

Estuarine Recruitment, Growth, and First-Year Survival of Juvenile Red Drum in North Carolina

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Abstract.—For many marine and estuarine fishes, there is growing evidence that processes occurring during the juvenile life stage can contribute to determining the relative success of recruitment of annual cohorts into the fishery. We studied two consecutive annual cohorts of juvenile red drum *Sciaenops ocellatus* from estuarine arrival through age 1 in two estuarine systems of southeastern North Carolina. For age-0 cohorts, relative abundance generally peaked in mid to late fall, and fish were present in shallow-water habitats through December before presumably moving to deeper waters during winter. Reappearance of red drum in shallow-water habitats during spring occurred between late March and late April depending on spring warming rates. Considerable differences in relative abundance of age-0 red drum were observed between estuaries; such differences may be related to variations in estuarine hydrology and flushing rates, which probably affect larval delivery and distribution. Otolith-derived hatch date distributions indicated that red drum juveniles in North Carolina were produced between July and October; interannual differences (of up to 30 d) in peak spawning times were correlated with variable nearshore water temperatures during summer. Juvenile growth rates during fall ranged from 0.45 to 0.75 mm/d, and mortality rates were between 1.6% and 4.1% per day; ratios of weight-specific instantaneous growth to instantaneous mortality were greater than 1.0 for all cohorts during their first fall. Both growth and mortality varied between estuaries and years, suggesting local-scale control of these vital rates. Discrete overwinter loss rates ranged from 35% to 67%, indicating that fall cohorts of juvenile red drum could be negatively affected by variable overwinter mortality. First-year vital rates and demographics of red drum cohorts in North Carolina displayed considerable spatial and temporal variability that could potentially affect eventual year-class success, highlighting the need for further understanding of the linkages between juvenile ecology and fishery recruitment.

Year-class strength in marine fishes is believed to be the result of multiple processes that often interact. Many species demonstrate a bipartite life history strategy that includes a pelagic larval stage followed by a demersal juvenile stage. Historically, research on recruitment variability has focused on the influence of the early larval period (Hjort 1914; Cushing 1990), and the effects of juvenile-stage events on year-class strength have been given less emphasis. Although the initial number of larval recruits may shape broad patterns of abundance from year to year (Leggett and Deblois 1994), high and variable mortality occurring after settlement to demersal habitats may disrupt associations between larval supply and eventual recruitment to the adult stage (Bailey 1994; Steele 1997). A meta-analysis conducted by Bradford (1992) concluded that abundance of early larval stages was generally poorly correlated with eventual fishery recruitment for many marine fish species, while the

numbers of postmetamorphic stages demonstrated stronger associations with ultimate recruitment. For many species, detailed knowledge of vital rates and processes generating variability during the juvenile life stage should enable a more complete understanding of the linkages between early life stages and eventual fishery recruitment.

The availability of otolith-derived age information has enabled accurate estimation of early life stage vital rates for annual cohorts and examination of within-cohort variation. The presence of discernable daily increments in otoliths provides a robust method of age estimation in most larval and juvenile fishes (Campana and Neilson 1985), and daily increment counts have been used to reconstruct birth timing and early growth histories of individual fish. Aging also enables more-refined estimates of cohort mortality that can be used to infer the relative influence of different life stage processes on year-class success. Several recent studies that have used microstructural aging approaches have revealed the potential importance of first-year post-larval processes in structuring year-classes of fishes. For example, daily aging was used to detect relatively high juvenile mortality that may have contributed to population biomass declines and demographic cohort

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shifts in American shad *Alosa sapidissima* within the Pamunkey River, Virginia (Hoffman and Olney 2005). Similarly, Pine et al. (2000) used daily increment counts to determine that juvenile largemouth bass *Micropterus salmoides* from early hatching groups experienced higher survival than late-hatching individuals, suggesting that juvenile-stage processes may help determine eventual recruitment success.

The red drum *Sciaenops ocellatus* is an estuarine-dependent species that is distributed in marine and estuarine waters of the western Atlantic Ocean (Chesapeake Bay to southern Florida) and throughout the Gulf of Mexico (Mercer 1984). Spawning occurs during the summer and early fall (Comyns et al. 1991; Wilson and Nieland 1994), when aggregations of adult red drum are observed near ocean inlets along the Atlantic and Gulf of Mexico coasts, as well as inside large sounds. After spending about 20 d as plankton, larvae are transported by tidal currents from spawning locations into shallow habitats of bays and estuaries (Holt et al. 1989; Rooker et al. 1999; Brown et al. 2004). Settlement initially occurs in structured benthic habitats close to inlets; as they age, individuals disperse into lower-salinity habitats toward the head of estuaries. Juvenile and subadult red drum are believed to remain in estuaries for 3–4 years before moving to oceanic waters, supporting inshore fisheries of considerable economic importance throughout their range.

General features of the early life history of red drum have been established for several subpopulations in the Gulf of Mexico (Peters and McMichael 1987; Rooker and Holt 1997; Scharf 2000; Stunz et al. 2002). However, along the U.S. Atlantic coast, red drum early life ecology has only been studied extensively in some South Carolina estuaries (Daniel 1988; Wenner et al. 1990). Despite the historic occurrence of red drum as far north as New Jersey (Welsh and Breder 1923), recent landings statistics (National Oceanic and Atmospheric Administration, Marine Recreational Fisheries Statistics Survey, unpublished data) indicate that adult red drum rarely occur north of Chesapeake Bay. The regular occurrence of age-0 juveniles appears to be further restricted to estuaries in North Carolina and more southerly states, based on infrequent captures of juveniles during extensive fishery-independent surveys in Chesapeake Bay and its tributaries (M. Fabrizio, Virginia Institute of Marine Science, Gloucester Point, personal communication). Thus, North Carolina estuaries are representative of conditions encountered by juvenile red drum life stages near the northern edge of the geographic distribution; thus, juvenile cohorts in North Carolina may experience more extreme seasonal variation in environmental

conditions (e.g., winter severity) relative to that experienced by fish in more southerly parts of the range. Being positioned near the northern edge of the species' geographic range, juvenile red drum in North Carolina may exhibit vital rates distinct from those of red drum in other areas. Furthermore, given that environment–recruitment correlations appear to be strongest near the edges of species' distributions (Myers 1998), year-class success of North Carolina red drum may be strongly influenced by environmental conditions that affect recruitment timing and first-year survival. Therefore, a better understanding of first-year ecological processes that influence red drum dynamics in North Carolina could have direct consequences for fishery management in this region and should also contribute to a greater appreciation of the importance of juvenile ecology throughout the species' range.

Here, we present results from a 2-year field study designed to estimate the relative abundance, distribution, hatch timing, growth, and mortality rate of age-0 juvenile red drum in two estuarine systems within southeastern North Carolina. Sampling was conducted across estuarine salinity gradients and with fine-scale temporal resolution to (1) identify the presence of any shifts in broad-scale distribution patterns and (2) quantify variation among individuals in vital rates (i.e., growth and mortality) throughout the first year of life. In addition, seasonal relative abundance estimates for three life stages (early stage juveniles during fall, late-stage juveniles during spring, and subadults during summer) allowed us to assess reductions in stage-specific relative abundance throughout the first year, particularly the potential for overwinter loss.

