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Patterns in Abundance, Growth, and Mortality of Juvenile Red Drum across Estuaries on the Texas Coast with Implications for Recruitment and Stock Enhancement

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Abstract.—The interannual variation in patterns of abundance, growth, and mortality of juvenile red drum *Sciaenops ocellatus* was examined with long-term monitoring data from nine estuaries along the Texas Gulf Coast during a 20-year period. Estimates of abundance and mortality exhibited order-of-magnitude differences. Growth rates varied two- to threefold across years within each estuary and across estuaries within a single year. For age-0 juveniles, abundance was typically highest in late fall, length increased exponentially, and mortality was generally low. Variation in growth and mortality was not related among estuaries, suggesting that the factors affecting the feeding and survival of young red drum are specific to individual estuarine systems. Estimates of age-0 red drum abundance were characterized by the intermittent occurrence of strong year-classes and were positively correlated across estuaries, indicating that factors determining abundance and distribution vary on a large spatial scale. Correlative evidence suggests that compensatory mechanisms affect the survival of age-0 red drum. Variation in abundance during early juvenile stages was not related to abundance variability in later juvenile stages and was significantly reduced by the end of the first year of life, indicating that processes occurring during the juvenile stage may be important in regulating the year-class strength of red drum. Clear effects of increased stocking rates of hatchery-reared fingerlings during the last decade on the abundance of age-0 and age-1 red drum were not detected.

Understanding variation in the abundance of fish populations has long been a central theme of fisheries research (Rothschild 1986). Much of this research has linked events occurring during the early life of fishes to subsequent recruitment. Various studies have demonstrated the importance of the biological and physical processes that occur during the early life stages, particularly the larval stage, in generating large interannual differences in year-class strength (Houde 1987; Bailey and Houde 1989; Cushing 1990; Leggett and DeBlois 1994).

Recent attention has focused on the effect of variation in growth and mortality during the juvenile stage on year-class strength (Sissenwine 1984; Bailey 1994; Campana 1996). Density-dependent and density-independent sources of variability in growth and mortality rates that act during postlarval stages may stabilize population fluctuations that originate in the larval stage (Myers and Cadigan 1993a; Leggett and DeBlois 1994). Many marine fishes are dependent on estuarine habitats that serve as nursery areas for young fishes throughout the first year of life. Annual changes in growth and mortality patterns that occur in estuarine environments may have important effects on future levels of population abundance. Knowledge of the estuarine ecology of juvenile fishes and the interactions among the patterns of abundance, growth, and mortality should improve our ability to forecast the contribution of individual cohorts to the adult population.

The red drum *Sciaenops ocellatus* is an estuarine-dependent fish that inhabits coastal waters of the western Atlantic Ocean and the Gulf of Mexico (Pattillo et al. 1997). Along the Texas coast, spawning occurs in coastal waters during late summer and early fall, and evidence suggests that mature adults congregate near the mouths of passes and inlets (Pearson 1929; Peters and McMichael 1987; Comyns et al. 1991). Tidal currents transport larvae through passes into estuaries, where they settle in shallow nursery habitats and remain through the juvenile stage (Holt et al. 1989; Rooker and Holt 1997). Red drum commonly occur year-round in Texas estuaries through at least age 4, whereas older red drum migrate to offshore waters during fall and winter (Pattillo et al. 1997). Red drum was an important commercial species in the northern Gulf of Mexico until 1990, when harvest was banned throughout the region. The

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recreational fishery is currently of both social and economic importance in the region, as red drum is one of the most targeted species throughout the Gulf of Mexico (Van Voorhees et al. 1992). Because of declining numbers along the Texas coast during the 1970s and the strong public interest in red drum as a sport fish, the state of Texas initiated a red drum stock enhancement program in 1983. The goal of the program is to supplement natural recruitment of red drum in Texas estuaries by stocking hatchery-reared juvenile fingerlings (25–30 mm total length) in suitable habitats during the recruitment season (McEachron and Daniels 1995).

This study examines spatial and temporal variation in the abundance, growth, and mortality of age-0 juvenile red drum in nine estuarine systems spanning the entire Texas Gulf Coast throughout a 20-year period. Annual estimates of abundance, growth, and mortality are examined to determine if interannual variation is correlated among estuaries and to identify factors that may generate the observed patterns. To assess the potential for processes operating during the early juvenile stage (age-0) to influence red drum recruitment success, seasonal patterns of decline in age-0 abundance and the effects of variable abundance on age-0 growth are evaluated. In addition, water temperature fluctuations among years and estuaries are examined for their potential influence on the growth and survival of age-0 red drum. The effectiveness of estimates of age-0 abundance, growth, and mortality in forecasting future population size is evaluated by comparing these age-0 traits with abundance at age-1. Yearly trends in the abundance of age-0 and age-1 red drum are compared to increased stocking rates during the last decade to evaluate the effects of stocking on recruitment of young fish.

Methods

Red drum were sampled in nine Texas estuaries throughout the study period. These major estuarine systems extend along the Texas coast for nearly 650 km, from Sabine Lake in the north, which is located on the Texas–Louisiana border, to the lower Laguna Madre in the south, which is near the Mexican border (Figure 1). With the exception of Sabine Lake, each of these estuaries is separated from the Gulf of Mexico by a barrier island chain that extends along much of the coast. Several passes or inlets that connect the estuaries with the Gulf of Mexico are located along this island chain.

Age-0 juvenile red drum were collected throughout a 20-year period from October 1977 to May 1997 in seven of nine Texas estuaries; collections occurred from October 1986 to May 1997 in Sabine Lake and from October 1984 to May 1997 in East Matagorda Bay. Age-0 red drum were captured with seines as part of Texas Parks and Wildlife's resource monitoring initiated in October 1977 (Fuls and McEachron 1997). Sample locations consisted of 1-square-nautical-mile (1.85-km^2) grids that were chosen randomly from all grids that contained shoreline throughout each estuary. For each sample, a single seine (18.3 m long × 1.8 m deep, with 1.9-cm and 1.3-cm stretched nylon mesh wings and bag, respectively) was pulled parallel to the shore for a distance of approximately 15.2–30.5 m. During each year, between 6 and 20 (mean = 13.05, SD = 5.38) seine samples were collected per month in each estuary. The number of monthly samples increased continually throughout the survey period, and beginning in 1992, 20 samples/month were collected in all estuaries except East Matagorda Bay (where 10 samples/month were collected). More specific details on amendments to the number of monthly samples completed throughout the study period are given in Fuls and McEachron (1997). Attempts were made to distribute sampling effort equally within each month, so that half of the seine samples were completed during the first half of the month and half during the second, with a maximum of five seines completed per sample day. For each sample, all fish and invertebrates were counted; for a subsample of randomly selected individuals from each species, total length (TL) was measured. In addition, several environmental variables were measured, including surface water temperature, salinity, dissolved oxygen, turbidity, bottom type, and aquatic vegetation density.

An index of the abundance of age-0 red drum was calculated as the geometric mean of catch per unit effort (CPUE = back-transformed mean of log[number of red drum per seine haul + 1] − 1). Sampling effort was stratified by month, and the relative abundance of each year-class was determined using monthly abundance estimates from October through June. No collections were included from July, August, or September because age-0 red drum were rarely captured during this time period. Monthly CPUE estimates were averaged over the 9-month period to obtain annual estimates of abundance for each year-class.

