Abstract—Offshore winter-spawned fishes dominate the nekton of southeastern United States estuaries. Their juveniles reside for several months in shallow, soft bottom estuarine creeks and bays called primary nursery areas. Despite similarity in many nursery characteristics, there is, between and within species, variability in the occupation of these habitats. Whether all occupied habitats are equally valuable to individuals of the same species or whether most recruiting juveniles end up in the best habitats is not known. If nursery quality varies, then factors controlling variation in pre-settlement fish distribution are important to year-class success. If nursery areas have similar values, interannual variation in distribution across nursery creeks should have less effect on population sizes or production. I used early nursery period age-specific growth and mortality rates of spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*)—two dominant estuarine fishes—to assess relative habitat quality across a wide variety of nursery conditions, assuming that fish growth and mortality rates were direct reflections of overall physical and biological conditions in the nurseries. I tested the hypothesis that habitat quality varies for these fishes by comparing growth and mortality rates and distribution patterns across a wide range of typical nursery habitats at extreme ends of two systems. Juvenile spot and Atlantic croaker were collected from 10 creeks in the Cape Fear River estuary and from 18 creeks in the Pamlico Sound system, North Carolina, during the 1987 recruitment season (mid-March–mid-June). Sampled creeks were similar in size, depth, and substrates but varied in salinities, tidal regimes, and distances from inlets. Spot was widely distributed among all the estuarine creeks, but was least abundant in the creeks in middle reaches of both systems. Atlantic croaker occurred in the greatest abundance in oligohaline creeks of both systems. Instantaneous growth rates derived from daily otolith ages were generally similar for all creeks and for both species, except that spot exhibited a short-term growth depression in the upriver Pamlico system creeks—perhaps the result of the long migration distance of this species to this area. Spot and Atlantic croaker from upriver oligohaline creeks exhibited lower mortality rates than fish from downstream polyhaline creeks. These results indicated that even though growth was similar at the ends of the estuaries, the upstream habitats provided conditions that may optimize fitness through improved survival.

The relative value of different estuarine nursery areas in North Carolina for transient juvenile marine fishes

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Offshore winter-spawned (OWS) fishes are a major component of the nekton of southeastern United States and Gulf of Mexico estuaries. Their larvae migrate across the shelf, enter estuaries, and the majority of juveniles reside for several months in shallow, soft bottom estuarine creeks and bays called primary nursery areas (PNAs). Very high concentrations of fishes in these PNAs suggest that they are valuable habitats, perhaps because they are good sources of food and shelter (Boesch and Turner, 1984; McIvor and Odum, 1988; Miltner et al., 1995). Despite similarity in some PNA physical characteristics, there is variability in habitats occupied (between and within species), especially with regard to salinity, tidal influence, accessibility (i.e. distance from inlets), and, perhaps, food and predator regimes (Weinstein, 1979; Ross and Epperly, 1985). Assessing the relative value of all PNA habitats to individuals of the same species is increasingly important (Weinstein, 1982; Sogard, 1992; Guindon and Miller, 1995; Beck et al., 2001). If PNA value varies, do most of the recruiting juveniles end up in the best habitats (Thresher, 1985)? Understanding variation in habitat quality during a major early life history phase should yield insight into causes of variability in year-class strength, particularly if juvenile fish distributions vary interannually. If PNA quality varies, then factors controlling variation in presettlement distribution are important to year class success because animals could be transported to habitats of unpredictable quality. If nursery areas have similar value, interannual variations in distribution across nursery creeks should have less effect on ultimate population sizes or production.

General estuarine distributions of two dominant OWS fishes, spot (*Leiostomus xanthurus*) and Atlantic croaker (*Micropogonias undulatus*), exhibit consistent patterns throughout their ranges. Juvenile Atlantic croaker routinely concentrate in oligohaline creeks or bays (Weinstein, 1979; Mercer, 1987a)—a pattern that suggests that the upstream regions are most valuable to this species. Spot, however, are more ubiquitously and variably distributed through the shallow PNAs (Ross and Epperly, 1985; Mercer, 1987b), perhaps indicating less dependence on a particular estuarine region. Despite these generalities, both species can be present in large numbers in almost any estuarine creek or bay over the full salinity range (e.g. Nelson et al., 1991). In general, juveniles of both species seem to avoid (or are unsuccessful in) more open water areas of estuaries during the early part of the nursery period.

The main purpose of this paper is to assess relative habitat value for two dominant members of the OWS fish group, spot and Atlantic croaker, across a wide variety of North Carolina PNA conditions. I assumed that fish growth and mortality rates were direct reflections (integrators) of overall physical and biological conditions in PNA habitats. Therefore, I used early nursery period age-specific growth and mortality rates of spot and Atlantic croaker, in addition to distribution data, to assess relative habitat quality, testing the hypothesis that habitat quality varies for these fishes across a broad range of typical PNAs in two very different estuarine systems. Growth and mortality can be influenced by fish density; however, Ross (1992) found similar growth and mortality rates for spot and Atlantic
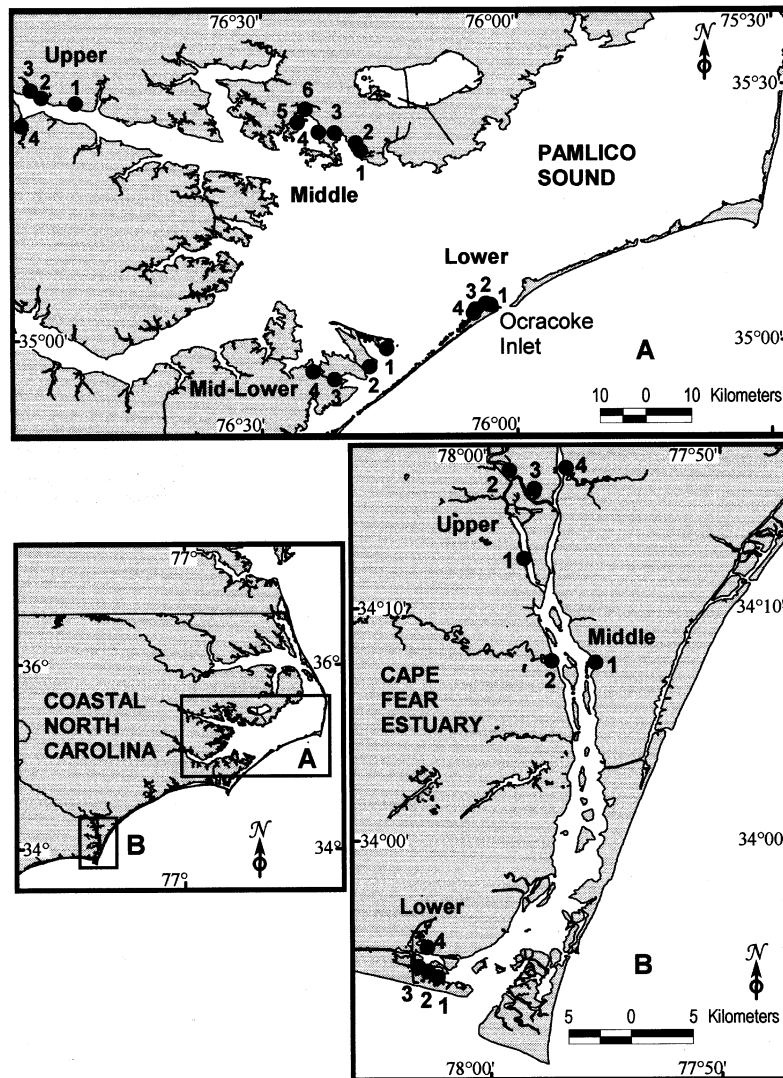
Figure 1

Pamlico Sound (**A**) and Cape Fear Estuary (**B**) in coastal North Carolina. General areas (e.g. upper, middle, lower) and sampling locations during March–June 1987 (solid dots) are labeled in the enlargements. Numbers correspond to station descriptions in Table 1.

croaker across wide ranges of densities in these systems. The similarity in these rates imply that PNAs were below carrying capacities. Thus, I did not consider density as a variable affecting growth or mortality for the following comparisons of PNA quality.