Methods

Study systems and sampling locations.—Sampling for red drum was conducted during a single year in the Cape Fear River and for two consecutive years in the New River. The two estuaries are located about 60 km apart in southeastern North Carolina (Figure 1). In each system, sampling sites were selected based on their orientation to the mouth of the estuary and their salinity profiles so that samples could be taken along an estuarine physicochemical gradient. Measured salinity in each estuary ranged from less than 5‰ to greater than 35‰ across sites and sampling periods. Within each estuary, sites were selected to allow similar habitats to be swept efficiently (or with similar efficiency) by active sampling gear. Sites were characterized by gently sloping shorelines with fringing marsh grasses and soft mud bottoms (sometimes containing scattered shells). Initially, 10 sampling sites were selected for fall sampling of the 2003 cohort in the New River. For spring sampling and for sampling

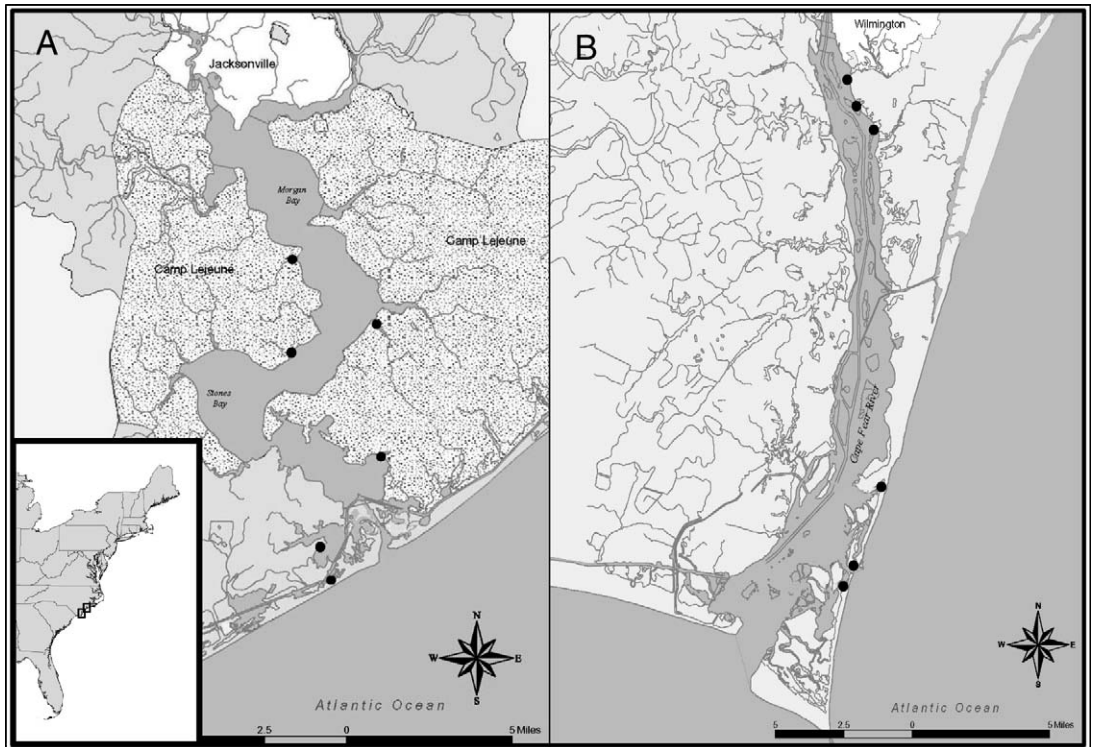


FIGURE 1.—Maps illustrating fixed locations (black circles) used for beach seine sampling of juvenile red drum in two North Carolina estuary systems: (A) New River and (B) Cape Fear River.

of the 2004 cohort, the number of sites was reduced to six to allow for greater sampling frequency at each site. In the Cape Fear River, exploratory sampling was initially conducted at 8–14 sites starting in September 2004. By November, six of these sites were selected and sampled for the remainder of the year.

Seining for recently settled juveniles.—In the New River, seine samples were collected biweekly beginning in early October 2003, and sampling continued through July 2004. In August 2004, the temporal frequency of sampling in the New River was increased to weekly collections that continued through December 2004; biweekly samples were collected from January to June 2005. In the Cape Fear River, weekly seine samples were collected during September through December 2004 and biweekly samples were collected during January through June 2005. Sampling was completed using a bag seine (30.5 × 1.8 m; 6.4-mm mesh in the wings; 3.2-mm mesh in the bag) that was set and retrieved by hand using standardized protocols at each site. At any site, if the lead line was snagged or raised from the bottom for an extended period during seining, the site was resampled at an adjacent section of shoreline within 100 m of the original site. At each site

and on each sample date, salinity, dissolved oxygen, and water temperature were recorded. All captured species (macroinvertebrates and vertebrates) were sorted and identified, and subsamples ($n = 50$) were measured for total length (TL). All captured red drum were counted, measured, weighed, and preserved in 95% ethanol to avoid otolith dissolution during storage.

Capture efficiency can be defined as the product of encirclement efficiency as the net is set and retention efficiency as the net is retrieved (Bayley and Herendeen 2000). Encirclement and retention efficiencies are generally believed to vary inversely relative to fish body size; encirclement efficiency decreases and retention efficiency increases as fish body size increases. In this study, we were mainly concerned about the potential for declining encirclement efficiency as red drum body sizes increased rapidly during spring. To evaluate the encirclement efficiency of the 30.5-m bag seine, we sampled a subset of New River sites using a larger seine (61.0-m seine; 6.4-mm mesh in the wings; 4.8-mm mesh in the bag) set by boat during April through June 2005. Twenty-five hauls were completed with the 61.0-m seine, and catches were compared with those observed in normal

biweekly sampling that employed the 30.5-m seine. Encirclement times generally ranged between 2 and 3 min for the 30.5-m seine, which was always deployed on foot and retrieved by hand. A 6.8-m skiff was used to deploy the 61.0-m seine in a semicircular pattern, resulting in relatively short encirclement times (<1 min). Once set, the 61.0-m seine was retrieved by hand. Sites were resampled at an adjacent section of shoreline if the lead line was snagged or if encirclement time for the 61.0-m seine exceeded 1 min. The size distributions of red drum captured in each seine type were compared to determine the size at which the fish were no longer vulnerable to capture in the 30.5-m seine.

Summer gill-net sampling for late-stage juveniles and subadults.—To assess the distribution and relative abundance of older, larger age-0 red drum (9–12 months old, 200–400 mm TL), gillnetting was conducted during summer months. In the New River, multipanel gill nets were fished biweekly from June to August during 2004 and 2005. In the Cape Fear River, gill nets were fished biweekly from July to September 2005. Gill nets were 45.7 m in length and consisted of six separate panels (panel length = 7.6 m; stretched-mesh sizes = 2.5–15.2 cm). To ensure that the gill nets were fished close to the bottom, each net was constructed with a 13.6-kg (30-lb) lead line with 3.6-kg (8-lb) anchors closely tied at each end. Gill nets were set within 1 h of sunset and were retrieved shortly after sunrise, resulting in a soak time of approximately 12 h or one complete tidal cycle. Gill nets were set perpendicular to the shoreline, and the panel with the smallest mesh was set nearest to the beach. At each site, salinity, dissolved oxygen, and water temperature were recorded during deployment and retrieval. All fish captured during each gill-net set were identified, counted, and measured in the field. All red drum captured were placed on ice until they could be returned to the laboratory for processing.