Growth in length for each year-class of red drum was initially calculated by means of linear, exponential, and nonlinear piecewise methods to de-

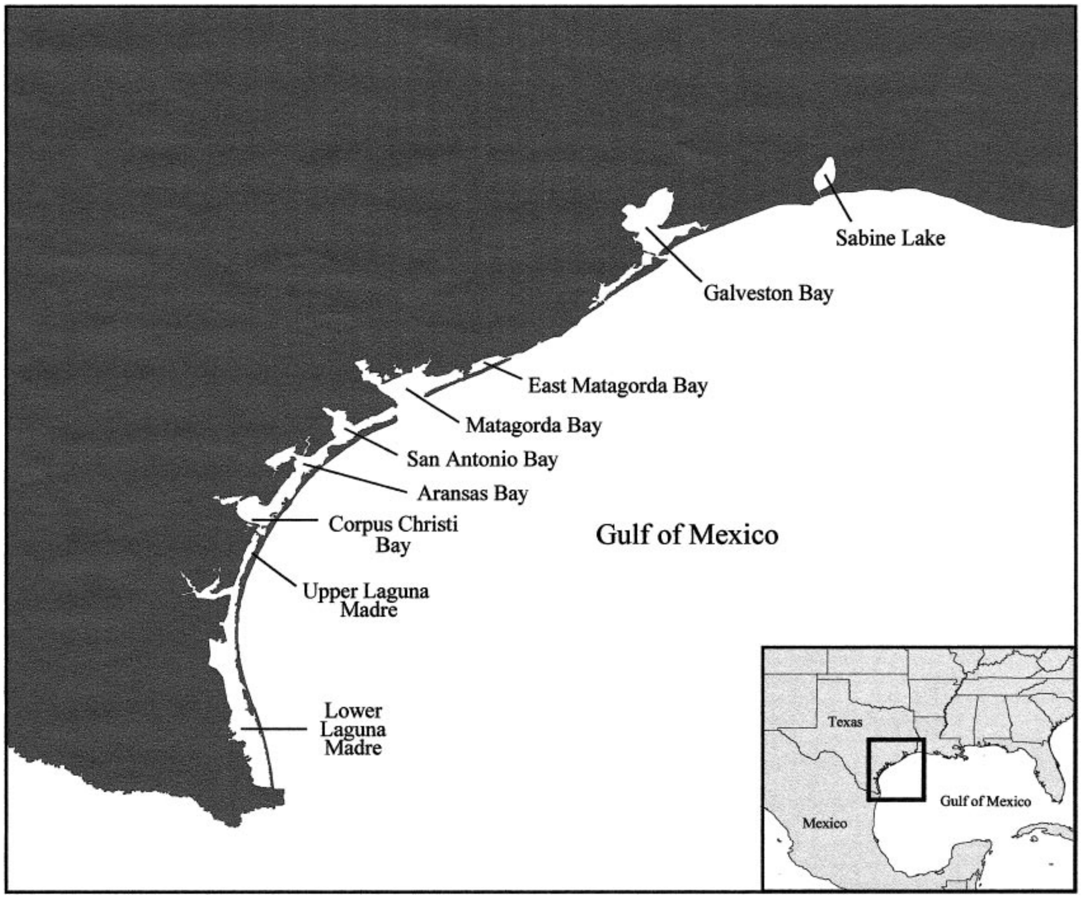

FIGURE 1.—Map of the Texas Gulf Coast showing the locations of the nine estuaries examined in this study.

termine the most appropriate growth model. Based on analysis of residuals and comparisons between predicted and observed sizes at age-1, exponential models provided the best fit to the data. Instantaneous growth rates were calculated by means of an exponential growth model,

$$\mathrm{TL} = ae^{gt}$$

where TL = red drum TL; t = the day of the year when capture occurred, and g = daily instantaneous growth coefficient. Instantaneous growth coefficients were converted to daily conditional growth rates (percent growth per day) by evaluating the expression $1 - e^{-g}$ (Ricker 1975).

Mortality rates for age-0 red drum were calculated by means of catch curve analysis (Ricker 1975) based on the exponential model of decline in CPUE with increasing date of capture:

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

where N_t = abundance at time t, N_0 = initial abundance, and Z_t = daily instantaneous mortality coefficient. For each year-class, CPUE was calculated separately for each month between October and June. Beginning with the data for the month having the highest CPUE estimate and ending in June, log-transformed monthly CPUE estimates were regressed against the midpoint date of capture of each month (i.e., the 15th of each month). Regression slopes represented the instantaneous mortality rate (Z). Daily conditional mortality rates (percent mortality per day) were calculated as $1 - e^{-Z}$. Calculation of mortality rates by using trends in catch data over time assumes that any observed declines in CPUE are not the result of increased emigration from the nearshore zone or the decreased catchability of fish with age or size.

Pearson's correlation analysis was used to compare annual estimates of the abundance, growth, and mortality of age-0 red drum across estuaries throughout the study period. To assess the potential for density-dependent processes to occur during the juvenile life stage, age-0 abundance in December was compared with age-0 abundance in April in each estuary across years. Correlation analysis was used to determine if the interannual patterns of variation in age-0 CPUE that were detected during the fall (December) remained similar after several months (April). Correlation analysis was also performed between the annual estimates of age-0 abundance and those of age-0 growth to evaluate the effects of density on growth rate.

The relationships between red drum life history traits and several indices of estuary water temperature were examined to evaluate a potential density-independent source of variation. Average surface water temperatures in each estuary were calculated for the fall (September–November), winter (December–February), and spring (March–May) of each year. The rate of spring warming was calculated each year as the slope of a piecewise regression of water temperature versus day of the year between September and May that occurred after the break point (break points usually occurred in late winter, when water temperatures began to increase). Also, as an index of winter severity, the number of days each year when water temperatures fell below 10°C were recorded for each estuary. This index should account for the potential effects of the freeze events that occur sporadically along the Texas Gulf Coast. Correlation analyses were performed between growth, mortality, and abundance of age-0 red drum and annual measures of water temperature variation to examine interannual and interestuary variation.

The age-1 red drum examined in this study were collected during the fall months (beginning in early to mid-September and ending in mid- to late November) throughout the 19-year period from 1978 to 1996 in eight of nine Texas estuaries; collections began in September 1986 in Sabine Lake. All age-1 red drum were captured with gill nets as part of a Texas Parks and Wildlife resource monitoring effort initiated in November 1975 (Fuls and McEachron 1997). Monofilament gill nets measured 183 m long × 1.2 m deep, with four separate 45.7-m sections of 7.6-cm, 10.2-cm, 12.7-cm, and 15.2-cm stretched mesh. Gill nets were set perpendicularly to the shore just off the beach with the section with the smallest mesh (7.6 cm) being closest to shore and were fished overnight (mean soak time = 14.21 h; SD = 1.13 h, range = 11.50−18.22 h). More details on gill-net sampling methods are given in Fuls and McEachron (1997). Each year beginning in 1981 (1986 in Sabine Lake), 45 gill nets were set during fall in each estuary except East Matagorda Bay, where up to 20 gill nets were set each fall. Before 1981, between 4 and 18 nets were set each fall. Sampling effort was distributed over a 10-week period, with four to five gill nets being set per week and a maximum of three nets set per sample day. All red drum captured in gill nets were counted, and TL was measured for a randomly selected subsample of individuals in each of the four mesh sizes per sample day.

Length-at-age keys (Colura and Buckley 1996) generated from red drum captured in estuarine systems only (i.e., excluding fish caught in the Gulf of Mexico) were used to estimate the maximum size of age-1 red drum caught during fall (12–15 months old). All red drum up to 370 mm TL that were captured in gill nets in the fall were assumed to be age-1 because age-0 red drum are too small to be caught in gill nets. The minimum size of age-2 red drum captured during fall is approximately 350 mm TL (Colura and Buckley 1996). Length-at-age data from 1993 and 1994 indicated that nearly all red drum of less than 350 mm TL were age-1 fish and that only 9–11% of red drum measuring 350–374 mm TL were age-2 fish (Colura and Buckley 1996). Although it probably excluded some larger age-1 fish from this study, the use of 370 mm TL as the maximum age-1 size during fall gill-net sampling minimized the effect of age-2 fish on age-1 CPUE estimates.

