common in estuarine habitats in south Texas (Montagna and Kalke, 1992), seasonal trends in prey abundance may

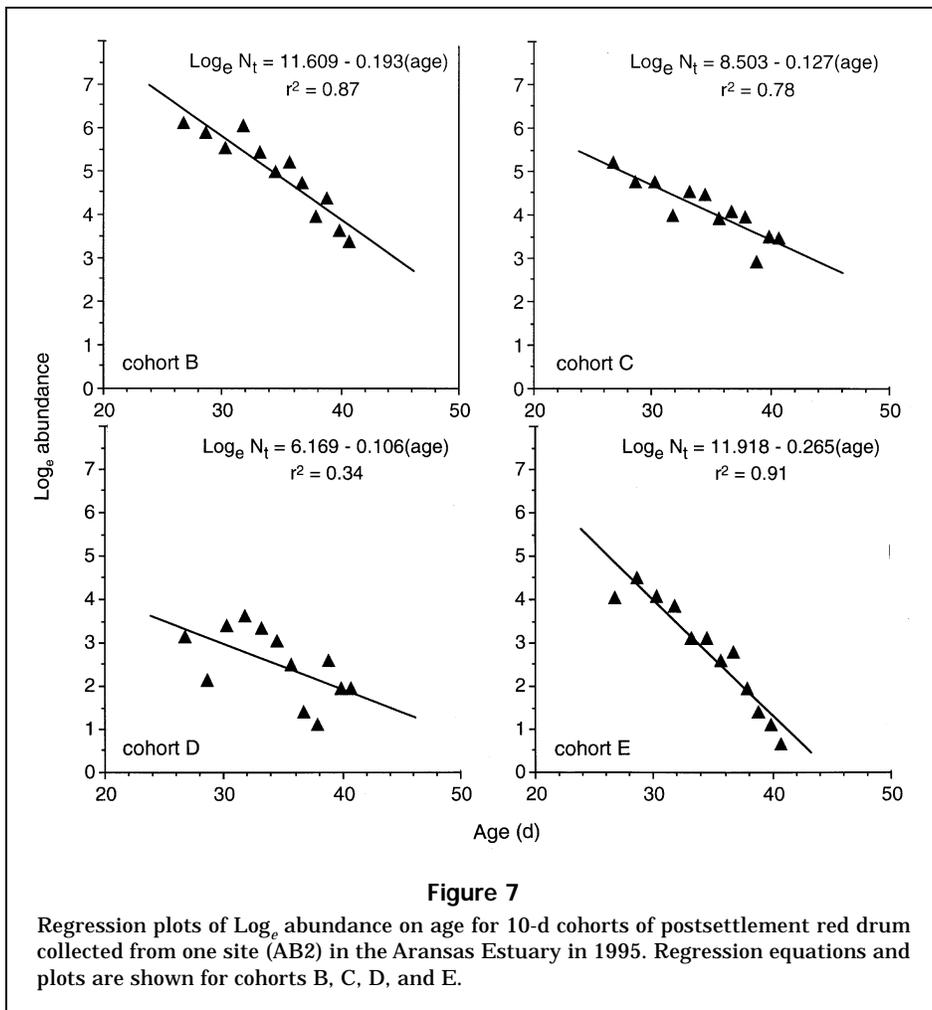


Figure 7

Regression plots of Log_e abundance on age for 10-d cohorts of postsettlement red drum collected from one site (AB2) in the Aransas Estuary in 1995. Regression equations and plots are shown for cohorts B, C, D, and E.

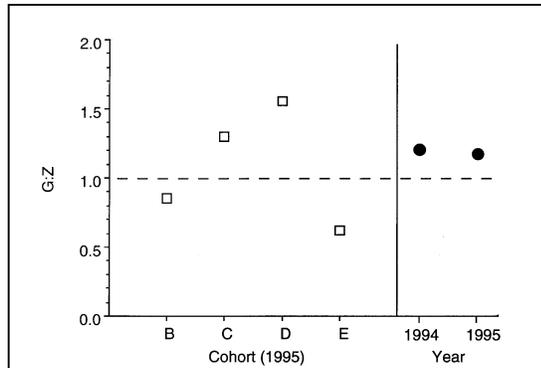


Figure 8

Recruitment potential ($G:Z$ ratios) of 10-d cohorts of postsettlement red drum collected from the Aransas Estuary in 1995. Interannual estimates of $G:Z$ are given.