Otolith microstructural analysis.—Sagittal otoliths have been used in a number of age and growth studies for red drum (Peters and McMichael 1987; Ross et al. 1995) and to validate the formation of daily increments in laboratory-reared red drum (Peters and McMichael 1987). Although no considerable morphological variation between left and right otoliths has been documented for red drum, we used the left sagittal otolith exclusively unless it was damaged, in which case the right sagittal otolith was used. Otoliths were embedded, sectioned transversely, and hand polished before age estimation.

Daily aging of red drum otoliths was completed using a light microscope at 100–400× magnification. Age (d) was estimated by counting all daily growth increments from the core to the posterior margin

(medial edge) of each otolith. Two blind counts were completed for each otolith; if the two counts differed by more than 10%, the otoliths were read a third time. If no two counts were less than 10% apart, the otolith was discarded from further analysis. For each otolith, separate counts that differed by less than 10% were averaged to estimate fish age.

Data analysis.—Catch-per-unit-effort (CPUE) data were first examined qualitatively to identify broad spatial and temporal patterns. Hatch dates were back-calculated by subtracting the estimated age (d) from the date of collection. Due to the high temporal frequency of sampling, hatch date distributions that were corrected for mortality (described below) did not differ significantly from uncorrected distributions (Kolmogorov–Smirnov two-sample test: all $P > 0.75$); thus, only uncorrected distributions were tested for differences among estuaries and years using Kolmogorov–Smirnov two-sample tests. Spatial and temporal patterns of CPUE were examined relative to variation in water temperature and salinity using both logistic regression and single-factor analysis of variance (ANOVA). Overall model significance for the logistic regression was determined using a likelihood ratio test and a chi-square distribution, and goodness of fit was assessed post hoc using Pearson's chi-square test.

Length-at-age relationships were constructed to estimate daily growth rates (mm/d) for fall cohorts in each estuary and year. Weight-specific instantaneous growth rates (G) were also calculated for each cohort based on the exponential growth model:

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

where W_t = wet weight (g) at age; W_0 = estimated weight at hatch; e = the base of the natural logarithm; G = weight-specific instantaneous growth coefficient (per d); and t = estimated age (d).

Daily instantaneous mortality rates (Z) were calculated based on catch-curve analysis using Ricker's (1975) model of exponential decline:

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

where N_t = number of fish at age t ; N_0 = estimated number of fish at hatch; and t = otolith-derived age (d posthatch). This model assumes that once the members of a cohort have settled in an estuary, there is no emigration or immigration during the period for which mortality is being calculated. Most evidence suggests that this assumption is reasonable for juvenile red drum, which are believed to reside in estuaries of initial settlement for up to 3–4 years before returning to the open ocean to spawn (Ross et al. 1995). Additionally, we only estimated mortality using fish captured

through November to avoid any artifacts due to temperature-dependent emigration from shallow-water habitats within the estuary. Catch curves were fitted to abundance-at-age data ($\log_e[n + 1]$ transformed), and regression slopes represented estimates of Z . To ensure that mortality was estimated only for fish that had fully recruited to the sampling gear, catch curves were fitted only for the age of peak abundance through the oldest age captured in November. Age-specific juvenile growth and mortality rates were compared among estuaries and years using analysis of covariance (ANCOVA). The $G:Z$ ratio was calculated for each fall cohort.

The fall (November) CPUE for age-0 red drum was compared with the subsequent spring (May) CPUE to estimate winter loss rate. During this study, recruitment of newly settled juveniles was mostly complete in November, since only 8% of captured fish were smaller than 30 mm TL; this percentage was 52–54% in October and 64% in September. Catches were also relatively stable during November before sharp declines in December, indicating that considerable emigration from shallow-water habitats had probably not yet occurred in November. After winter, the re-entry of juvenile red drum into shallow-water habitats appeared to be temperature dependent and generally occurred abruptly. Re-entry was mostly complete in May of both years, and at that time fish were not yet large enough (160 mm TL) to avoid encirclement in the 30.5-m seine. Thus, for the 2 years examined, the difference in capture rates between November and May should provide a reliable estimate of overwinter reductions in relative abundance.

Results

Relative Abundance and Distribution

Fall beach seine sampling resulted in the capture of age-0 juvenile red drum from September to December; peak catches generally occurred between late October and early November, although CPUE peaked in early December 2004 in the New River (Figure 2). Fish were first captured at sizes of 15–20 mm TL in late August or early September, and abundances increased as fall progressed and new recruits continued to enter each system. Although our beach seine sampling did not begin until early October in 2003, fishery-independent sampling conducted by North Carolina state biologists detected juvenile red drum during mid-September of that year. The probability of encountering red drum during seining trips was positively related to water temperature in the estuary (Figure 3). The logistic regression model was significant ($P = 0.004$), and the data distribution was not significantly different from that predicted by the model (Pearson's chi-square

goodness-of-fit test: $P > 0.05$). Fish were captured in shallow habitats usually until mid-December, before emigrating from shoreline habitats as water temperatures fell. Above-normal temperatures appeared to enable members of the 2004 cohort to use shallow-water habitats in New River through mid-January 2005 (Figure 2). We did not collect sufficient water temperature data during January 2004 to make interannual comparisons, but average air temperatures measured at a U.S. Marine Corps base adjacent to the New River during the first 2 weeks of January were significantly warmer during 2005 (mean = 14.7°C) than during 2004 (mean = 6.9°C; ANOVA: $P < 0.005$), which coincided with larger red drum CPUE in early January 2005 (2.8 fish/haul versus 0.3 fish/haul in 2004). Fall (September–December) CPUE did not differ statistically (ANOVA: $P = 0.84$) between the 2003 (5.9 fish/haul) and 2004 (6.4 fish/haul) cohorts in the New River. During fall 2004, when both estuaries were sampled, we detected a significant (ANOVA: $P < 0.001$) difference in the relative abundance of juvenile red drum between estuaries; CPUE was more than three times higher in the New River (6.4 fish/haul) than in the Cape Fear River (1.9 fish/haul).

Postwinter juveniles returned to shallow-water habitats as nearshore estuarine water temperatures warmed above approximately 16°C (age-0 red drum were only captured by seining once during spring at water temperatures less than 16°C). Fish were captured in beach seines as early as the end of March and were caught regularly through May; the lower CPUE observed in June (Figure 2) was at least partly due to size-based gear avoidance. The rate of spring warming appeared to contribute to interannual differences (as much as 30 d) in the timing of juvenile red drum re-appearance in shallow-water habitats. For instance, average March water temperatures at sites in the New River were significantly warmer during 2004 (mean = 17.9°C) than during 2005 (mean = 11.6°C; ANOVA: $P < 0.001$), and fish were initially encountered more than a month earlier during spring 2004 than during spring 2005. In the Cape Fear River estuary, spring seining failed to regularly capture juvenile red drum; only a single individual was captured in 23 seine hauls conducted between March and May 2005.