An annual index of age-1 red drum abundance was calculated as the geometric mean of CPUE (back-transformed mean of log[number of red drum per hour of soak time + 1] − 1) based on all gill nets set each fall. The abundance of a given age-0 year-class was thus based on age-1 fish captured during fall of the following year (e.g., the abundance of age-0 fish from the 1977 year-class was based on age-1 fish captured during fall 1978).

To determine whether the abundance of age-0 red drum was proficient in forecasting year-class strength, correlative relationships between the abundances of age-0 and age-1 red drum were examined in each estuary and coastwide by pooling abundance data from all years and estuaries. Relationships between age-0 red drum growth and mortality rates and age-1 red drum abundance were also examined in each estuary and coastwide. General trends in interannual water temperature variation during the first year of life (age-0) were compared with age-1 abundance the following year.

Trends in annual stocking rates of hatchery-reared red drum fingerlings were examined during 1989–1996. Correlations between stocking rates and age-0 or age-1 CPUE estimates were performed across estuaries to assess the effects of hatchery plantings on the abundance of young red drum.

Results

In all, 10,984 age-0 juvenile red drum were captured from 1977 to 1997. Order-of-magnitude differences in annual abundance were observed within each estuary, with three- to fivefold differences being common. Age-0 abundance also varied three- to fivefold among estuaries within a given year (Figure 2A). Generally, East Matagorda Bay and lower Laguna Madre had higher average age-0 red drum abundance compared with other estuaries, with Sabine Lake and upper Laguna Madre having low abundance throughout most of the study period. Strong year-classes were apparent in 1981–1982 and 1990–1991, with moderate year-classes in each year after 1990 (Figure 2A). Age-0 red drum abundance was positively correlated across estuaries. All significant Pearson's correlation coefficients (15 of 36) were positive (Table 1). Only Sabine Lake and upper Laguna Madre, the two estuaries with the lowest catch rates, showed a lack of correlation with other estuaries.

General growth patterns indicated that red drum length increased exponentially during the first year of the juvenile life stage (Figure 3). Daily conditional growth rates were generally about 0.75% and were rarely greater than 1.00% (Table 2), which translates to average growth increases of about 0.6 mm/d. Within each estuary, two- to threefold differences in growth coefficients were observed among years. Growth also varied two- to threefold among estuaries within each year. Growth was generally higher in estuaries at more southern latitudes, with lower Laguna Madre red drum having the highest growth rates and Sabine Lake red drum the lowest growth rates during the study period (Table 2). Although residual analyses indicated that the sizes of older age-0 red drum tended to be underestimated somewhat by the exponential growth model, the predicted sizes on September 15 the following fall (approximately age-1) agreed well with the actual sizes of age-1 red drum captured during this time period. Predicted size at age-1 ranged from 271 to 383 mm TL across estuaries, and the actual mean size of age-1 fish captured in September gill-net sampling was 325 mm TL. Growth rates were not correlated across estuaries; only 3 of 36 correlations were significant, ($P < 0.05$) and 12 of 36 correlation coefficients were negative.

From the peak months in fall and winter to the end of spring, age-0 red drum abundance declined exponentially. Within each estuary, the highest CPUE was typically observed during November and December, with a general decline thereafter (Figure 4). Age-0 juvenile mortality rates were generally around 0.50% per day and only rarely exceeded 2.00% per day in any estuary (Table 3). Order-of-magnitude differences in mortality rates were observed among years within each estuary and among estuaries within each year. Mortality rates showed no evidence of correlation among estuaries, as only 3 of 36 correlations were significant ($P < 0.05$) and 17 of 36 correlation coefficients were negative.

Significant positive correlations between the December and April age-0 CPUE estimates were detected in only two of nine estuaries (Table 4). Correlations between initial peak age-0 abundance and seasonal growth rates were negative for six of nine estuaries (Table 4); however, only one relationship was significant ($P < 0.05$), and all were generally weak.

Interannual variation in estuary surface water temperatures did not appear to have a strong influence on the variations in age-0 red drum abundance, growth, and mortality across years. Although average spring water temperature was positively related to later body size (estimated on August 1) in some estuaries ($P < 0.05$ in one estuary, $P < 0.10$ in three others), the pattern was not consistent coastwide. The rate of spring warming and the number of days with water temperatures below 10°C were not strongly related to age-0 growth, mortality, or abundance (no significant correlations; most P-values > 0.25). Interannual variation in average fall and winter temperatures was also not significantly related to interannual variation in age-0 red drum life history traits (most P-values > 0.50). Similarly, temperature variation among estuaries appeared to have only a minor influence on interestuary variation in age-0 red drum abundance, growth, and mortality. Average seasonal water temperatures, rates of spring warming, and frequency of freeze events across estuaries were not related to interestuary variation in abundance or mortality rates (no significant correlations; most P-values > 0.40). Only average winter temperatures across estuaries were positively correlated with growth variability among estuaries (15 of 19 correlations between average winter temperature and growth were positive; $P < 0.15$ for 8 of these).