Methods

Study area

To encompass the greatest variability possible in estuarine habitats, I sampled nursery creeks in two widely separated, geophysically different North Carolina estuarine systems: 1) Pamlico Sound and River and 2) the Cape Fear River (Fig. 1). Each system was partitioned into general areas (e.g.

upper, middle, lower) and stations were selected to represent these areas. Stations were located in creeks throughout both systems that previous sampling (Weinstein, 1979; Ross and Epperly, 1985; NC Division of Marine Fisheries[1]) indicated were consistently productive for juvenile marine fishes during the spring-summer season. All creeks were similar in depth, size, and sediment type. The greatest physical differences between stations were the salinities, tidal regimes, and distances from the nearest inlets (Table 1).

Pamlico Sound is a shallow lagoon estuary whose hydrography is controlled by wind (Giese et al., 1979; Pietrafesa et al., 1986a; Pietrafesa and Janowitz, 1988).

Table 1

Distances to nearest inlets (D in km), salinity (‰) ranges and means, mean depths (m), and sediments of stations sampled from mid-March through mid-June 1987 in the Pamlico Sound and Cape Fear systems. Sediment symbols are m = mud, fs = fine sand, g = grass, and fs-m = fine sand and mud.

Area	D	Salinity range (mean)	Mean depth	Sediment
Pamlico Sound				
Lower				
"Coastguard" Creek	3	15.5–23.0 (18.9)	0.9	m
"Doctors" Creek	4	15.0–24.5 (18.6)	0.7	m
"Tom Bragg Slough"	7	13.0–22.0 (17.4)	0.9	fs-m
Royal Point Bay	8	17.0–20.4 (18.6)	0.7	fs
Mid–Lower				
Oyster Creek	26	11.0–15.0 (13.5)	0.9	m
Southwest Prong	33	13.5–23.0 (17.8)	1.0	m [1]
Merkle Hammock Creek	41	11.0–14.5 (15.1)	0.9	fs-g[1]
Codduggen Creek	46	9.0–14.5 (12.3)	0.9	fs-m[1]
Middle				
Caffee Creek	46	10.8–18.5 (13.4)	1.8	m
Oyster Creek	48	10.8–17.8 (13.2)	1.2	m[1]
unnamed Creek	51	10.9–18.0 (13.7)	1.6	fs-m
"Swan" Creek	60	10.0–15.9 (12.4)	1.1	m
Tooley Cr	61	10.2–17.1 (12.5)	1.3	m[1]
Head Rose Bay	64	10.0–13.3 (11.1)	2.5	m
Upper				
Mallard Creek	92	1.3–7.2 (3.5)	1.2	m
Flatty Creek	99	0.9–4.0 (2.6)	1.0	m
Broad Creek	101	0.3–8.7 (2.4)	1.4	m
Little Creek	104	0.6–3.9 (2.3)	1.0	m
Cape Fear estuary				
Lower				
Molasses Creek	4	15.4–29.0 (21.5)	1.0	m
Piney Pt. Creek	6	15.0–29.9 (22.5)	0.6	m
Dennis Creek	7	11.8–31.0 (21.7)	1.0	m-fs
Dutchman Creek	7	12.6–24.6 (17.7)	0.6	m
Middle				
Town Creek	29	0.0–10.2 (3.7)	2.0	m
Mott Creek	29	0.0–13.4 (5.6)	1.0	m
Upper				
Jackeys Creek	36	0.0–6.9 (1.7)	0.5	m
Toomers Creek	44	0.0–2.3 (0.3)	3.0	m
Horseshoe Bend	43	0.0–2.3 (0.4)	0.6	m
Smith Creek	44	0.0–4.8 (1.5)	1.3	m

[1] See Ross and Epperly (1985) for additional sediment data.

Eighteen stations were located in creeks in four areas along an approximately 100-km transect from Ocracoke Inlet to the upper Pamlico River (Fig. 1). Four polyhaline stations were located on Portsmouth Island (lower area). Water depths there were largely controlled by semidiurnal lunar tides (range usually <0.7 m, Giese et al., 1979); however, on one occasion I observed that northerly winds (≥37 km/h) moved large quantities of water into these creeks. The mid-lower area consisted of four stations on Cedar Island, which exhibited less depth variation (dampened lunar tides) than creeks on Portsmouth Island. Six creeks were sampled in the middle area: three each in Rose and Swanquarter bays. Tidal influence was negligible here (Pietrafesa et al., 1986a). The creeks in the above three areas were largely surrounded by *Spartina* and *Juncus* marsh grasses. The upper area was represented by four creeks (oligohaline or freshwater) surrounded by a mixture of woodlands and patches of marsh. Water levels and currents here were almost entirely controlled by winds or river flow (or both) (Hobbie, 1970; Pietrafesa et al., 1986a).

The Cape Fear River is more typical (compared to the Pamlico Sound system) of United States East and Gulf

coasts estuaries (i.e. a drowned river valley). Diurnal lunar tides (average range about 1.5 m) were a dominant feature throughout the study area (Welch and Parker, 1979; Pietrafesa and Janowitz, 1988). Ten stations were located along a 50-km transect of the Cape Fear system (Fig. 1). In the lower estuary, four polyhaline creeks were sampled on the west side of the inlet (Oak Island). Two creeks were sampled on opposite sides of the middle of the estuary and four oligohaline creeks were sampled in the upper estuary near Wilmington. All stations in this system were surrounded by *Spartina* marshes.

Field sampling

All stations were sampled during daylight with two one-minute tows (68.6 m each) of a small-mesh trawl (3.2-m headrope length, 6.4-mm bar mesh wings and body, 3.2-mm tail bag mesh). Catches from the two tows were combined for the station sample. Surface and bottom salinities (nearest ‰) and water temperatures (nearest °C) were recorded after each sample. Mean salinities and temperatures for each area were analyzed for differences by using *t*-tests for all possible combinations of area pairs.

Sampling was designed to provide biological data during the time of early residency in the nursery creeks, but before significant emigration. Most recruitment of young juvenile fishes into these creeks has ended by late-April, and some fishes begin to emigrate by June–July (Weinstein, 1979; Ross and Epperly, 1985; author's pers. obs.). To minimize the influence of emigration on the calculation of growth and mortality rates, sampling occurred during seven periods, every other week from mid-March through mid-June 1987 (about 14 d between samples). Synoptic samples over this large region were generated by assigning areas to four crews for trawling during the same period of each sample week.

Newly recruiting OWS juvenile fishes of the 1987 year class were sorted from the catches and preserved in the field in 100% ethyl alcohol. About one month after collection the fishes were identified, counted, and standard lengths (SL) were measured to the nearest mm. Analyses were limited to spot and Atlantic croaker, the two most abundant species. Catch per unit of effort (CPUE) was calculated by dividing the total number of individuals of a species captured by the number of trawl tows in a time period or area. Subsamples of these fishes representing several collection dates and all areas were measured for SL, blotted, and weighed to the nearest 0.01 g and were used to develop a weight-length relationship using linear regression. Differences in weight-length relationships between areas were assessed by using analysis of covariance (covariate=log*SL*) in a general linear model procedure (SAS Institute, 1988).