Summer gill-net sampling yielded 334 fish between 172 and 406 mm TL (mean \pm SE = 284.4 \pm 2.7 mm TL) across systems and years. Similar to CPUEs for spring beach seines, the gill-net CPUE in the New River (0.344 fish/h) was significantly higher than that in the Cape Fear River (0.013 fish/h) during summer 2005 (ANOVA: $P < 0.001$; Figure 2). Gill-net CPUE in the New River did not differ between 2004 (0.251 fish/h) and 2005 (ANOVA: $P = 0.150$).

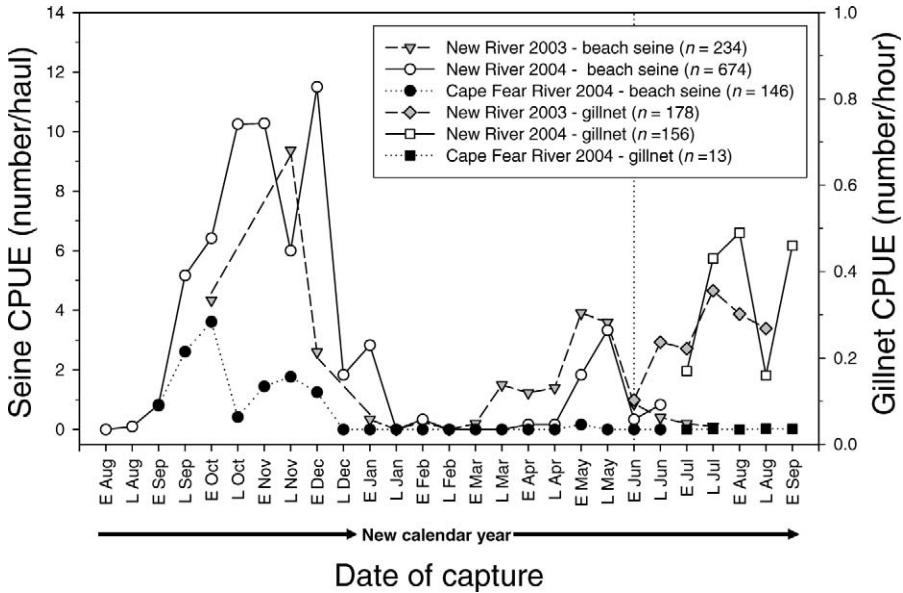


FIGURE 2.—Biweekly seine and gill-net catch per unit effort (CPUE) for first-year red drum in the New River (2003 and 2004 cohort) and Cape Fear River (2004 cohort) estuaries, North Carolina (n = total number of fish captured; E = early [first half of a given month]; L = late [second half of the month]). The vertical dotted line indicates the approximate initiation of gill-net sampling in each year.

By spring, New River juveniles shifted up-estuary and were relatively concentrated, in contrast to the more homogeneous spatial distribution exhibited during fall. Capture rates of recently settled red drum did not differ between lower-estuary (three sites closest to the ocean

inlet; see Figure 1) and mid-estuary sites during fall 2003 (ANOVA: $P = 0.467$) or fall 2004 (ANOVA: $P = 0.757$). However, postwinter age-0 red drum were rarely captured during spring seining in the lower estuary and were instead concentrated in the mid-estuary (Figure 4). Throughout the study period, salinity differed significantly (ANOVA: $P < 0.001$) between lower-estuary (polyhaline; mean = 27.2‰) and mid-estuary sites (mesohaline; mean = 13.5‰). Spring beach seine CPUEs were approximately five times higher at mid-estuary sites than at lower-estuary sites in the New River during both study years, but differences were significant only during spring 2004 (ANOVA for 2004: $P = 0.021$; 2005: $P = 0.215$). The spatial distribution of larger individuals during summer gill-net sampling in the New River continued to reflect higher relative abundances at mid-estuary sites (Figure 4). Although red drum were captured consistently in gill nets fished in the lower estuary during both summers, CPUEs at mid-estuary sites were significantly higher than those at lower-estuary sites during summer 2004 (ANOVA: $P < 0.001$) and were marginally higher during summer 2005 (ANOVA: $P = 0.076$).

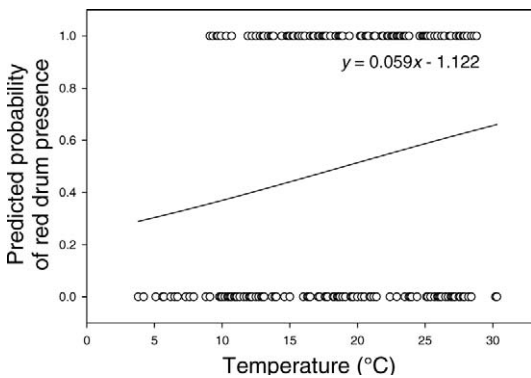


FIGURE 3.—Predicted probability of red drum presence as a function of estuarine water temperature (solid line) based on a logistic regression model (likelihood ratio = 8.28, $P = 0.004$, $n = 245$) of catch in the New River, North Carolina, between September and May (2003–2005 sampling of the 2003 and 2004 cohorts). The linear equation describes the expected change in the log-odds of presence for each unit of change in water temperature. Open circles are the raw presence-absence observations.

Beach Seine Capture Efficiency

Size distributions of red drum captured in the 30.5- and 61.0-m beach seines were nearly identical