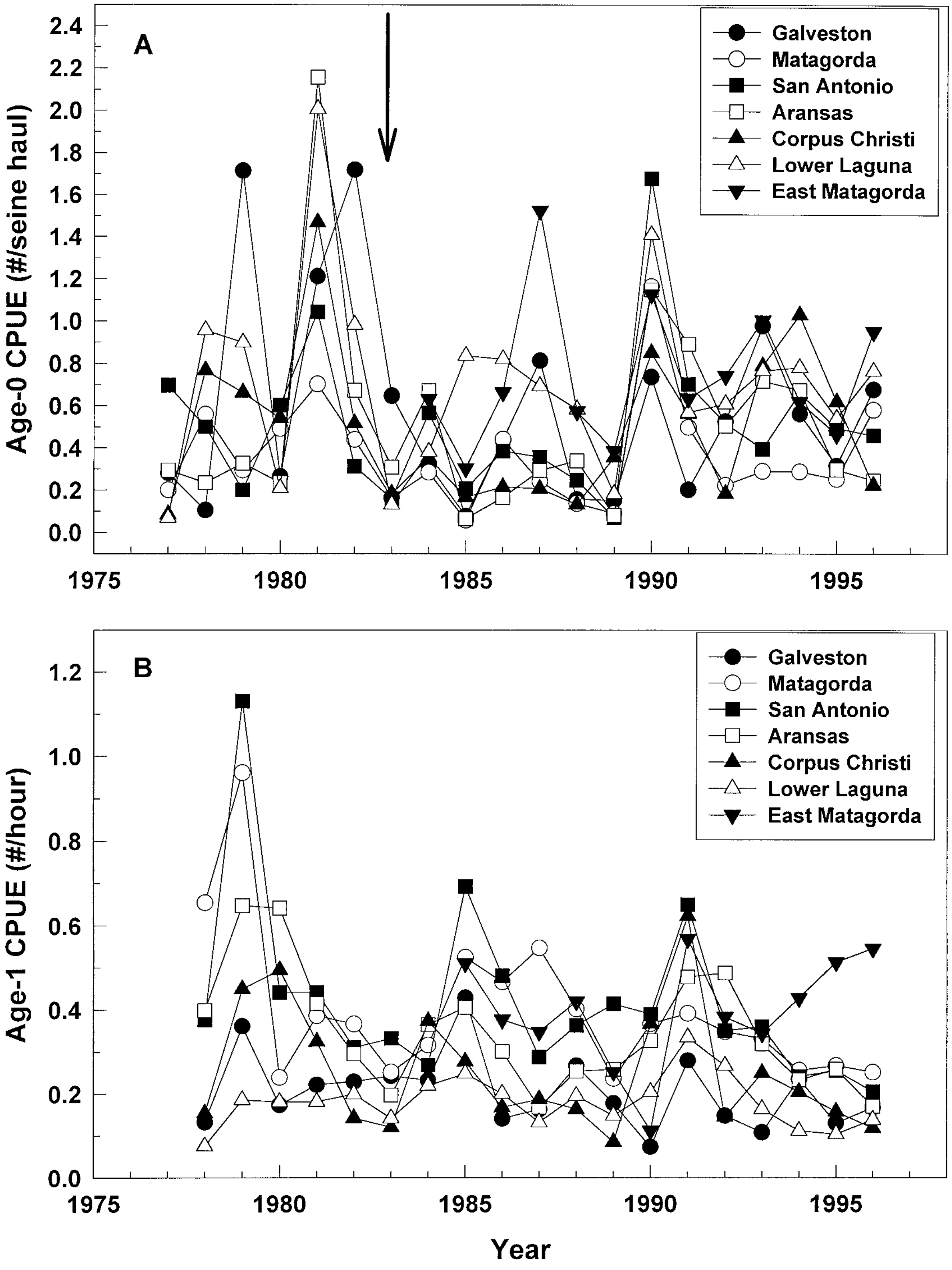

FIGURE 2.—Catch per unit effort (CPUE = number per seine haul or number per hour) of **(A)** age-0 and **(B)** age-1 red drum each year from 1977 to 1997 in seven Texas estuaries. Two of the estuaries examined in the study, Sabine Lake and upper Laguna Madre, were excluded from this figure because of generally low catch rates throughout the study period. Age-0 CPUE is the average monthly CPUE for October–June; age-1 CPUE is the average monthly CPUE for September–November only. For age-0 fish, each year refers to the first-year juvenile

In all, 22,502 age-1 red drum were captured during fall between 1978 and 1996. Two- to threefold differences in age-1 abundance were observed between years within each estuary and among estuaries within each year (Figure 2B). High abundance coupled with large variation was evident during the late 1970s, followed by several years of low abundance and low variability during the early to mid-1980s. After 1991, the abundance of age-1 red drum declined steadily in each estuary, with the exception of East Matagorda Bay, and variation among estuaries was low. Interannual variation in abundance was lower for age-1 red drum than for age-0 red drum in each estuary (Table 5). In most estuaries, the coefficient of variation ($100 \cdot \mathrm{SD/mean}$) in CPUE declined by 25–45% from age-0 to age-1 fish (range $= 7-57\%$).

The presence of a strong age-0 year-class in 1990 was evident in fall 1991 age-1 abundance estimates; however, a strong 1981 age-0 year-class was not apparent in fall 1982 age-1 estimates. Correlations between age-0 abundance and age-1 abundance the following year were positive (Figure 5), but most were very weak and only one was statistically significant ($P < 0.05$). Within each estuary, no correlations were evident between the growth or mortality rates of age-0 red drum and the abundance of age-1 fish. Furthermore, no relationship was observed between the growth or mortality rates of age-0 fish and the abundance of age-1 fish when data from all estuaries and years were pooled (Figure 6). Pooled data also revealed that the relationship between age-0 abundance and age-1 abundance was highly variable ($r = 0.13$; $P = 0.11$).

Interannual and interestuary variation in water temperatures did not appear to have strong effects on age-1 abundance levels. Average seasonal water temperatures and the frequency of freeze events during the first year of life were not consistently related to age-1 CPUE (most correlation P-values > 0.25; significant correlations were both positive and negative).

Stocking rates of hatchery-reared red drum fingerlings have shown an increasing trend during recent years, with coastwide numbers stocked rising from about 7 million in 1989 to 25–30 million by the mid-1990s (Table 6). Clear effects of increased stocking rates on age-0 or age-1 abundance were not apparent, as age-0 CPUE was relatively constant after 1990 and age-1 CPUE showed a slight declining trend during this time (Figure 2A, B). Within each year during the period 1990–1996, correlations across estuaries between stocking rates and age-0 or age-1 CPUE were not significant (P-values > 0.25 for 5 of 7 years for age-0 fish; all P-values > 0.40 for age-1 fish). Similarly, within each estuary, no correlations across years between stocking rates and age-0 or age-1 CPUE were significant ($P > 0.50$ for 6 of 9 correlations for age-0 fish, and 5 of 9 correlations were negative; $P > 0.30$ for 6 of 9 correlations for age-1 fish, and 8 of 9 correlations were negative).

Discussion

A considerable degree of intra- and interannual variability in abundance, growth, and mortality of age-0 juvenile red drum was present across Texas estuaries. Abundance was typically highest early in the juvenile stage, growth was rapid, and mortality was generally low. Previous studies of the early life history of red drum in the Gulf of Mexico indicate that spawning occurs from August through October and that larvae settle into estuarine habitats within approximately 3 weeks at sizes of 8–10 mm (Peters and McMichael 1987; Rooker et al. 1999). Once in the estuary, larval red drum grow quickly and mortality is high. Average growth rates reported for larval and early juvenile red drum (0.6 mm/d; Peters and McMichael 1987; Rooker and Holt 1997; Rooker et al. 1999) are similar to those reported for age-0 juveniles in this study. However, published daily larval mortality rates (12–13% Rooker et al. 1999) are one to two orders of magnitude greater than the daily mortality rates of juveniles ($< 1-2\%$) observed in this study. Order-of-magnitude differences between natural mortality rates of larvae and juveniles are typical for many marine fishes (Houde 1987). Assuming an average larval growth rate of 0.6 mm/d, hatch dates for the early juvenile red drum between 30 and 40 mm long that were captured during October in this study would have occurred sometime between mid-August and early

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growing season beginning in the fall of that year (e.g., 1977 = the 1977–78 season). For age-1 fish, each year refers to the fall season following the previous year's age-0 growing season (e.g., 1978 = the 1977–78 season). The arrow in panel A indicates initiation of the stock enhancement program. Data for East Matagorda Bay were collected from 1984 to 1997.

TABLE 1.—Pearson's correlation matrix for annual values of catch per unit effort (number per seine haul) of age-0 red drum in nine Texas estuaries from 1977 to 1997. An asterisk indicates that $P < 0.05$, a dagger that $0.05 \leq P < 0.10$.

Estuary	Sabine	Galveston	East Matagorda	Matagorda	San Antonio	Aransas	Corpus Christi	Upper Laguna Madre	Lower Laguna Madre
Sabine	1.00								
Galveston	−0.21	1.00							
East Matagorda	−0.27	0.84*	1.00						
Matagorda	−0.29	0.24	0.46*	1.00					
San Antonio	−0.19	0.04	0.38	0.84*	1.00				
Aransas	−0.14	0.40*	0.34	0.58*	0.68*	1.00			
Corpus Christi	−0.07	0.38*	0.10	0.55*	0.54*	0.76*	1.00		
Upper Laguna Madre	−0.13	−0.07	0.43†	0.16	−0.07	−0.20	0.27	1.00	
Lower Laguna Madre	−0.07	0.49*	0.45†	0.64*	0.53*	0.74*	0.71*	0.08	1.00