Otolith aging

Subsamples for aging were randomly selected from early (early and mid-April) and late (mid and late May) dates and from downstream (lower) and upstream (upper) areas in each system. Sagittae were removed from these fishes,

mounted on microscope slides with thermoplastic cement, and polished (often on both sides) until thin sections were obtained. Otoliths were viewed with oil immersion and transmitted polarized light at magnifications between 500 and 625×, and images were projected through a video system to a screen. Rings, presumed to be daily, were counted. The formation of daily rings has either been validated (Peters et al., 1978; Baldevarona, 1987; Siegfried and Weinstein, 1989) or assumed (Warlen and Chester, 1985; Cowan, 1988) for the two species in the size ranges used here. Even so, the counted rings need not be deposited daily for growth rate comparisons, nor is it necessary to know their periodicity. It is required that groups of fish being compared exhibit the same ring formation periodicity over the time and space of the comparison. Spot and Atlantic croaker do not form growth rings until after yolksac absorption, about four to five days after spawning (Peters et al., 1978; Warlen, 1980). Therefore, to estimate actual ages for mortality calculations, five days were added to the ring counts.
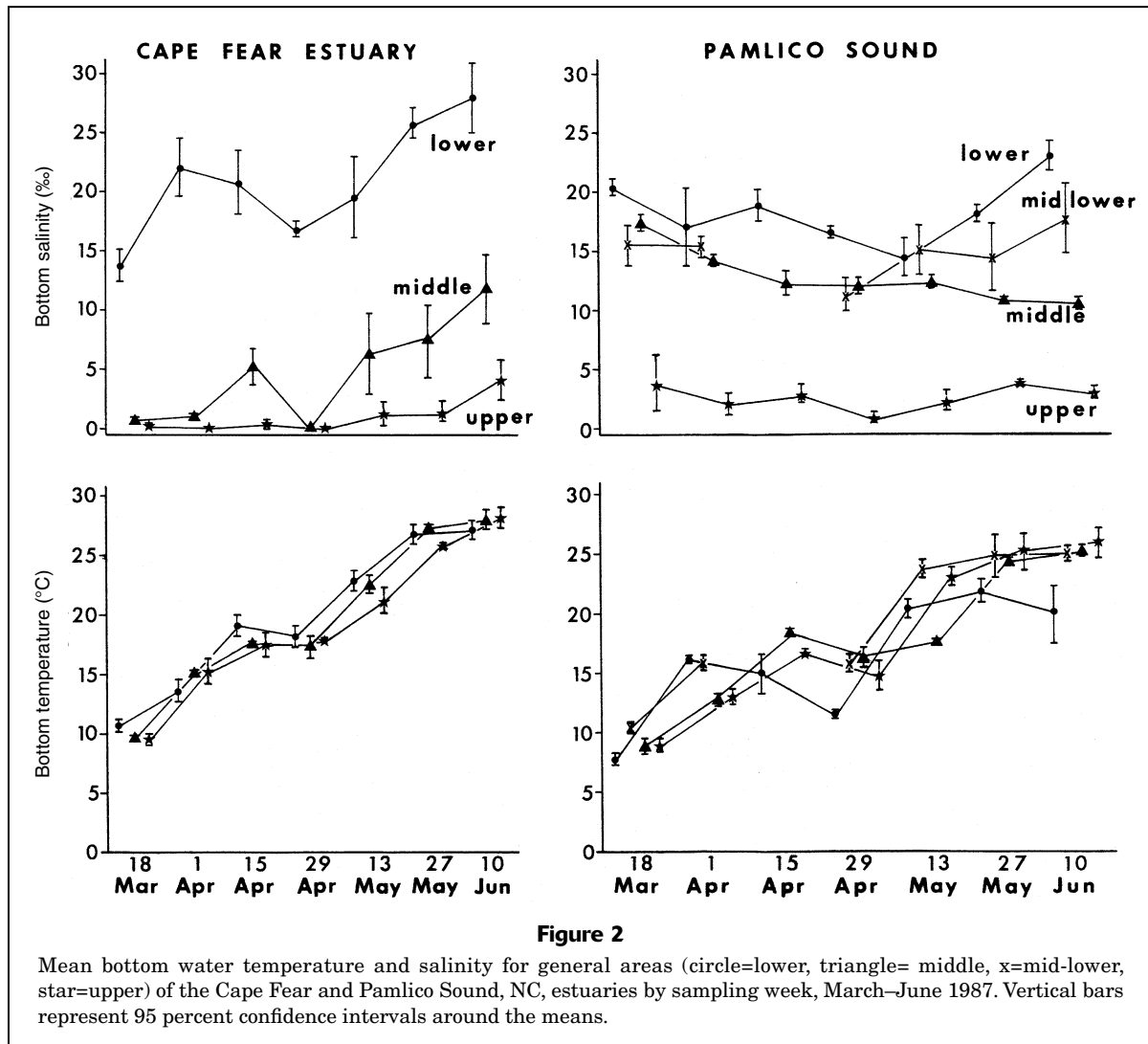
Although it seems reasonable to assume that juvenile spot and Atlantic croaker form daily sagittae rings, the precision (repeatability) of ring counts and the ability to identify daily rings needs addressing. Before aging the samples used in this study, I examined several hundred spot and Atlantic croaker otoliths. Counts by myself and 2–3 other otolith readers were compared. Our ring identifications were compared to samples of known age spot and Atlantic croaker provided by the National Marine Fisheries Service (Warlen[2]). These preliminary samples were used as a training device to ensure that daily rings were accurately identified and were not confused with shadows or subdaily rings. Subdaily rings may not even be resolvable at the magnifications (≤625×) used in the present study (Campana et al., 1987; Isely[3]). After aging the samples used in this study, I re-aged a random selection of spot (without knowledge of previous age assignments) and obtained a mean difference in counts of 2.85 (SD=2.03, *n*=27). Because Atlantic croaker otolith rings were usually easier to count, I assumed that the above count difference was generally similar for this species. I assumed that the ages reported here had a count precision of ±3 days. I also assumed that any aging errors were randomly distributed throughout the samples and were not spatially or temporally biased.

Growth and mortality

Linear regression of the form $\text{Log}_{10}SL = b + m(age)$ was used to model growth. The slope of this line, *m*, is the instantaneous daily growth rate. Differences in growth rates between areas were assessed by using analysis of covariance (covariate=age) in a general linear model procedure (SAS Institute, 1988). Absolute and relative daily growth rates were calculated by using values predicted with the age-SL regression equation (Ricker, 1975). For each sampling date, mean SLs were compared between all

[2] Warlen, S. M. 1989. Personal commun. National Marine Fisheries Service Beaufort Lab, Beaufort, NC 28516.

[3] Isely, J. 1989. Personal commun. Zoology Dept., NC State Univ., Raleigh, NC 27695.

Figure 2

Mean bottom water temperature and salinity for general areas (circle=lower, triangle= middle, x=mid-lower, star=upper) of the Cape Fear and Pamlico Sound, NC, estuaries by sampling week, March–June 1987. Vertical bars represent 95 percent confidence intervals around the means.

areas and systems by using pairwise t-tests for all possible pair combinations as an option in the general linear models procedure (SAS Institute, 1988).