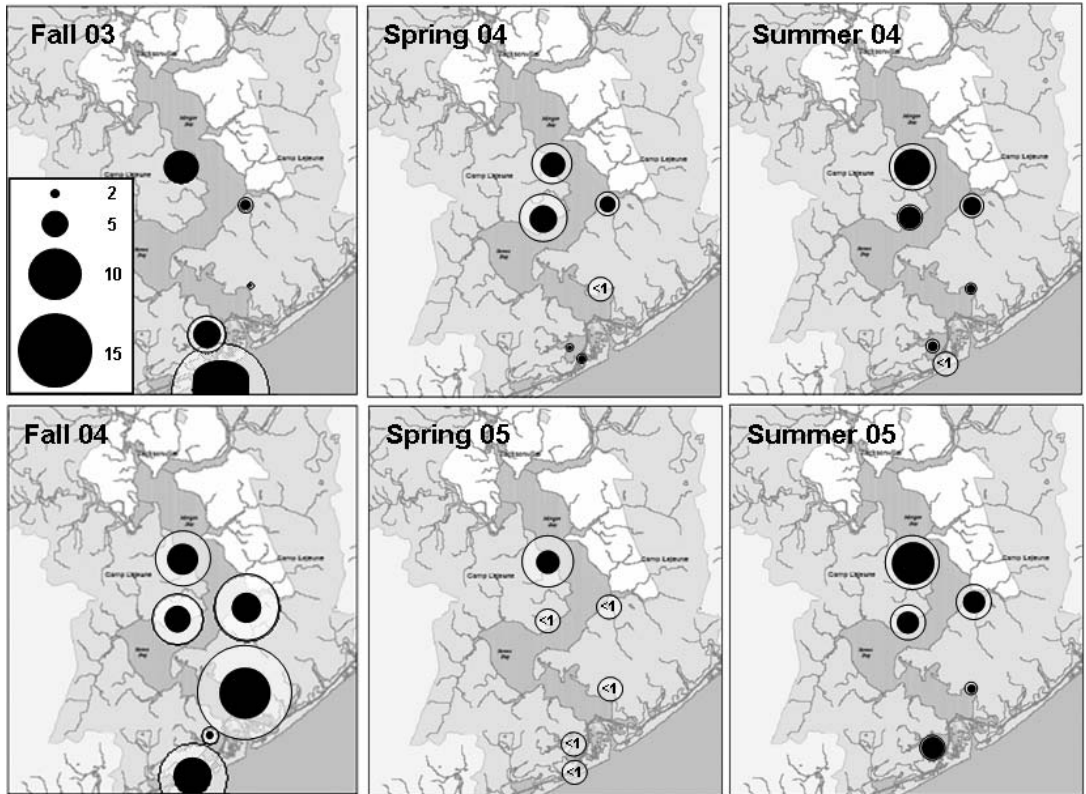


FIGURE 4.—Maps illustrating the seasonal spatial distribution of 2003 and 2004 red drum cohorts in the New River estuary, North Carolina (black circles = mean catch per unit effort [CPUE] at each site; white areas surrounding the black circles = 1 SE of CPUE; inset scale values refer to CPUE). Fall (September–December) and spring (March–June) panels represent beach seine sampling (CPUE in fish/seine haul); summer (June–September) panels represent gill-net sampling (CPUE in fish/h).

for fish up to 160 mm TL, above which the catch in the 30.5-m seine abruptly decreased (Figure 5). The length frequency distributions were not significantly different from normality (Shapiro–Wilk and Kolmogorov–Smirnov tests: $P > 0.05$) or from each other (Kolmogorov–Smirnov two-sample test: $P > 0.05$), although the statistical power of these tests is compromised (Sokal and Rohlf 1995) at low sample sizes such as ours ($n < 50$). Graphical interpretation suggests that capture efficiency of the 30.5-m seine (the standard gear) was stable until fish reached 160 mm TL and then abruptly declined for fish of larger sizes. In contrast, the size distribution of fish captured in the 61.0-m seine illustrated a gradual descending limb for larger body sizes. Length distributions of red drum in May of both years revealed that only 2 of 105 captured fish were larger than 160 mm TL, whereas 20 of 24 fish captured during June were larger than 160 mm TL. Thus, capture rates of the standard gear were comparable from late fall to May in both years.

Hatch Date Distributions

The distribution of red drum hatch dates demonstrated a moderately protracted spawning period (Figure 6). Estimated hatch dates for the 2003 New River cohort extended from July 21 to October 18; however, 97% of the fish hatched during August and September. A similar range of hatch timing (July 4–October 18) was estimated for the 2004 New River cohort; however, peak spawning occurred earlier (early to mid-August) than that for the 2003 cohort (late August to early September). The hatch date distributions differed significantly between the 2003 and 2004 New River cohorts (Kolmogorov–Smirnov two-sample test: $P < 0.05$). In the Cape Fear River, estimated hatch dates for the 2004 cohort extended over a similar range of dates but ended earlier (late September) than those of the 2004 New River cohort. Similar to the New River in 2004, peak spawning of red drum that settled in the Cape Fear River occurred in early to mid-August. Despite the lack of October hatch dates in the

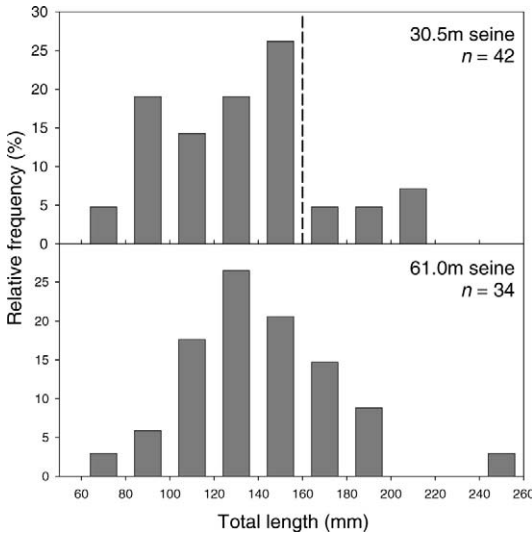


FIGURE 5.—Length frequency distributions (total length, mm) of red drum captured in 30.5- and 61.0-m beach seines during April–June 2005 in the New River estuary, North Carolina. Dashed line in upper panel denotes the abrupt decrease in capture rate for fish larger than 160 mm.

Cape Fear River, there was no significant difference between the hatch date distributions of the two estuaries in 2004 (Kolmogorov–Smirnov two-sample test: $0.25 < P < 0.50$).

Age-0 Red Drum Length at Age

Length-at-age relationships were developed for age-0 red drum captured during fall 2003 in the New River and fall 2004 in both rivers (Figure 7). Slow growth during winter months resulted in close spacing of otolith daily increments, which prevented accurate age estimation for postwinter fish captured during spring. Across estuaries and years, otolith-aged fish ranged in size between 13 and 81 mm TL, and age estimates ranged from 24 to 126 d. In the New River estuary, red drum lengths in 2003 and 2004 were similar through about 60 d of age, after which the 2004 cohort demonstrated significantly faster growth (slope heterogeneity test: $F = 21.21, P < 0.001$). A significant difference in red drum growth was also detected between estuaries during 2004 (slope heterogeneity test: $F = 101.15, P < 0.001$), which indicated faster growth rates in the New River (0.755 mm/d) than in the Cape Fear River (0.447 mm/d). Maximum sizes attained by December ranged between 63 and 81 mm TL. Initial sizes of red drum in spring generally ranged between 70 and 100 mm TL; subsequent rapid growth resulted in TLs greater than 200 mm by late June.

Mortality Estimates, G:Z Ratios, and Potential Overwinter Loss

During fall 2004, age-specific mortality of red drum was estimated at about 4.1% per day ($Z = 0.042$) in the New River and about 1.6% per day ($Z = 0.016$) in the Cape Fear River (Figure 8); significant differences were observed between the two estuaries (slope heterogeneity test: $F = 10.08, P < 0.005$). The estimated mortality rate in the New River during fall 2004 was also significantly higher (slope heterogeneity test: $F = 4.91, P < 0.05$) than the 2003 estimate (~2.2% per day; $Z = 0.022$). Despite the presence of significant variability in growth and mortality rates between estuaries and years, each juvenile cohort experienced increases in biomass during the fall, as evidenced by positive *G:Z* ratios (Table 1). All three cohorts demonstrated *G:Z* ratios greater than 1.0; the 2004 New River cohort exhibited a ratio that was about 30% lower than those of the other two cohorts. The fastest-growing cohort (New River, 2004) also experienced the highest mortality rate, whereas the lowest mortality rate was observed for the slowest-growing cohort (Cape Fear River, 2004).

Declines in beach seine CPUE between November and May indicated considerable overwinter loss rates in the New River during both 2003 and 2004 (Figure 9). Red drum CPUE decreased from 9.4 fish/haul in November 2003 to 6.1 fish/haul in May 2004, representing a discrete loss rate of 35%. An even greater decline was observed for the 2004 cohort; CPUE decreased from 8.6 fish/haul in November 2004 to 2.8 fish/haul in May 2005 (discrete loss rate = 67%). The near-complete absence of age-0 red drum from the Cape Fear River during spring 2005 indicated either substantial overwinter mortality or a considerable shift in habitat distribution that relocated fish outside of our sampling area.