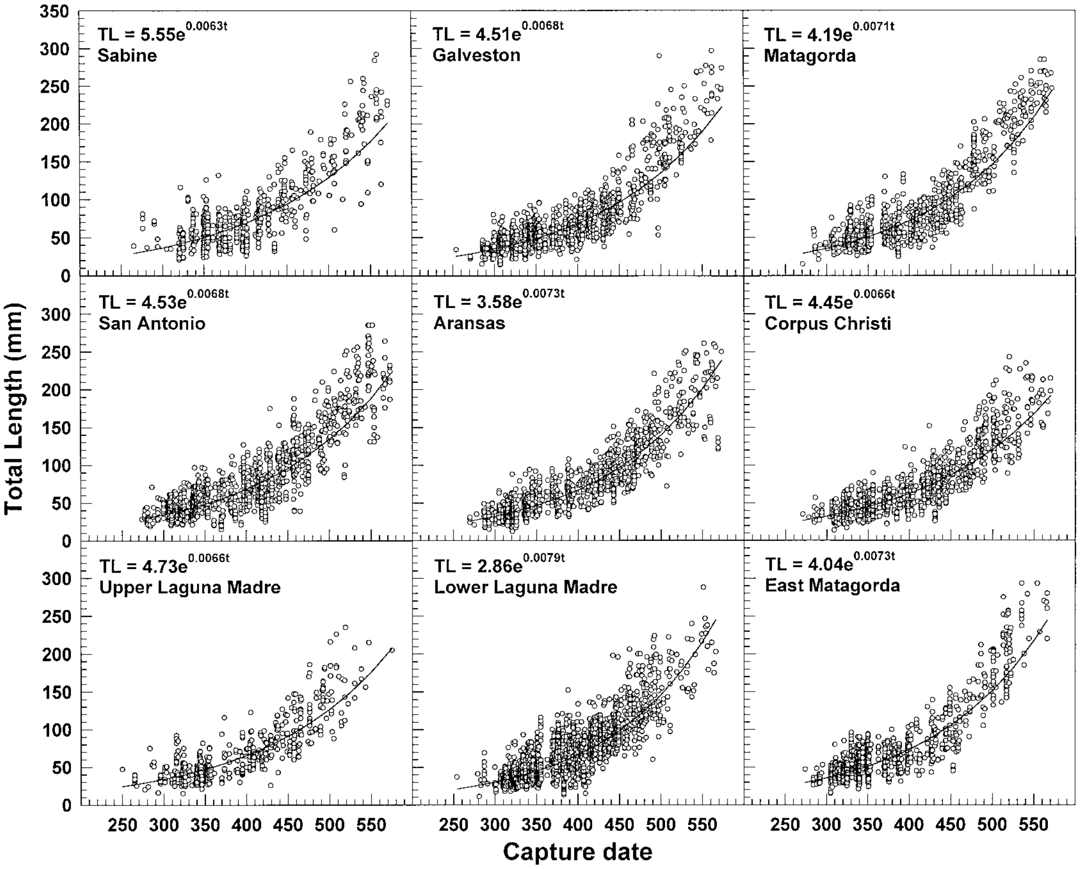

FIGURE 3.—Instantaneous growth equations for age-0 red drum captured in nine Texas estuaries from 1977 to 1997. Length data are presented for all years combined; one equation was fit to the data in each estuary to illustrate the general patterns of age-0 growth. The capture date extends beyond day 365 because the growing season for age-0 red drum examined in this study extends from September of one calendar year through July of the next. Data for Sabine Lake were collected from 1986 to 1997; data for East Matagorda Bay were collected from 1984 to 1997.

TABLE 2.—Daily conditional growth rates (percent per day) for age-0 red drum in nine Texas estuaries from 1977 to 1997; ND = insufficient data. All growth coefficients were significant ($P < 0.05$).

Year	Sabine	Galveston	East Matagorda	Matagorda	San Antonio	Aransas	Corpus Christi	Upper Laguna Madre	Lower Laguna Madre
1977–1978		0.86		0.52	0.50	0.69	0.61	1.04	0.47
1978–1979		0.74		0.81	0.60	0.57	0.65	0.64	0.74
1979–1980		0.56		0.82	0.69	0.65	0.61	0.65	0.79
1980–1981		0.56		0.74	0.64	0.73	0.56	ND	1.12
1981–1982		0.68		0.33	0.63	0.80	0.62	0.39	0.67
1982–1983		0.67		0.76	0.71	0.77	0.69	0.65	0.74
1983–1984		0.54		0.79	0.49	0.73	0.78	ND	0.91
1984–1985		0.69	0.63	0.87	0.75	0.68	0.65	0.56	0.55
1985–1986		0.60	0.50	0.92	0.73	0.58	0.89	1.09	0.83
1986–1987	0.53	0.68	0.58	0.67	0.75	0.99	1.12	0.78	0.71
1987–1988	0.61	0.59	0.67	0.61	0.74	0.75	1.28	ND	1.02
1988–1989	0.61	0.76	0.45	0.82	0.67	0.63	0.73	0.77	0.73
1989–1990	0.83	0.71	0.68	0.78	0.60	0.90	0.96	ND	1.21
1990–1991	0.68	0.79	0.84	0.91	0.80	0.76	0.86	1.12	1.01
1991–1992	0.67	0.80	0.82	0.67	0.72	0.73	0.64	0.70	0.87
1992–1993	0.61	0.73	0.73	0.80	0.77	0.63	0.61	0.41	0.79
1993–1994	0.47	0.51	0.67	0.68	0.61	0.74	0.58	0.58	0.88
1994–1995	0.67	0.67	0.79	0.62	0.74	0.73	0.66	0.68	0.88
1995–1996	0.58	0.62	0.70	0.68	0.69	0.75	0.64	0.60	0.71
1996–1997	0.61	0.66	0.70	0.73	0.58	0.91	0.75	0.75	0.76
Mean	0.62	0.67	0.67	0.73	0.67	0.74	0.74	0.71	0.82

September, which corresponds well with past estimates of the spawning period for red drum in the Gulf of Mexico (Peters and McMichael 1987; Murphy and Taylor 1990; Wilson and Nieland 1994; Rooker and Holt 1997).

Juvenile red drum grew exponentially in length during their first year of life in Texas estuaries. Growth was slower during fall and winter months and increased rapidly beginning in early March. Similar patterns of rapid spring growth have been observed for juvenile red drum in Gulf of Mexico estuaries (Pearson 1929; Simmons and Breuer 1962; Bass and Avault 1975; Peters and McMichael 1987) and typically coincide with seasonally increasing water temperatures along the Gulf Coast. Seasonal variation in water temperature is known to be an important determinant of growth in young red drum and other juvenile estuarine fishes (Lee et al. 1984; Sogard 1992; Rooker and Holt 1997). The timing of the increase in the growth rate of juvenile red drum also corresponds with a dietary shift from the mysids, amphipods, and polychaetes that are mainly consumed by smaller juveniles (< 75 mm) to the fish, crabs, and shrimp that are the primary diet of larger juveniles (Bass and Avault 1975; Peters and McMichael 1987). Ontogenetic dietary shifts in fishes, particularly shifts to include piscine prey in the diet, have been shown to substantially increase growth rates (Paloheimo and Dickie 1966; Stergiou and Fourtouni 1991; Juanes and Conover 1994) and may be important in determining the growth of juvenile red drum.

Growth of juvenile red drum probably remains rapid during summer months at the end of the first year of life (between 9 and 12 months of age). Although the sizes of red drum between 7 and 9 months of age were slightly underestimated by the exponential growth model for some estuaries, the model's predictions of size at age 1 were accurate. Exponential increase in length is atypical for most fish, which usually show linear increases in length and exponential increases in weight with age (Paloheimo and Dickie 1966). The exponential growth in length observed for red drum may reflect the broad time interval over which growth patterns were examined in this study. The growth patterns observed were probably a result of depressed winter growth coupled with rapid spring growth and were evident only when growth was examined across seasons.