Instantaneous and daily mortality rates were calculated for spot and Atlantic croaker by using methods similar to Crecco et al. (1983) and Essig and Cole (1986). Inverse regression (Zar, 1984) of the relationship between age and SL was used to estimate age from SL. Ages were then calculated for all fish sampled, and the natural logarithm of the slope of the descending limb of the catch curve was the instantaneous natural mortality rate (Z). Analysis of covariance (covariate=age) in a general lineal model procedure was used to test for differences in mortality rates between areas (SAS Institute, 1988). The daily mortality rate (M, %/d) for the whole time period was calculated as $M = 1-e^{Z}$ (Ricker, 1975).
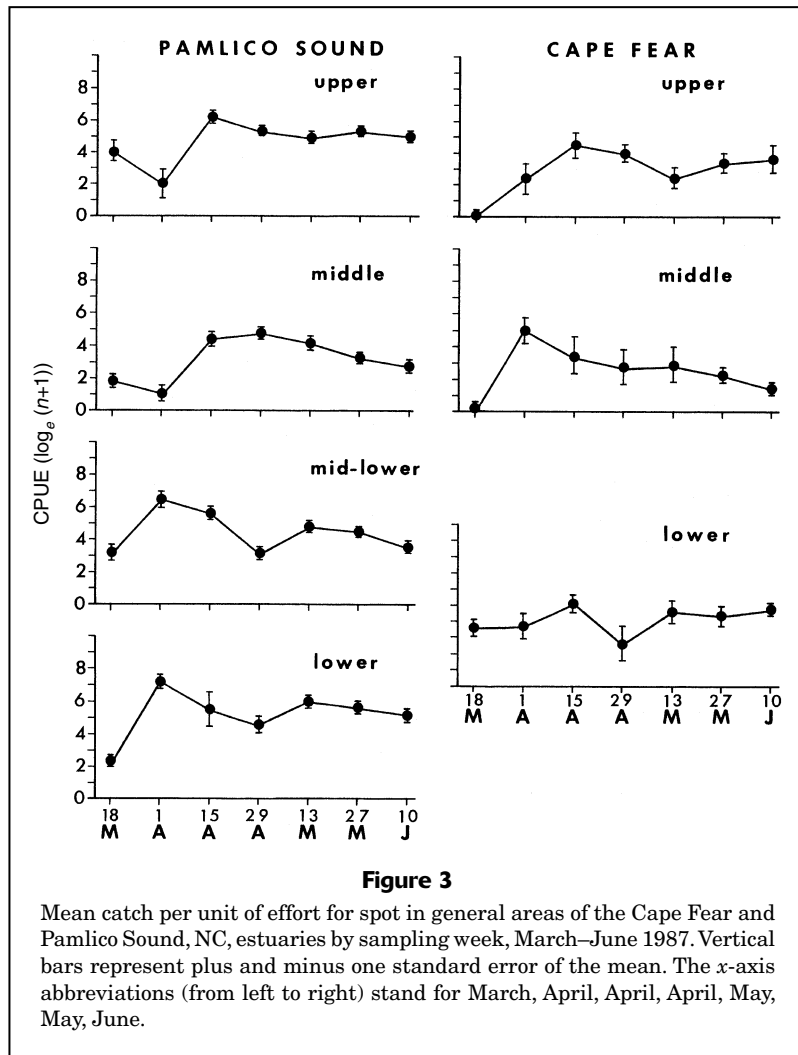
Because null hypotheses of no differences in growth or mortality rates between areas were accepted in many cases, probabilities of type-II errors (B, H_0 actually false) existed. Calculations of power ($1-B$), the probability of correctly rejecting H_0, are difficult with ANOVA or ANCOVA (Zar,

1984; Neter et al., 1985). A power analysis was probably unnecessary for spot and Atlantic croaker age-SL regressions because the precisions of the slope estimates were good (i.e. proportional SEs of the estimates were 2–4% of the slopes).

Results

Hydrographic data

Only bottom hydrographic data are presented because the waters of these shallow stations were well mixed. Bottom water temperatures in all areas of both systems were similar on a given sampling date (Fig. 2). In the Cape Fear estuary, mean water temperatures were not significantly different (t-test, $P>0.05$) between areas. Mean temperatures throughout the Pamlico system were not significantly different ($P>0.05$), except that the lower area was cooler than the others ($P<0.05$). Comparisons between systems revealed no significant differences ($P>0.05$) between middle or upper area temperatures. Lower Cape Fear creeks were

Figure 3

Mean catch per unit of effort for spot in general areas of the Cape Fear and Pamlico Sound, NC, estuaries by sampling week, March–June 1987. Vertical bars represent plus and minus one standard error of the mean. The *x*-axis abbreviations (from left to right) stand for March, April, April, April, May, May, June.

significantly (*P*<0.05) warmer than those of the lower Pamlico. The cooler temperatures in the lower Pamlico may have resulted from sampling there at earlier times of the day or on different days of the sampling week.

Salinity was more variable than temperature, particularly within the mesohaline and polyhaline areas (Fig. 2). Within both the Pamlico and Cape Fear systems all areas exhibited significantly different (*t*-test, P<0.05) bottom salinities from each other. As expected, the Cape Fear estuary, with its larger, more channeled river flow and obvious tidal effects, was a more variable system than the Pamlico system. During this study mean salinities within the lower and middle areas of the Cape Fear system varied over a range of 11.8‰ and 14.2‰, respectively, whereas mean salinities in all other areas (including the Pamlico) varied over a range less than 9‰. The lower Cape Fear creeks had significantly higher (*P*<0.05) salinities than those of the lower Pamlico; however, the middle and upper Pamlico areas had significantly higher (*P*<0.05) salinities than their counterparts in the Cape Fear, even though the upper Pamlico area was twice as far from an inlet as the upper Cape Fear. Salinities declined rapidly in the Cape

Fear with increasing distance from the inlet; however, this relationship was more variable in the Pamlico System (Fig. 2). In both systems, overall mean salinity (S) was accurately predicted by distance (D, in km) from the inlet: Cape Fear: $S=23.5 - 0.55(D)$, $r^2=0.95$, $n=10$ and Pamlico: $S=20.4 - 0.17(D)$, $r^2=0.92$, $n=18$.

Leiostomus xanthurus

Distribution Spot was the more widely distributed of the two species (Figs. 3–5). At the earliest sample date, small numbers of spot had accumulated in all areas of the Pamlico system (Fig. 3). Peak abundance was observed in the lower and mid-lower areas by the second sample date and in the middle and upper areas by the third sample date. Although more spot were collected in the lower Pamlico, numerical differences between areas were not extreme (Figs. 3 and 4). Overall, the least numbers of spot occurred in the middle region (Figs. 3 and 4).