Discussion

Spatial and Temporal Patterns of Relative Abundance and Distribution

The reproductive success of many marine fishes is linked to the movement of young life stages into or out of estuaries. Several factors, such as local hydrodynamics, temperature, salinity, stratification, turbidity, and riverine discharge, are thought to influence the distribution and retention of marine fishes in estuarine systems (Norcross and Shaw 1984). Strong temporal correlations in the relative abundance of age-0 red drum among large estuaries along the Texas coast suggested that patterns of recruit delivery were influenced by nearshore, wind-driven currents over a broad spatial scale (Scharf 2000). Using oceanographic

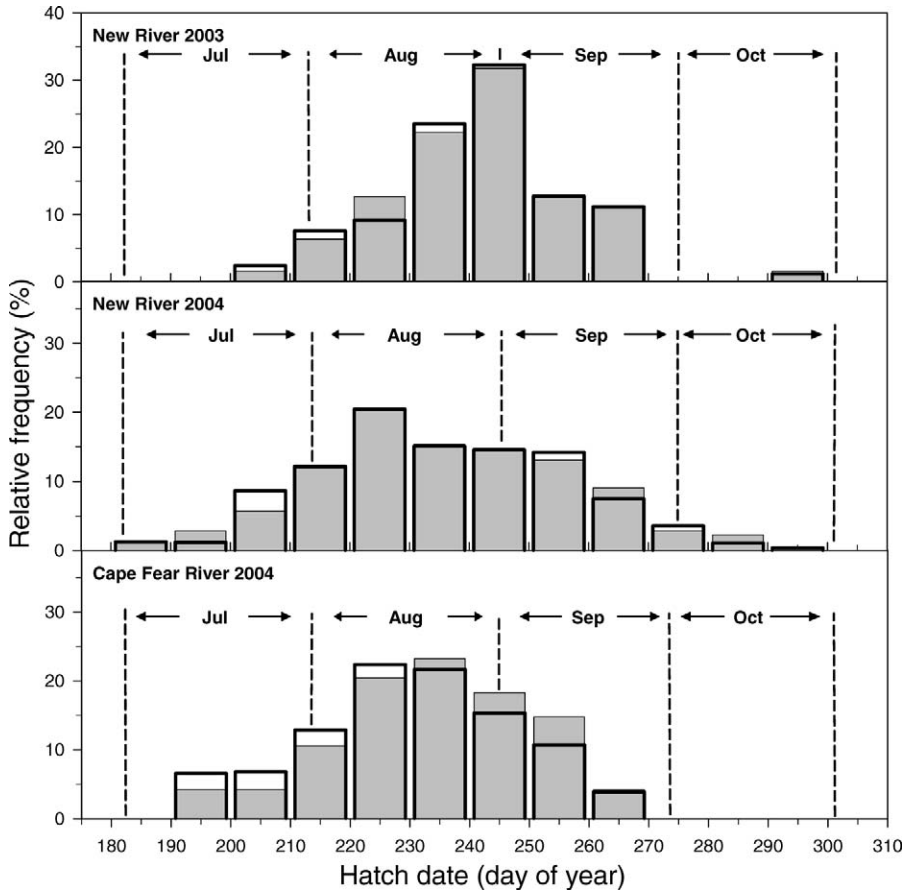


FIGURE 6.—Estimated hatch date distributions for red drum collected during fall in the New River (2003 and 2004) and Cape Fear River (2004), North Carolina. Open bars with thickened edges represent hatch date distributions that were adjusted for mortality.

models to simulate settlement patterns of red drum larvae, Brown et al. (2004) also concluded that wind forcing, combined with estuarine circulation patterns and bathymetry, dictated spatial and temporal patterns of abundance in a Texas estuary. Similarly, physical processes have been found to influence spatiotemporal variation in the larval supply of several Atlantic coast fishes (e.g., Atlantic menhaden *Brevoortia tyrannus*, spot *Leiostomus xanthurus*, and several flounders *Paralichthys* spp.) entering Beaufort Inlet, North Carolina (Churchill et al. 1999; Forward et al. 1999; Luettich et al. 1999). Although we did not measure these processes directly, we propose that wind-driven nearshore currents and estuarine circulation patterns have the potential to influence the delivery and retention of early life stage red drum in the two study estuaries and thus probably contributed to the initial distribution patterns.

Hydrologic differences in the estuarine portions of

the New and Cape Fear rivers may partly explain the disparate levels of abundance of juvenile red drum observed between estuaries. The lower Cape Fear River has been characterized as a deep, narrow, partially mixed estuary that is strongly influenced by tide-driven flow (Giese et al. 1985; Ensign et al. 2004). The Cape Fear River is also unique, as it is the only major estuary in North Carolina that has relatively free, direct water access to the ocean (Giese et al. 1985). The New River, on the other hand, is a broad, shallow, highly eutrophic estuary (Mallin et al. 1999). In a recent study using digital bathymetric data to calculate estuarine flushing time, the estuarine portion of the Cape Fear River was found to receive considerably greater freshwater inflow (Ensign et al. 2004) that generated much shorter flushing times (1–22 d) than those of the New River (8–187 d). The two rivers showed similar seasonal patterns, wherein longer flushing times generally occurred during warmer months (May–October). Long

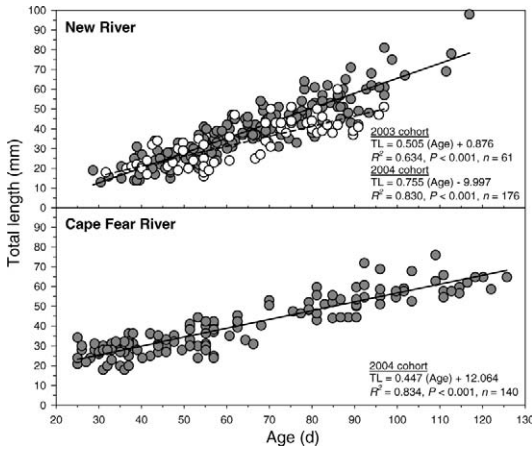


FIGURE 7.—Total length (TL, mm) at age (d) of juvenile red drum in the New River (top panel; white symbols, dashed line = fall 2003; gray symbols, solid line = fall 2004) and Cape Fear River (bottom panel; fall 2004 only) estuaries, North Carolina. Least-squares regression coefficients estimate daily growth rate (mm/d).

flushing times in the New River, coupled with extended flushing times during summer, could promote higher larval retention and subsequent settlement in the estuary during the peak red drum spawning and larval

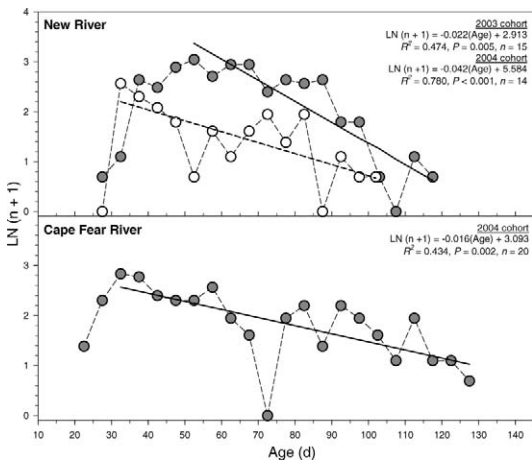


FIGURE 8.—Abundance ($\log_e [n + 1]$ transformed) at age of juvenile red drum in the New River (top panel; white symbols, dashed line = fall 2003; gray symbols, solid line = fall 2004) and Cape Fear River (bottom panel; fall 2004 only) estuaries, North Carolina. Least-squares regression coefficients estimate total instantaneous mortality rate. Regression lines extend only across the range of ages used to estimate mortality (fish used in mortality calculations: New River 2003, $n = 78$; New River 2004, $n = 149$; Cape Fear River 2004, $n = 129$). In the top panel, symbols at age 100–105 d are offset slightly for clarity.