The estimation of growth and mortality from size and abundance information over multiple dates of capture has some potential flaws. The 2–3 month spawning period of red drum produces several cohorts of small juveniles that recruit to the sampling gear throughout late fall and early winter. The inclusion of newly recruiting fish during later months will tend to suppress estimates of growth calculated during this time period. Because

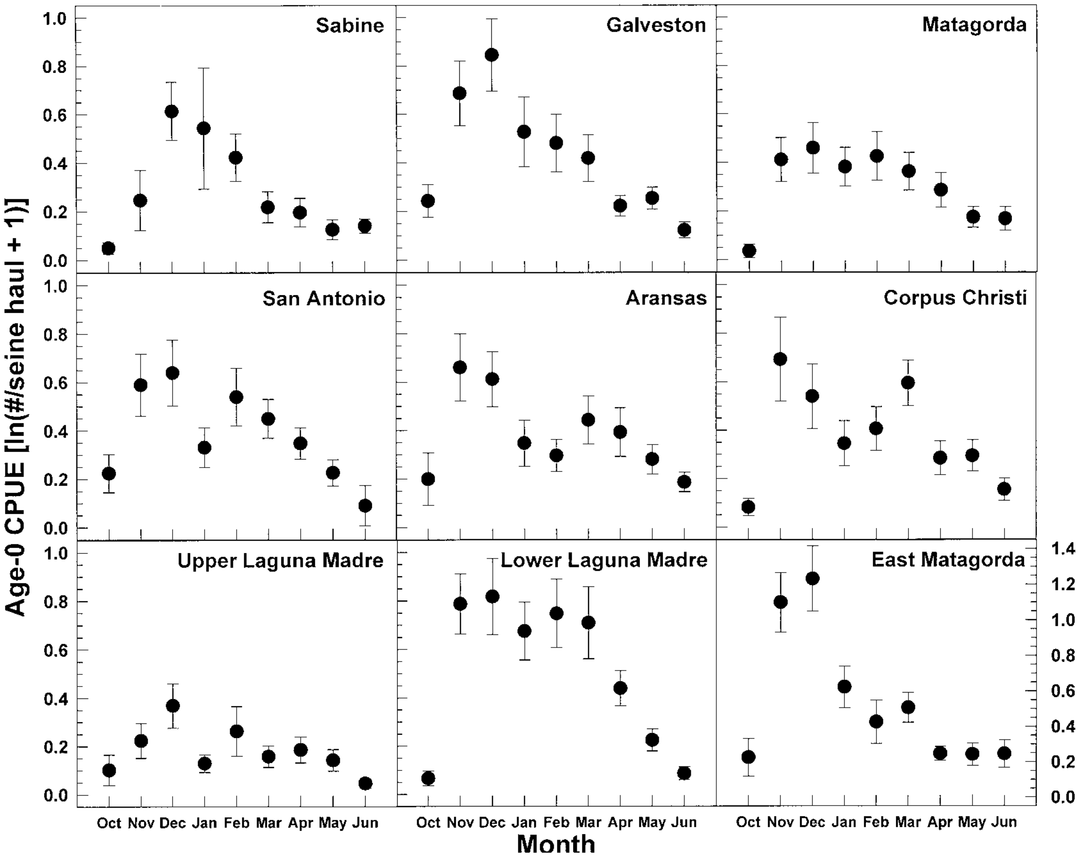

FIGURE 4.—Mean monthly catch per unit effort [CPUE = log(number per seine haul + 1)] ± SE of age-0 red drum in nine Texas estuaries from 1977 to 1997. Note different *y*-axis for East Matagorda Bay. Data for Sabine Lake were collected from 1986 to 1997; data for East Matagorda Bay were collected from 1984 to 1997.

red drum growth was slow during fall and winter, linear estimates of growth for the largest and smallest juveniles captured from October through February were calculated using quantile regression techniques (95th quantile = largest red drum, 5th quantile = smallest red drum; Scharf et al. 1998; Cade et al. 1999). In each estuary, these linear growth coefficients were always slightly higher for the largest red drum. That faster growth estimates were obtained from data on larger fish alone suggests that the general growth rates are underestimates, a bias that may have resulted from the continuous influx of newly recruiting individuals during fall.

The potential for size-based emigration and gear avoidance also presents difficulties when one is estimating growth and mortality rates in the field. Seasonal movements to deeper, warmer waters during the coldest months have been observed for several fish species and probably occur among red drum in Texas estuaries (note the drop in age-0 CPUE during January, followed by a higher CPUE in February, that occurred in several estuaries; Figure 4). Although very little is known about the patterns of movement of age-0 red drum in the estuary, substantial emigration from the nearshore zone as a function of size or age may have important implications, particularly for estimating mortality. The only evidence available suggests that movement away from nearshore areas is limited; trawl data from monitoring surveys in Texas estuaries indicate that juvenile red drum are only rarely captured in deeper waters (> 1−2 m) and that the average size of those fish typically exceeds 200 mm (Fuls and McEachron 1997). Size-based avoidance of the sampling gear is likely to affect mortality estimates more than estimates of growth. The extent of gear avoidance by juvenile red drum as a result of increasing body size is unknown, but it may be important late in the first juvenile grow-

TABLE 3.—Daily conditional mortality rates (percent per day) for age-0 red drum in nine Texas estuaries from 1977 to 1997. ND = insufficient data. An asterisk indicates that $P < 0.05$, a dagger that $0.05 \leq P < 0.10$.

Year	Sabine	Galveston	East Matagorda	Matagorda	San Antonio	Aransas	Corpus Christi	Upper Laguna Madre	Lower Laguna Madre
1977–1978		0.29*		0.27†	0.60*	0.21	0.47	0.52	0.33*
1978–1979		0.09		0.73	0.25	0.08	1.07	1.13*	0.53
1979–1980		1.33*		0.83*	0.03	0.20	0.20	0.27†	0.97*
1980–1981		0.04		0.14	0.78†	0.26	0.48†	ND	1.12
1981–1982		1.55		1.03	0.23	2.20	1.08*	0.33	1.12*
1982–1983		0.76*		0.11	0.14	0.00	0.27	0.42†	3.19†
1983–1984		0.56		0.71	0.17	0.14	0.23	ND	0.39*
1984–1985		0.29	0.27	0.75	0.30†	0.55	0.45*	0.24†	0.23
1985–1986		0.67	0.53*	0.30†	0.34	0.12	0.62	0.22	1.28*
1986–1987	0.20	0.39	0.70*	0.45*	0.64	1.07	0.64	0.50	0.87†
1987–1988	0.87	0.81	0.51†	0.14	0.22†	0.26	1.30	ND	0.65
1988–1989	1.53	0.20	0.34*	0.12	0.87	0.49	0.32	0.33*	0.73*
1989–1990	0.26*	0.13	0.64*	0.07	0.16	0.09	0.84	ND	0.35
1990–1991	0.20	0.75*	0.73*	0.79	0.99*	0.88*	0.54†	0.17	1.69*
1991–1992	0.03	0.03	0.65*	0.63*	1.35	0.49*	0.36	0.19*	0.44*
1992–1993	0.26	0.64*	0.74*	0.45	0.47†	0.36*	0.07	0.35†	0.34*
1993–1994	0.59*	0.53*	0.72†	0.30	0.29*	0.24	0.56	0.32†	0.35
1994–1995	0.40	0.64*	0.84†	0.22†	0.82†	0.64*	0.87*	0.32	0.80*
1995–1996	0.52*	0.24*	0.56*	0.33	0.91	0.34†	0.58*	0.51*	0.64*
1996–1997	0.54*	0.58*	0.71*	0.58*	0.51*	0.96	0.60*	0.17	0.72*
Mean	0.49	0.53	0.61	0.45	0.50	0.48	0.58	0.38	0.84

ing season. If substantial gear avoidance occurs at larger sizes, mortality rate estimates may not be reliable. The actual effect of size-dependent emigration and changes in catchability on the estimates of age-0 red drum growth and mortality in this study are unknown. However, any inherent biases in the estimation of red drum early life history traits were present during all years and in all estuaries.

Age-0 red drum abundance was positively correlated across estuarine systems. The appearance of only two strong year-classes during the 20-year study period indicates the potential for time periods of up to 10 years without a strong cohort, which can be common for marine fishes (Rothschild 1986). Strong cohorts that occur infrequently can be critical for the maintenance of fish populations during subsequent years of relatively low recruitment success. Once mature, a single robust year-class can sustain spawning stock size for several years under heavy fishing pressure, such as that imposed by the recreational fishery for red drum along the Gulf Coast (Van Voorhees et al.