In the Cape Fear system, overall spot abundance was similar between the upper and lower regions, and, as in the Pamlico, the least numbers were collected from the middle
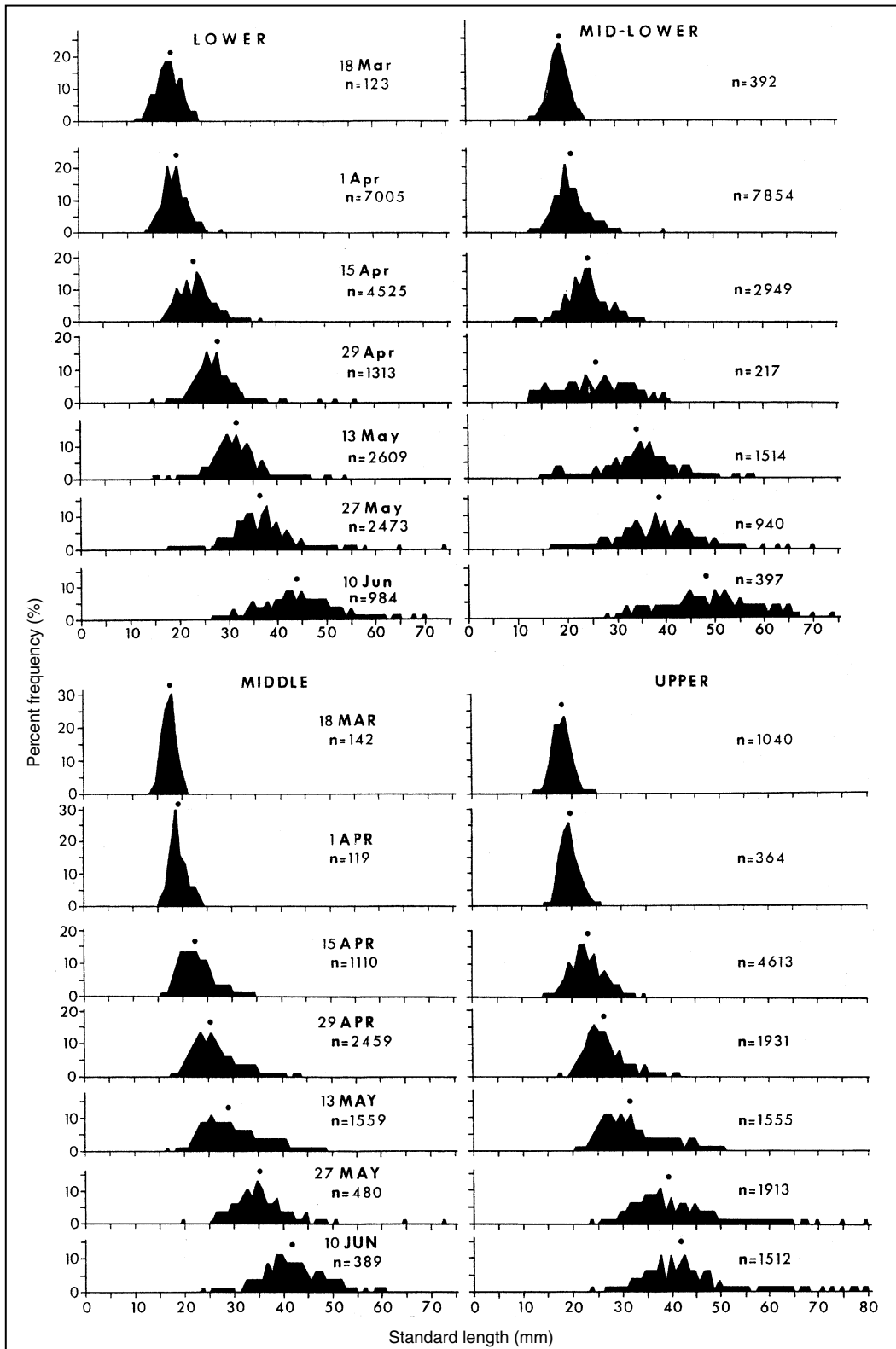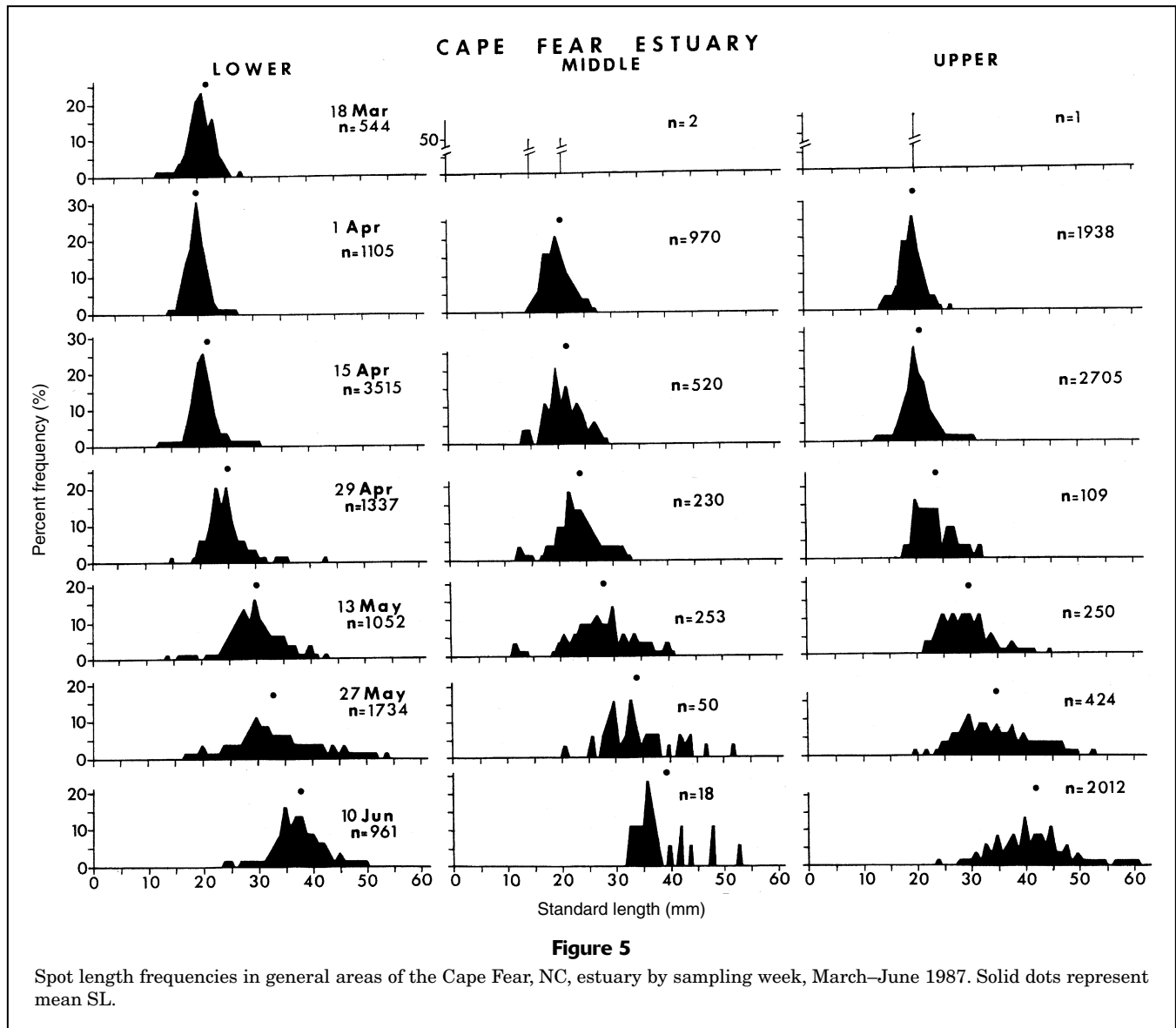
Figure 4

Spot length frequencies in general areas of the Pamlico Sound, NC, estuary by sampling week, March–June 1987. Solid dots represent mean SL.