TABLE 1.—Weight-specific instantaneous growth rate (G), instantaneous mortality rate (Z), and $G:Z$ ratio calculated for fall cohorts of juvenile red drum in two North Carolina estuaries.

Estuary	Year	G	Z	$G:Z$ ratio
New River	2003	0.047	0.022	2.136
	2004	0.056	0.042	1.333
Cape Fear River	2004	0.031	0.016	1.938

transport period (August–September). Reduced tidal exchange at the mouth of the estuary may also contribute to the lengthened flushing time of the New River, while the Cape Fear River has greater tidal exchange due to a more-direct connection to the ocean (Ensign et al. 2004). Along the Texas coast, Brown et al. (2000) determined that accelerated ebb tidal flow at the inlet was the primary mechanism responsible for transporting surface particles offshore and could impede the movement of larval fishes through the inlet. Therefore, high flow rates during ebb tides in the Cape Fear River (Weinstein et al. 1980) may limit upstream transport of red drum postlarvae and could be partly responsible for the observed differences in relative abundance between rivers.

Early fall (August–October) sampling, before permanent sample site selection was completed in the Cape Fear River, demonstrated no occurrences of recently settled red drum along the western edge of the river. In contrast, fish were evenly distributed along both the eastern and western edges of the New River. Large across-channel variation in the subtidal flow passing through ocean inlets may influence the up-estuary transport of larval fishes. For instance, net inflow in the eastern and central regions of Beaufort Inlet, North Carolina, was correlated with large

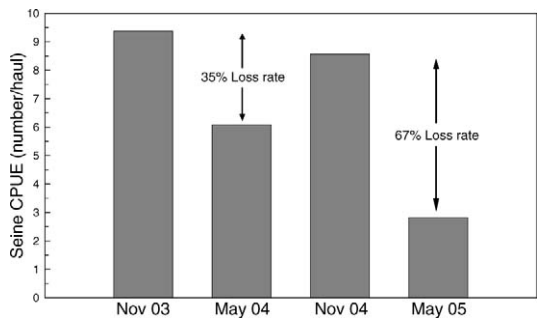


FIGURE 9.—Red drum catch per unit effort (CPUE; fish/haul) in beach seining conducted during fall and spring for the 2003 cohort (November 2003 and May 2004) and the 2004 cohort (November 2004 and May 2005) in the New River, North Carolina. Seasonal differences in CPUE were used to estimate annual overwinter loss.

concentrations of larvae along the eastern side of the inlet, whereas the net outflow on the western side tended to hinder transport (Churchill et al. 1999; Forward et al. 1999). Data collected by Weinstein et al. (1980) indicated that water and larvae tended to move upriver along the eastern shoals of the Cape Fear River and that net flow out of the river occurred along the western edge. Thus, the uneven distribution of juvenile red drum in the Cape Fear River may have resulted partly from across-channel variation in tidal flow.

As fish grow, their ecological and physiological requirements change and fish often demonstrate adaptive life history strategies to maximize energy gains and reduce mortality risks. We observed a temporal habitat shift in the relative abundance of age-0 red drum juveniles in the New River estuary during both 2003 and 2004. Beach seine and gill-net CPUEs indicated that by spring and summer, most fish were distributed farther upriver relative to the more-even fall distributions. The capture of only a single age-0 red drum during spring sampling in the Cape Fear River suggests that fish relocated to upriver habitats beyond our sampling area. A similar habitat shift was noted by Peters and McMichael (1987), who captured older juvenile red drum in greater numbers within low-salinity tidal creeks far upstream from the ocean inlet in Tampa Bay, Florida. Other sciaenid fishes have also been found to use mesohaline, and even oligohaline, habitats during juvenile life stages. Although growth efficiency was lower, juvenile weakfish *Cynoscion regalis* consistently used habitats of low to moderate salinity, prompting Lankford and Targett (1994) to suggest that low salinity acts as a physiological barrier to many piscivorous fishes that prey upon juvenile weakfish. Summer gill-nets in both estuaries captured more potential predators (summer flounder *Paralichthys dentatus*, bluefish *Pomatomus saltatrix*, Atlantic sharpnose shark *Rhizoprionodon terraenovae*, and spiny dogfish *Squalus acanthias*) of juvenile red drum in polyhaline waters than in areas farther upriver (authors' unpublished data), supporting the idea that low-salinity habitats provide a predation refuge. Our observations suggest that juvenile red drum reduce predation risk by concentrating in mesohaline habitats during early ontogeny. However, distributional shifts may also have a physiological basis related to higher growth (Lanier and Scharf 2007), lowered metabolic costs (Wakeman and Wohlschlag 1983) or size-based tolerance of cold temperatures (e.g., Atlantic croaker *Micropogonias undulatus*; Lankford and Targett 2001) in low- to moderate-salinity habitats.

Recruitment Timing

For marine fishes with protracted spawning periods, the timing of hatch and recruitment to estuarine

habitats shapes initial patterns of abundance and distribution but can also have lasting effects on eventual cohort success (e.g., Pine et al. 2000). Gradients in hatch timing across stocks located at different latitudes can generate variation in the timing of initial settlement, which has potential implications for growth and size-dependent ecological processes occurring after settlement. In Chesapeake Bay, red drum were observed to spawn as early as July, and peak spawning occurred in late September and October (Mansueti 1960). However, in Tampa Bay, the timing of appearance of larval and juvenile red drum indicated that spawning begins somewhat later (from mid-August to mid-November) and that peak spawning occurs between late August and mid-October (Peters and McMichael 1987). The timing of red drum appearance in Aransas Bay, Texas, indicated that spawning activity was relatively high and continuous during September and October (Rooker and Holt 1997). Hatch dates estimated during our study indicated that recently settled red drum in both estuaries were the product of spawning that was initiated earlier than generally observed along the Gulf Coast. Ross et al. (1995) noted the occurrence of mature individuals with high gonadosomatic indices off North Carolina in July and concluded that red drum were capable of initiating spawning at this time; peak spawning activity occurred during August and September. Field experiments have shown that growth of juvenile red drum in North Carolina estuaries is compromised by declining water temperatures in late fall (Lanier and Scharf 2007); thus, moderately earlier spawning off North Carolina may be a way of lengthening the growing season before winter.