have affected early life survival. Conversely, predator fields also vary spatially and temporally and survival may be a function of predator abundance. Postsettlement red drum are exposed to a suite of predators in the seagrass meadows and the abundance and distribution of these predators are highly variable (senior author's unpubl. data). Rooker et al. (1998a) examined predation rates on newly settled red drum in experimental mesocosms and demonstrated that predators inhabiting these seagrass meadows, are capable of consuming large numbers of red drum ($Z=2-7\%/h \cdot \text{predator}$). Consequently, fluctuations in prey and predator densities appear critical to the survival of red drum and the addition of this information to future studies should enhance our understanding of early life mortality.

Growth and mortality estimates were combined to evaluate the relative recruitment potential ($G:Z$) of red drum cohorts. According to Houde and Zastrow's (1993) review of 188 species, $G:Z$ ratios for marine fish larvae are generally less than 1.0 (mean $G:Z=0.89$) and larvae inhabiting estuarine ecosystems tend to have low $G:Z$ ratios (range: 0.34–0.82). However, recent work in Chesapeake Bay on striped bass (*Morone saxatilis*) has demonstrated that $G:Z$ ratios can be >1 in estuarine ecosystems (Rutherford and Houde, 1995; Secor and Houde, 1995). Similarly, $G:Z$ ratios for postsettlement red drum in the Aransas Estuary were >1 in both 1994 and 1995 (1.21 and 1.19, respectively) and, as a result, gross growth efficiency was positive and the recruitment potential of 1994 and 1995 year classes appears to have been favorable.

A high degree of correspondence in $G:Z$ ratios between years was present, suggesting that conditions for growth and survival were similar in 1994 and

1995. Although the assessment of physical and biological conditions was limited (no data on prey availability or predator fields), parameters measured in this study (e.g. temperature, salinity, settlement size, and density) were relatively equal between years. In contrast, $G:Z$ ratios of 10-d cohorts and the environmental conditions experienced by these individuals were highly variable within a single season. The $G:Z$ ratios were highest (1.3–1.6) for midseason cohorts and settlement densities at these times were at maximum levels. Thus, it appears that physical and biological conditions in the seagrass meadows were optimal for growth or survival, or for both. The opposite trend was observed for individuals arriving early and late in the season. Because $G:Z$ ratios of individuals from these cohorts were low (0.6–0.9), we postulated that nursery conditions experienced by early and late-season cohorts do not favor early life survival (low recruitment potential).

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Literature cited

- Bailey, K. M., and E. D. Houde
1989. Predation on egg and larvae of marine fishes and the recruitment problem. *Adv. Mar. Biol.* 25:1–83.
- Baltz, D. M., C. Rakocinski, and J. W. Fleeger.
1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. *Environ. Biol. Fish.* 36:109–126.
- Campana, S. E., and J. D. Neilson
1985. Microstructure of fish otoliths. *Can. J. Fish. Aquat. Sci.* 42:1014–1032.
- Comyns, B. H., J. Lyczkowski-Shultz, D. L. Nieland, and C. A. Wilson.
1991. Reproduction of red drum, *Sciaenops ocellatus*, in the northcentral Gulf of Mexico: seasonality and spawner biomass. U.S. Dep. Commer., NOAA Tech Rep NMFS 95:17–26.
- Comyns, B. H., J. Lyczkowski-Shultz, C. F. Rakocinski, and J. R. Steen Jr.
1989. Age and growth of red drum larvae in the north-central Gulf of Mexico. *Trans. Am. Fish. Soc.* 118:159–167.
- Cushing, D. H.
1975. Marine ecology and fisheries. Cambridge Univ. Press, Cambridge, England, 278 p.