Figure 5

Spot length frequencies in general areas of the Cape Fear, NC, estuary by sampling week, March–June 1987. Solid dots represent mean SL.
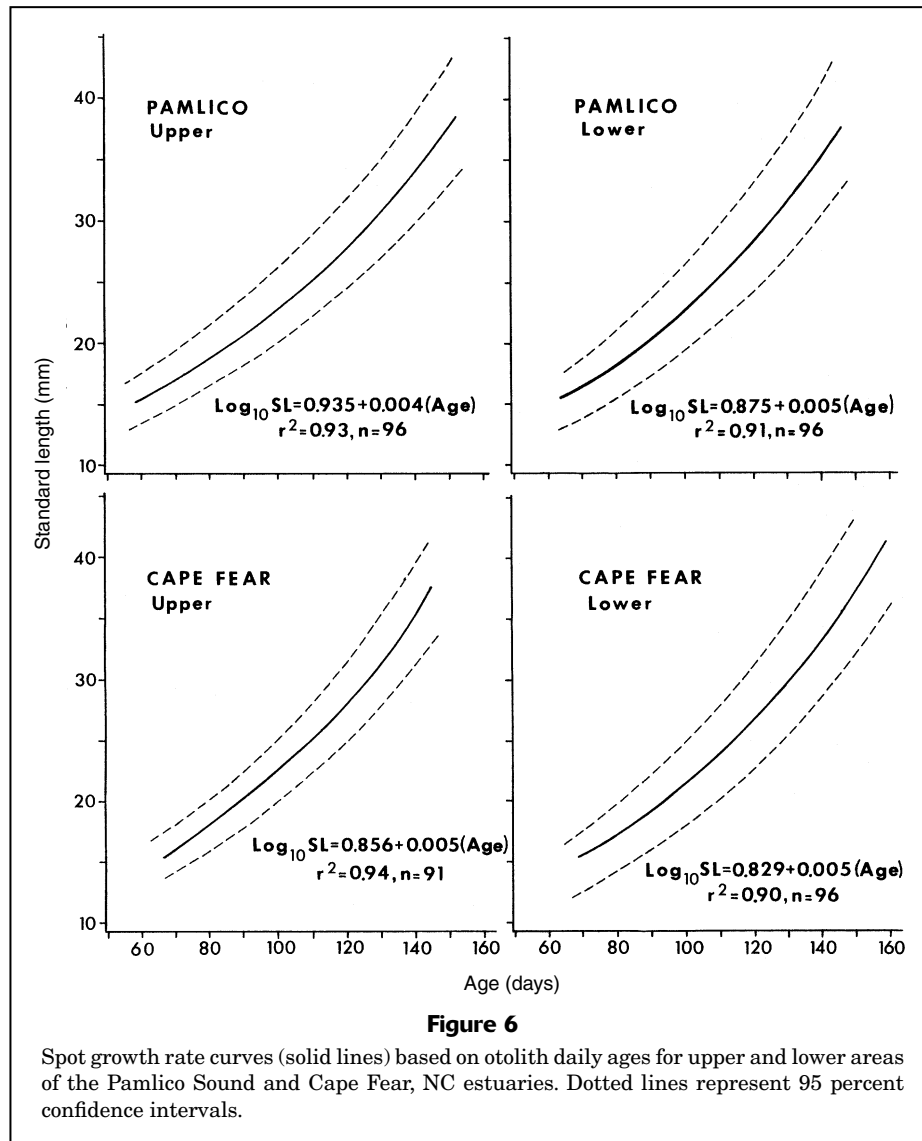
area creeks (Figs. 3 and 5). Initial recruitment was high in the lower Cape Fear area, whereas it lagged behind in the middle and upper areas (Fig. 3). Nevertheless, all Cape Fear areas reached peak numbers by the second or third sampling dates (Fig. 3).

Size distributions The bulk of the spot year class recruited to all creeks from mid-March to early April; however, some small fish ($\leq$25 mm) continued to enter the creeks through the end of May (Figs. 4 and 5). The smallest spot captured in both systems were always between 13 and 15 mm SL (Figs. 4 and 5). Because the trawl can collect spot and Atlantic croaker at least to 10 mm SL , 13–15 mm probably represented the smallest recruitment sizes of spot to nursery habitats.

Differences in mean spot SLs between areas steadily increased during the study from <1 mm (through mid-April) to 4.3 mm in the Cape Fear and from 1 to 6.2 mm in the

Pamlico. Although mean spot SLs exhibited the smallest variations between areas in the Cape Fear system (Fig. 5), they were significantly different (paired t-tests, P<0.05) between areas on most sampling dates. No area in the Cape Fear had consistently larger or smaller mean spot SLs. After mid-April mean SLs of spot from all four Pamlico areas were larger than those from the Cape Fear. Within the Pamlico system (Fig. 4) spot in the mid-lower area had significantly larger (P<0.05) mean SL (except sampling weeks four and six), and fish in the middle area were always significantly smaller (P<0.05) than those in the other three areas.

Growth Estimated spot ages ranged from 61 to 157 days (17–35 mm SL, n=379). All of the age-SL relationships used to assess growth rates (Fig. 6) were highly significant (P<0.0001). Regression residuals were evenly distributed around zero, indicating that the exponential growth model

Figure 6

Spot growth rate curves (solid lines) based on otolith daily ages for upper and lower areas of the Pamlico Sound and Cape Fear, NC estuaries. Dotted lines represent 95 percent confidence intervals.

$(\log_{10}SL = b + m(age))$ was appropriate. Instantaneous daily growth rates (slopes of the regressions) were similar (analysis of covariance, $P>0.05$) between upper and lower areas in the Cape Fear and the lower Pamlico (Fig. 6). Therefore, a combined age-*SL* regression for all spot in the upper and lower Cape Fear estuary and the lower Pamlico area was developed: $\log_{10}SL = 0.861 + 0.0048(age)$, $r^2=0.90$, $n=283$. Analysis of covariance indicated that spot from the upper Pamlico region exhibited significantly slower ($P>0.05$) overall growth rates (Fig. 6) than fish from the other three areas.

Age-specific absolute and relative growth of spot was predicted from the age-SL regression for the upper and lower Cape Fear and lower Pamlico combined and the upper Pamlico (Table 2). Predicted absolute growth rates in the Cape Fear and lower Pamlico areas increased from 0.16 mm/d between 60 and 65 days of age to 0.43 mm/d between ages 150 and 155 days of age, and the largest increase in absolute growth occurred between ages 95 and 105 days of

age (Table 2). Relative growth remained constant around 1.13–1.14 %/d SL over the whole age range examined (Table 2). Although predicted sizes at ages were larger in the upper Pamlico area than those of the other three areas, the absolute growth rates were lower, increasing from 0.16 mm/d between ages 60 and 65 d to 0.39 mm/d between ages 150 and 155 d (Table 2). Absolute growth rates in this area also exhibited the largest increases around 100–105 days. Relative growth rates in the upper Pamlico were lower than in the other areas and averaged 1.01 %/d SL (Table 2). The ages when absolute growth in all areas was greatest (95–105 d) translated to SL ranges around 21–23 mm. This SL range dominated the length frequencies in all areas during the first two weeks of April (Figs. 4 and 5). Water temperatures were steadily increasing in all areas prior to mid-April (Fig. 2).

Growth was also compared by using weight-length relationships. These relationships for spot were highly significant (analysis of covariance, $P<0.0001$) and took the usual

Table 2

Predicted age-specific mean standard lengths (SL), absolute (mm/d), and relative (%/d SL) growth rates for spot from the upper and lower Cape Fear and lower Pamlico combined (CFR + LPAM) and the upper Pamlico area (UPPAM).

Age (days)	CFR + LPAM				UPPAM		
	Mean SL	Absolute growth rate	Relative growth rate		Mean SL	Absolute growth rate	Relative growth rate
60	14.09				15.60		
65	14.89	0.16	1.14		16.39	0.16	1.01
70	15.74				17.22		
75	16.63	0.18	1.13		18.09	0.17	1.01
80	17.58				19.01		
85	18.58	0.20	1.14		19.98	0.19	0.99
90	19.63				20.99		
95	20.75	0.22	1.14		22.05	0.21	1.00
100	21.93				23.17		
105	23.17	0.25	1.13		24.35	0.24	1.04
110	24.49				25.59		
115	25.88	0.28	1.14		26.88	0.26	1.02
120	27.35				28.24		
125	28.91	0.31	1.13		29.68	0.29	1.03
130	30.55				31.19		
135	32.28	0.35	1.15		32.77	0.32	0.99
140	34.12				34.43		
145	36.06	0.39	1.14		36.18	0.35	1.02
150	38.11				38.02		
155	40.27	0.43	1.13		39.95	0.39	1.03

Table 3

Weight-standard length (W-SL) relationships for spot and Atlantic croaker from all areas of the Cape Fear and Pamlico systems, March–June 1987.