TABLE 4.—Pearson's correlation coefficients for growth rate versus peak catch per unit effort (CPUE) and for December CPUE versus April CPUE for age-0 juvenile red drum from 1977 to 1997. Peak CPUE = single highest monthly CPUE estimate during each year (usually December). An asterisk indicates that $P < 0.05$, a dagger that $0.05 \leq P < 0.10$.

Estuary	Growth rate versus peak CPUE	December CPUE versus April CPUE
Sabine	−0.16	−0.30
Galveston	−0.34	−0.15
East Matagorda	0.72*	0.62*
Matagorda	0.00	0.38†
San Antonio	−0.27	0.10
Aransas	0.12	0.48*
Corpus Christi	−0.11	−0.14
Upper Laguna Madre	−0.23	0.17
Lower Laguna Madre	−0.15	0.12

TABLE 5.—Coefficients of variation (CV = 100 · SD/mean) for age-0 and age-1 red drum annual abundance indices in nine Texas estuaries from 1978 to 1996. The CVs were calculated from 19 annual catch per unit effort estimates over the entire study period. Symbols next to age-1 values indicate a significant decrease in the CV from age-0 to age-1 based on variance-ratio tests. An asterisk indicates that $P < 0.05$, a dagger that $0.05 \leq P < 0.10$.

Estuary	Age-0 CV	Age-1 CV
Sabine	0.73	0.68
Galveston	0.82	0.42*
East Matagorda	0.45	0.33
Matagorda	0.69	0.45*
San Antonio	0.70	0.51*
Aransas	0.93	0.40*
Corpus Christi	0.72	0.59†
Upper Laguna Madre	0.90	0.63
Lower Laguna Madre	0.63	0.34*

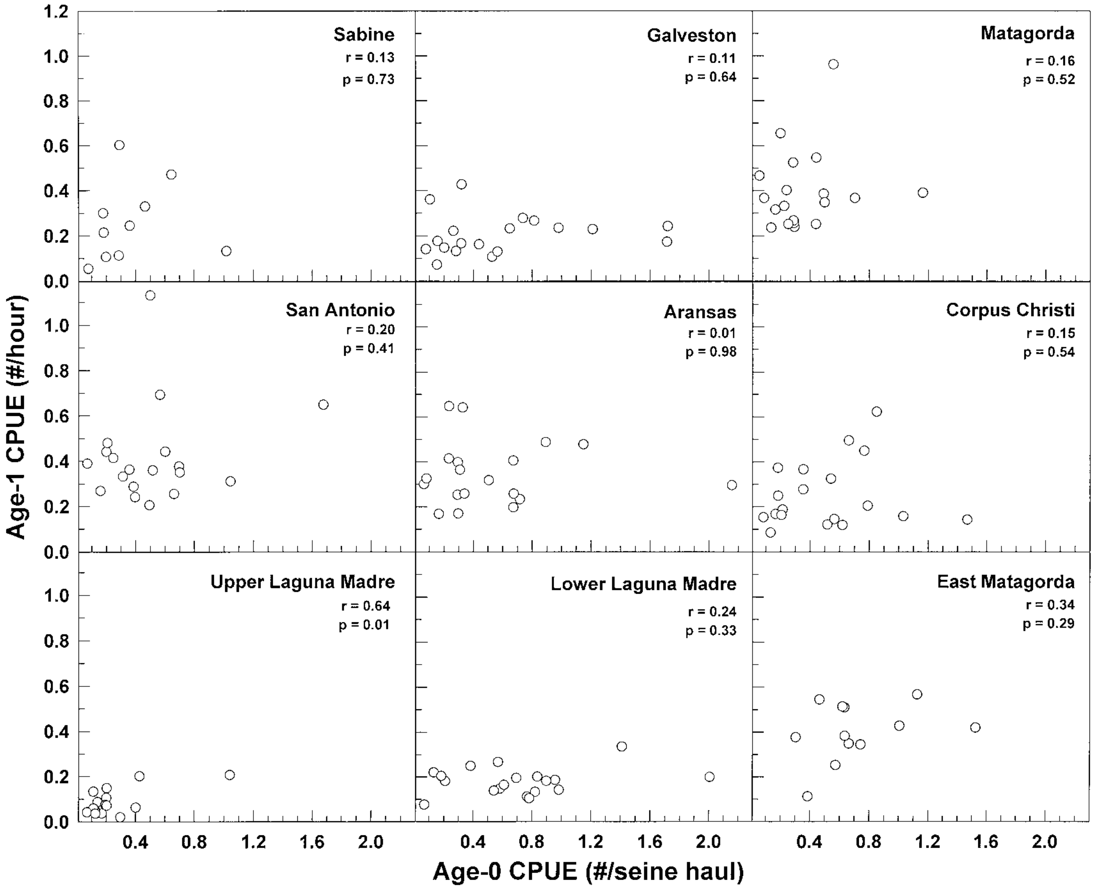

FIGURE 5.—Catch per unit effort (CPUE = number per hour) for age-1 red drum captured in gill nets in the fall versus CPUE (number per seine haul) for age-0 red drum captured in seines the previous year in nine Texas estuaries from 1977 to 1997. Pearson's correlation coefficients and probability values are indicated. Data for Sabine Lake were collected from 1986 to 1997; data for East Matagorda Bay were collected from 1984 to 1997.

1992). For example, the strong 1990 year-class of red drum detected in this study represented a substantial proportion of the coastwide red drum population until at least 1995 (Colura and Buckley 1996). The relative strength of the 1990 year-class may be solely responsible for the dramatic increase in gill-net catch rates of age 1–5 red drum observed during the early 1990s in Texas estuaries (McEachron and Daniels 1995; McEachron et al. 1998). The likely importance of strong year-classes

TABLE 6.—Numbers of red drum fingerlings (25–30 mm total length) stocked in Texas estuaries from 1989 to 1996.

Estuary	1989	1990	1991	1992	1993	1994
Sabine	0	277,820	712,842	530,938	511,442	705,003
Galveston	929,615	2,947,597	4,564,151	3,757,385	6,040,230	4,742,473
East Matagorda	1,019,603	655,598	953,018	552,396	247,931	682,049
Matagorda	1,809,201	2,973,432	2,589,751	3,065,408	8,371,914	5,687,041
San Antonio	1,003,698	1,316,155	963,995	1,052,705	1,303,960	2,622,002
Aransas	1,029,368	1,038,305	1,248,740	513,794	2,098,667	2,550,400
Corpus Christi	984,585	792,796	2,309,178	975,420	4,283,122	1,972,890
Upper Laguna Madre	219,315	2,451,096	5,242,595	3,459,122	5,921,279	4,162,300
Lower Laguna Madre	0	2,870,834	874,490	2,092,834	3,377,571	5,740,759
Coastwide totals	6,995,385	15,323,633	19,458,760	16,000,002	32,156,116	28,864,917

of red drum, coupled with their infrequency, underscores the need to manage on a year-class basis.