- Frederick, J. L.**
1997. Post-settlement movement of coral reef fishes and bias in survival estimates. *Mar. Ecol. Prog. Ser.* 150:65-74.
- Fuiman, L. A., and A. E. Magurran.**
1994. Development of predator defences in fishes. *Rev. Fish. Biol. Fish.* 4:145-183.
- Holt, G. J., R. Godbout, and C. R. Arnold.**
1981. Effects of temperature and salinity on egg hatching and larval survival of red drum, *Sciaenops ocellatus*. *Fish. Bull.* 79:569-573.
- Holt, S. A., G. J. Holt, and C. R. Arnold.**
1989. Tidal stream transport of larval fishes into non-stratified estuaries. *Rapp. P.V. Réun. Cons. Int. Explor. Mer* 191:100-104.
- Houde, E. D.**
1987. Fish early life dynamics and recruitment variability. *Am. Fish. Soc. Symp.* 2: 17-29.
1996. Evaluating stage-specific survival during the early life of fish. *In* Y. Watanabe, Y. Yamashita, and Y. Oozeki (eds.), *Survival strategies in early life stages of marine resources*. AA Balkema, Rotterdam, p 51-66.
- Houde, E. D., and C. E. Zastrow.**
1993. Ecosystem- and taxon-specific dynamic and energetics properties of larval fish assemblages. *Bull. Mar. Sci.* 53:290-335.
- Jones, C.**
1986. Determining the age of larval fish with the otolith increment technique. *Fish. Bull.* 84:91-103.
- Lee, W. Y., G. J. Holt, and C. R. Arnold.**
1984. Growth of red drum larvae in the laboratory. *Trans. Am. Fish. Soc.* 113:243-246.
- McGurk, M. D.**
1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. *Mar. Ecol. Prog. Ser.* 34:227-242.
- Montagna, P. A., and R. D. Kalke.**
1992. The effect of freshwater inflow on meiofaunal and macrofaunal populations in the Guadalupe and Nueces Estuaries, Texas. *Estuaries* 15:307-326.
- NOAA (National Oceanic and Atmospheric Administration).**
1991. Our living oceans: First annual report on the status of U.S. living marine resources. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-F/SPO-1:47-48.
- Peters, K. M., and R. H. McMichael Jr.**
1987. Early life history of the red drum *Sciaenops ocellatus* (Pisces: Sciaenidae) in Tampa Bay, Florida. *Estuaries* 10:92-107.
- Ricker, W. E.**
1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* 191, 382 p.
- Rooker, J. R.**
1997. Early life history of red drum (*Sciaenops ocellatus*) in subtropical seagrass meadows: patterns of condition, growth, and mortality. Ph.D. diss., Univ. Texas at Austin, Austin, TX, 192 p.
- Rooker, J. R., and S. A. Holt.**
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., G. J. Holt, and S. A. Holt.**
1997. Condition of larval and juvenile red drum (*Sciaenops ocellatus*) from estuarine nursery habitats. *Mar. Biol.* 127:387-394.
- Rooker, J. R., G. J. Holt, and S. A. Holt.**
1998a. Vulnerability of newly settled red drum (*Sciaenops ocellatus*) to predatory fish: is early survival enhanced by seagrass meadows? *Mar. Biol.* 131:145-151.
- Rooker, J. R., S. A. Holt, M. A. Soto, and G. J. Holt.**
1998b. Post-settlement patterns of habitat use by sciaenid fishes in subtropical seagrass meadows. *Estuaries* 21:315-324.
- Rutherford, E. S., and E. D. Houde.**
1995. The influence of temperature on cohort-specific growth, survival, and recruitment of striped bass, *Morone saxatilis*, larvae in Chesapeake Bay. *Fish. Bull.* 93:315-332.
- Secor, D. H., and E. D. Houde.**
1995. Temperature effects on the timing of striped bass egg production, larval viability, and recruitment potential in the Patuxent River (Chesapeake Bay). *Estuaries* 18:527-544.
- Sokal, R. R., and F. J. Rohlf.**
1981. *Biometry*, 2nd edition. W. H. Freeman, San Francisco, CA, 859 p.
- Swingle, W. E.**
1990. Status of the commercial and recreational fishery. *In* Red drum aquaculture, p. 22-24. Texas A&M Sea Grant Program report TAMU-SG-90-603, College Station, Texas.
- Werner, E. E., and J. F. Gilliam.**
1984. The ontogenetic niche and species interactions in size-structured populations. *Ann. Rev. Ecol. Syst.* 15:393-425.