Area	Formula	r^2	n
Spot			
Cape Fear Upper	$W = 10^{-6.25}(SL^{4.02})$	0.96	100
Cape Fear Middle	$W = 10^{-4.90}(SL^{3.05})$	0.97	134
Cape Fear Lower	$W = 10^{-5.00}(SL^{3.12})$	0.97	212
Pamlico Upper	$W = 10^{-6.09}(SL^{3.87})$	0.98	456
Pamlico Middle	$W = 10^{-5.73}(SL^{3.62})$	0.97	252
Pamlico Mid-Lower	$W = 10^{-6.12}(SL^{3.89})$	0.98	246
Pamlico Lower	$W = 10^{-6.22}(SL^{3.95})$	0.97	250
Atlantic croaker			
Cape Fear Upper	$W = 10^{-5.80}(SL^{3.64})$	0.97	138
Cape Fear Middle	$W = 10^{-5.30}(SL^{3.31})$	0.86	118
Cape Fear Lower	$W = 10^{-5.64}(SL^{3.48})$	0.93	98
Pamlico Upper	$W = 10^{-5.55}(SL^{3.43})$	0.96	188
Pamlico Lower	$W = 10^{-4.85}(SL^{2.98})$	0.88	46

curvilinear form (Table 3, Fig. 7). In the Pamlico system differences between areas were not large; however, middle area spot had significantly ($P<0.05$) lower weights per length, especially in larger individuals (Fig. 7). In the Cape Fear system, spot in the upper area had significantly ($P<0.05$) larger weights per length than those from the other two areas.

Mortality Spot mortality rates were based on individuals aged ≥85 days. All regression slopes describing the declining numbers of spot with increasing ages were significantly different from zero ($P<0.0001$). Instantaneous mortality rates over this time period ranged from 0.037 to 0.066 (Fig. 8). Analysis of covariance indicated that within each
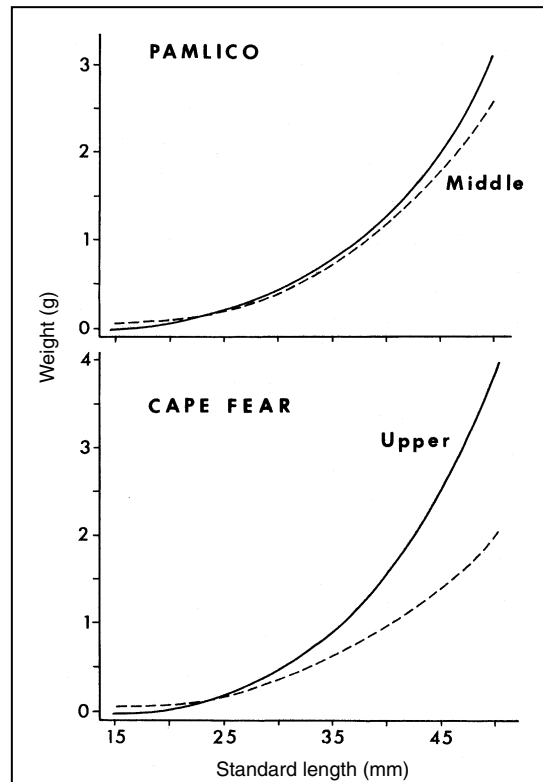
Figure 7

Spot weight-length relationships for the Pamlico and Cape Fear, NC, estuaries, March–June 1987. The line for the area that exhibited a significant difference was labeled (i.e. Pamlico Middle area, dashed line, was different and Cape Fear Upper area, solid line was different); the remaining line in each panel represented the relationship for all other areas combined.

system, upper area spot displayed significantly ($P<0.05$) lower instantaneous mortality rates than did fish from the lower estuaries, especially in Cape Fear. Lower Cape Fear spot exhibited a statistically similar ($P>0.05$) instantaneous mortality rate to those in the lower and upper Pamlico creeks. Daily mortality rates during the present study were 4.97 %/d in the upper Pamlico, 6.39 %/d in the lower Pamlico, 3.63 %/d in the upper Cape Fear, and 6.01 %/d in the lower Cape Fear.
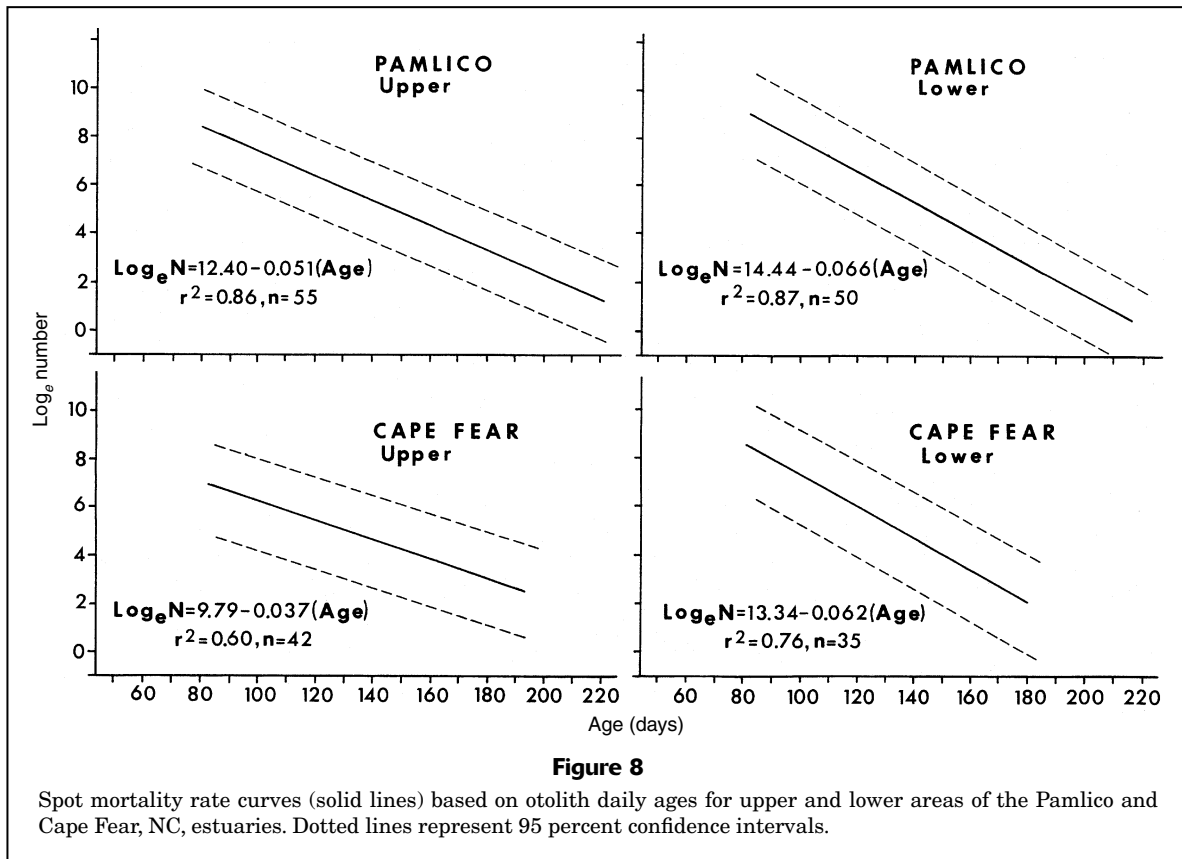
Micropogonias undulatus

Distribution Atlantic croaker distributions in both systems were skewed toward upstream, oligohaline creeks (Fig. 9–11). In the Pamlico system almost no Atlantic croaker were collected in the lower or middle areas (Fig. 9). Atlantic croaker recruitment in the Pamlico lagged behind the Cape Fear in abundance and timing (Fig. 9), and peak densities occurred throughout the Pamlico near the end of the sampling.