The strong association of juvenile abundance among estuaries suggests that the survival and distribution of egg and larval stages within each year are affected by large-scale processes acting along the entire Gulf Coast of Texas. The spawning strategy of red drum, in which adults spawn in coastal waters near the mouths of inlets and passes, is thought to depend on tidal flow to transport larvae into estuarine habitats (King 1971; Holt et al. 1989). The offshore location of most spawning activity would make the egg and early larval stages of red drum susceptible to variation in coastal hydrodynamic processes. Oceanographic data indicate that nearshore currents along the Texas Gulf Coast are driven primarily by wind and maintain a downcoast (west or south) direction throughout most of the year; the exception is the summer months, when nearshore currents reverse (Watson and Behrens 1970; Smith 1975; Smith 1978; Cochrane and Kelly 1986). Several authors have hypothesized that alongshore advection, combined with potential Ekman transport in surface waters, is the primary mechanism by which larvae are transported in nearshore waters of the northern Gulf of Mexico and that the spawning of several sciaenids and other fishes is timed to coincide with currents that are likely to transport larvae downcoast and into favorable estuarine habitats (Standard and Chittenden 1984; Shaw et al. 1985; Cowan and Shaw 1988; Shaw et al. 1988). Variation in several factors, including temperature, the abundance and distribution of prey, predator fields, and hydrodynamic processes, may lead to variation in the abundance of young red drum in Texas coastal estuaries. The correlative relationships among age-0 juvenile abundance across estuaries indicate that annual cohorts of red drum eggs and larvae spawned in nearshore waters along the Texas Gulf Coast may experience similar conditions for growth and survival and that the factors that determine their abundance and distribution vary on a large spatial scale.

TABLE 6.—Extended.

Estuary	1995	1996
Sabine	1,031,547	1,183,492
Galveston	3,224,063	5,546,391
East Matagorda	1,183,803	0
Matagorda	5,914,778	5,226,210
San Antonio	2,229,598	1,799,325
Aransas	2,343,542	2,735,557
Corpus Christi	1,865,921	1,955,504
Upper Laguna Madre	2,040,317	2,902,655
Lower Laguna Madre	4,203,447	4,167,013
Coastwide totals	24,037,016	25,516,147

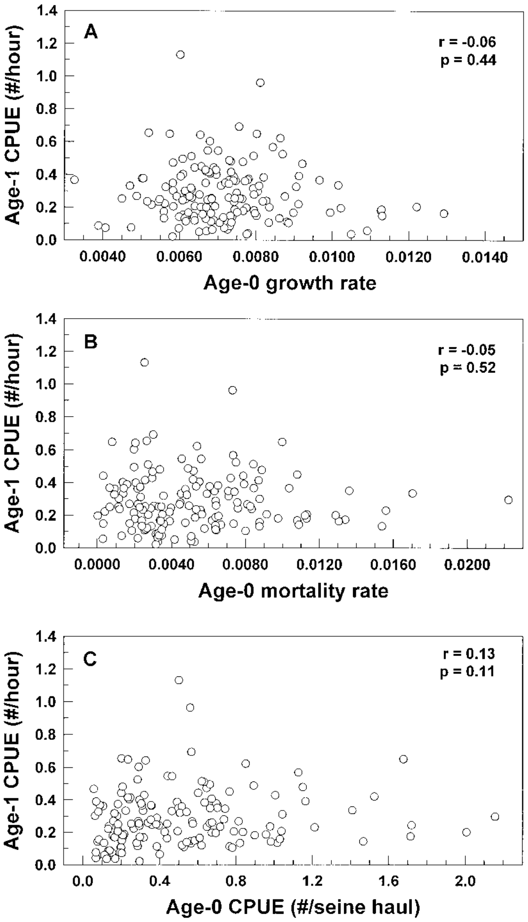

FIGURE 6.—Catch per unit effort (CPUE = number per hour) of age-1 red drum versus age-0 growth rate **(A),** age-0 mortality rate **(B),** and age-0 CPUE (number per seine haul) **(C)** in nine Texas estuaries from 1977 to 1997. Data are pooled for all estuaries and years. Pearson's correlation coefficients and probability values are indicated.

Growth and mortality rates of age-0 red drum were not correlated among Texas estuaries, indicating that conditions for growth and mortality are localized and unique to each estuary. Sogard (1992) proposed that variation in the growth of juvenile fishes in different estuarine habitats is probably caused by differences in water temperature and food availability. Although differences in winter temperatures may account for some of the interestuary variation in growth within each year, only a weak relationship between growth and winter temperature was observed among estuaries in this study. Because of the geographic distances between estuaries, physical and chemical characteristics and prey and predator fields probably differ among estuaries, thus resulting in disparate rates of growth and mortality. Future studies that examine the fine-scale temporal and spatial relationships between environmental factors and variability in juvenile red drum growth and mortality may provide information on the mechanisms that generate the variation that was observed across estuaries in this study.

Within each estuary, the weak correlations between CPUE of age-0 and age-1 red drum imply that processes operating during the juvenile stage may play an important role in determining year-class strength. The lack of significant correlations between age-0 CPUE in December and April indicates that density-dependent mortality of age-0 red drum is one potential explanation for the weak relationship between age-0 and age-1 abundance. Several recent studies have noted the existence of density-dependent mortality during the juvenile stage of marine fishes and its potential contribution to population regulation (van der Veer 1986; Myers and Cadigan 1993a, 1993b). Density-dependent processes in juvenile fish are believed to reduce the interannual variation in abundance levels between juvenile and later life stages. The reduction in variance among annual CPUE estimates between age-0 and age-1 red drum that was observed in Texas estuaries is consistent with this hypothesis. Although correlative evidence suggests that density-dependent age-0 mortality may be important in regulating red drum populations, other potential explanations for the weak relationship between age-0 and age-1 abundance include variable sampling error and variation in density-independent sources of age-0 mortality.

The release of hatchery-reared individuals into Texas estuaries may contribute significantly to variation in CPUE estimates for age-0 and age-1 juvenile red drum. Stocking of red drum occurred throughout most of the time period of this study, with large increases in numbers stocked during recent years. Previous research that compared red drum length frequencies in stocked versus unstocked estuaries and analyzed the capture rates of fish with chemically marked otoliths indicates that stocked red drum can contribute to wild populations at a local scale, but the results are not definitive (McEachron et al. 1998). The data necessary for an accurate estimate of the proportion of hatchery-reared fish remaining in the estuary after several years and their proportional contribution to the red drum population is difficult to obtain and not available currently (McEachron et al. 1998). In this study, the recent upward trend in numbers stocked did not appear to affect age-0 or age-1 abundance levels, which remained stable or declined after 1990–1991. Correlations between annual stocking rates and age-0 or age-1 CPUE were not significant across estuaries or years, suggesting no population-level effects of consistent annual increases in stocking or interestuary variation in stocking rates. However, because all estuaries received some hatchery-reared fish during the period of this study, abundance levels of age-0 and age-1 fish in the absence of stocking cannot be inferred. Therefore, although trends in resource monitoring data did not demonstrate clear stocking effects, release of hatchery-reared fish may still have enhanced red drum populations.

The evidence presented in this study may have important implications for coastwide stock enhancement programs now in place. If cohort year-class strength is not determined until late in the juvenile stage, stocking of early juveniles may be ineffectual. Regulatory processes occurring during the first year of life may negate any surplus production achieved through release of hatchery-reared individuals. Therefore, the age at which stocked red drum are released may be critical in determining their ability to enhance wild populations. To maximize stocking efficiency, future research should thus be aimed at identifying the age, size, or life stage when year-class strength is set.

The findings of this study imply that the year-class strength of red drum may not be simply a function of the supply of larvae and early juveniles to the estuary. The relative strength of specific cohorts may not be set until later in the juvenile stage, after the cohorts spend considerable time in the estuary. A large body of data suggests that variation in the year-class strength of many marine fishes is determined during prejuvenile stages, with finer controls on recruitment variation occurring during later life stages through compensatory effects on growth and mortality (Crecco et al. 1983; Smith 1985; van der Veer 1986; Houde 1987; Bradford 1992; Myers and Cadigan 1993a; 1993b; Leggett and DeBlois 1994). Recent evidence for flatfish *Pleuronectes* and *Paralichthys* spp. and Atlantic cod *Gadus morhua* implicates variability in growth and mortality of juveniles as making important contributions to recruitment variation (Bailey 1994; Campana 1996). The evidence presented for red drum populations supports the potential importance of postlarval processes in regulating marine fish populations.

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