The level of interannual variation in the hatch date distributions observed in this study was considerable and may be indicative of plasticity in the initiation of spawning activity along the coast. Hatch date distributions suggested that peak spawning activity in 2004 occurred about 2–3 weeks earlier than the peak in 2003. In the northern Gulf of Mexico, peak egg and larval abundances indicated that most red drum spawned when water temperatures over the shelf decreased from 27–29°C to 24–25°C (Comyns et al. 1991). Laboratory experiments have demonstrated that the optimum temperature for hatching success and larval survival is about 25°C and that high temperatures (30–35°C) are associated with poor survival of yolk sac larvae (Holt et al. 1981). During our study, interannual variation in hatch date distributions was correlated with yearly differences in summer coastal water temperatures. Between June and August, mean nearshore water temperatures off Hatteras Inlet, North Carolina, were significantly higher (ANOVA: $P < 0.001$) in 2004

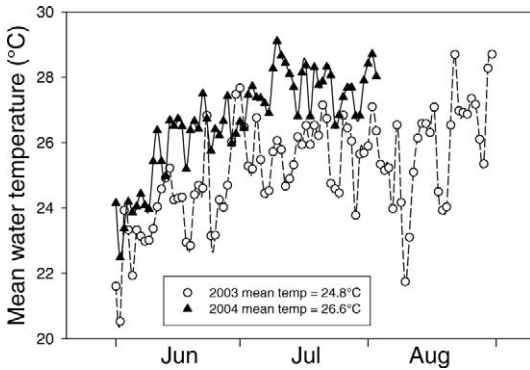


FIGURE 10.—Nearshore mean water temperature recorded during summer 2003 (open circles) and 2004 (black triangles) at the Diamond Shoals buoy (National Oceanic and Atmospheric Administration station 41025) near Cape Hatteras Inlet, North Carolina (35°00'N, 75°24'W). Overall (June 1–August 1) average water temperatures are indicated in the legend.

(mean = 26.6°C) than in 2003 (mean = 24.8°C; Figure 10). Water temperatures were also nearly 2°C higher in early August 2004 (mean = 28.4°C) than in late August 2003 (mean = 26.5°C). Similar to northern Gulf of Mexico stocks, red drum egg and larval success off North Carolina are probably influenced by ocean water temperature. Thus, peak spawning activity off North Carolina may vary from year to year in response to large-scale temperature variation.

Juvenile Growth and Mortality

The relative length of the juvenile life stage and the cumulative nature of growth and mortality imply that variation in juvenile vital rates have important effects on the abundance of annual cohorts. We observed significant spatial and temporal variability in juvenile red drum growth rates in North Carolina estuaries. Fall growth rates in the New River during 2004 (0.755 mm/d) were significantly higher than those during 2003 (0.505 mm/d) and those in the Cape Fear River (0.447 mm/d). Controlled laboratory and field experiments have found that temperature, salinity, prey resources, and fish density can each influence growth in early life stage red drum (Holt et al. 1981; Lee et al. 1984; Stunz et al. 2002; Smith and Fuiman 2003; Lanier and Scharf 2007). The disparity in growth rates observed between estuaries and years in the present study was probably caused by differences in abiotic factors (temperature and salinity) and potential prey availability rather than by negative effects of high cohort densities, since both growth rate and relative abundance (apparent density) of juvenile red drum were highest in the New River during 2004. Our

findings provide additional evidence that juvenile growth rates do not necessarily correspond among adjacent estuarine systems (Scharf 2000) and that growth rate variation is generated by factors operating at a local scale. Although growth rates varied between estuaries and years, our estimates of juvenile red drum growth were similar in magnitude to those reported for areas elsewhere in the species' range (Peters and McMichael 1987; Scharf 2000; Stunz et al. 2002).

There is growing evidence that mortality during the juvenile life stage influences year-class strength in marine fishes. Observational and experimental studies conducted across a range of species (Steele 1997; Fromentin et al. 2001; Shima 2001) have revealed the importance of postsettlement survival in determining eventual cohort success. Specifically, high mortality or highly variable mortality during the juvenile period can dampen strong larval recruitment events (Bailey 1994) and may alter the spatial and temporal patterns of abundance established before estuarine settlement. Differences in juvenile red drum mortality rates between estuaries and years were over twofold. Similar levels of interannual and interestuary variability (two- to fourfold differences) were evident along the Texas coast over a 20-year period (Scharf 2000), indicating that considerable variability typifies juvenile red drum mortality. Therefore, the potential is high for estuarine processes that affect juvenile survival to modify the eventual contribution of annual red drum cohorts to the fishery. We also observed the highest mortality rates in the New River during 2004, which coincided with the highest relative abundance estimates. If our CPUE estimates are positively correlated with fish density, then this observation suggests the potential for density-dependent mortality among early juveniles. Although our data do not provide direct evidence of density-dependent juvenile mortality in the study area, they are consistent with time series data from the Texas coast that indicate density-dependent loss rates during the juvenile stage (Scharf 2000). When combined with past studies of red drum, our results illustrate a continuum in juvenile mortality; mortality rates are as high as 12–13% per day for very early postsettlement individuals (8–20 mm TL; Rooper et al. 1999), decline to 2–4% per day throughout the fall (15–80 mm TL; this study), and eventually decrease to 0.5–1.0% per day for the majority of the first year (October–June; 25–250 mm TL; Scharf 2000). This pattern indicates stabilization of juvenile mortality throughout the first year as size rapidly increases.

The transition from larval to juvenile life stages in marine fishes is thought to mark the beginning of biomass accumulation for cohorts. Generally during the late larval or early juvenile period, the addition of

biomass generated through individual growth begins to exceed the biomass losses that are due to mortality (Houde 1997). The timing of the transition from decreasing to increasing cohort biomass varies among cohorts due to environmental factors (Secor and Houde 1995) and may have a considerable influence on recruitment success. Each cohort we examined achieved *G:Z* ratios greater than 1.0, indicating increasing biomass during the fall. In addition, Rooker et al. (1999) estimated a *G:Z* ratio of approximately 1.2 for two consecutive annual cohorts of very early juvenile red drum in a Texas estuary. Therefore, red drum cohorts appear to achieve increasing biomass near the time of larval–juvenile transition.

Winter is an important period of size-dependent mortality for many temperate fishes during the first year of life. For instance, Post and Evans (1989) concluded that overwinter mortality of age-0 yellow perch *Perca flavescens* was strongly size related and that smaller fish should have higher mortality as a result of low energy reserves coupled with high energetic demands. Garvey et al. (1998) proposed that overwinter survival and recruitment of age-0 large-mouth bass increase with improved first-summer growth resulting from earlier hatching. Because red drum in North Carolina estuaries are near the northern edge of the species' current distribution, hatch timing and fall growth may be particularly important for age-0 survival. Reduced body size (from late hatch timing or slow fall growth) coupled with extreme cold winter temperatures could lead to substantial overwinter losses. Osmoregulatory failure due to prolonged cold temperature exposure influences age-0 survival in several freshwater and marine fishes, including white crappies *Pomoxis annularis* (McCollum et al. 2003) and Atlantic croakers (Lankford and Targett 2001). In the New River estuary, discrete overwinter loss rates ranged from 35% to 67%, indicating that age-0 mortality during the winter is considerable in North Carolina estuaries. Mortality due to exposure to harsh winter conditions may be common for red drum in North Carolina, given that episodic freeze events or longer periods of prolonged cold temperatures have been implicated in winter mortality of red drum at lower latitudes (McEachron et al. 1995). Lankford and Targett (2001) proposed that temperature-mediated overwinter mortality may regulate the recruitment success and subsequent year-class strength of Atlantic croakers in some Middle Atlantic Bight estuaries. We conclude that conditions experienced before and during the first winter of life may contribute significantly to the structuring of red drum year-classes in North Carolina estuaries.

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