Patterns of Atlantic croaker recruitment were like those of spot in the upper and middle Cape Fear. Like spot, most

of the Atlantic croaker year class had recruited to these areas by mid-April, although small Atlantic croaker (≤20 mm) continued to colonize these creeks through mid-late May (Fig. 10). Also, peak abundance was reached in the middle and upper Cape Fear during the same weeks as those for spot (2nd and 3rd, respectively) (Fig. 9). Except for the larger CPUE in mid-March, Atlantic croaker recruitment in the lower Cape Fear was similar to that of most Pamlico system creeks (Fig. 9).

Atlantic croaker entering PNAs from mid-March through late April in both systems appeared to bypass lower and middle area nursery creeks (unlike spot) to a greater extent than fish recruiting after April (Fig. 9). Late recruitment of small Atlantic croaker was especially apparent in the mid-lower Pamlico (Fig. 11).

Size distribution Atlantic croaker initially collected in the Cape Fear creeks through the first week of April spanned a size range of 11–23 mm (Fig. 10, 15.4 mm SL mean), and mean sizes were not significantly different (paired *t*-test, $P>0.05$) between areas in the first or second sampling week. After this time, Atlantic croaker from the middle

Figure 8

Spot mortality rate curves (solid lines) based on otolith daily ages for upper and lower areas of the Pamlico and Cape Fear, NC, estuaries. Dotted lines represent 95 percent confidence intervals.

Cape Fear area were usually significantly shorter ($P<0.05$) than those from other areas, and Atlantic croaker from the lower Cape Fear were significantly longer ($P<0.05$) than those of other areas.

Atlantic croaker collected from the upper Pamlico creeks were significantly larger ($P<0.05$) on all sample dates than those occupying any area of the Cape Fear during the same weeks. Within the Pamlico, upper and mid-lower mean SLs were the same ($P>0.05$) except in the last week when mid-lower mean SL was significantly larger ($P<0.05$).
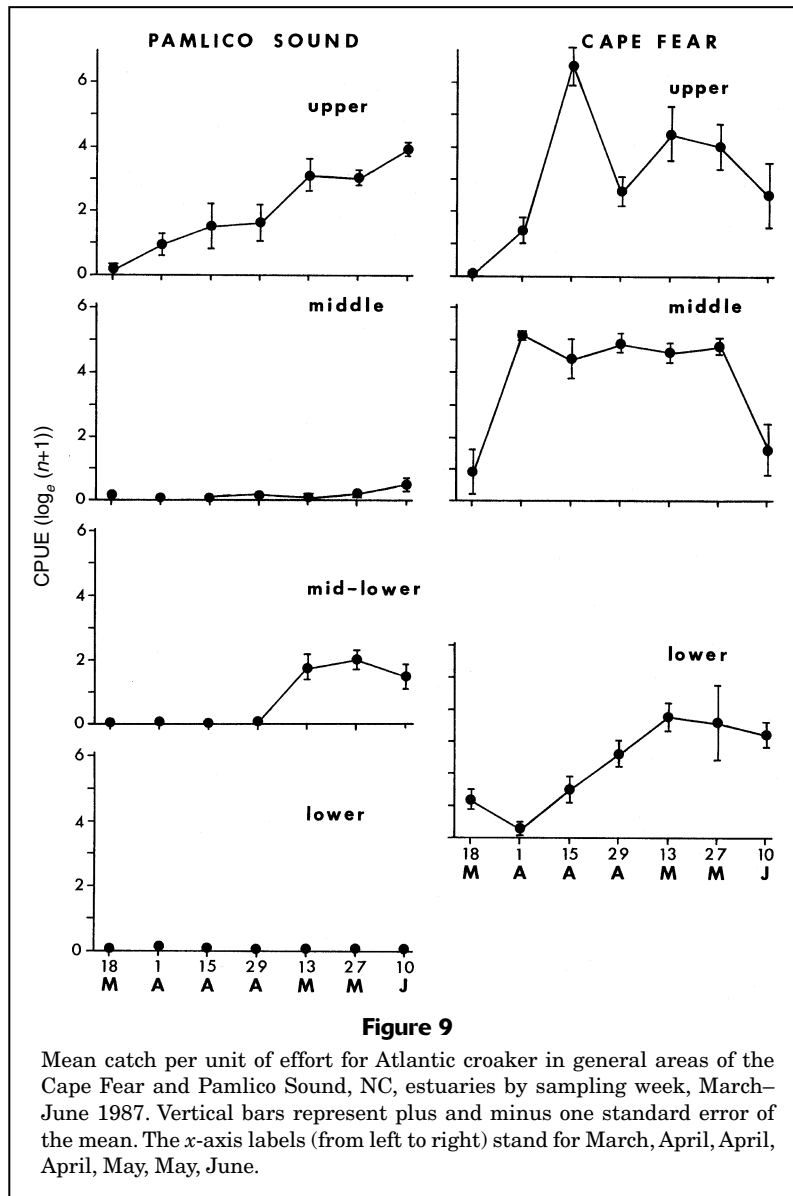
Growth   Atlantic croaker (12–35 mm SL, n=383) ages estimated from otoliths ranged from 62 to 234 days, and all age-SL relationships (Fig. 12) were significant ($P<0.0001$). Residuals of these regressions exhibited no pattern; therefore, the growth models appeared to be appropriate. The instantaneous daily growth rates within each system were not significantly different (analysis of covariance, $P<0.05$) between upper and lower areas (Fig. 12). Between systems, upper Pamlico Atlantic croaker grew more slowly than those from the upper Cape Fear ($P<0.05$). Overall age-length relationships for upper and lower Cape Fear combined and for the upper and lower Pamlico Atlantic croaker combined were the following: for Cape Fear—$\log_{10}SL = 0.915 + 0.0027(age)$, r^2=0.87, n=229; for Pamlico—$\log_{10}SL = 0.970 + 0.0024(age)$, r^2=0.87, n=158.

The above combined equations for each system were used to calculate age-specific absolute and relative Atlantic croaker growth rates (Table 4). Early absolute Atlantic

croaker growth rates in the Cape Fear system increased most rapidly in ages <105 days, averaging 0.085 mm/d (Table 4). After this age, Cape Fear growth rates increased at a steady, slow rate, reaching 0.19 mm/d by age 215 days. Relative Atlantic croaker growth rates in the Cape Fear were constant over the whole age range at about 0.63 %/d SL. The larger Pamlico system Atlantic croaker exhibited similar absolute growth rates to Cape Fear fish and these increased rapidly from 0.077 mm/d between ages 60 and 65 d to 0.106 mm/d between ages 120 and 125 d to 0.175 mm/d between ages 210 and 215 d (Table 4). Relative growth rates were less than those from the Cape Fear and were constant around 0.56 %/d SL.

Weight-length relationships for Atlantic croaker were highly significant in all areas ($P<0.0001$) (Table 3). In both systems fish from upper area creeks exhibited significantly larger ($P<0.05$) weights per length than those from other areas, particularly at the larger sizes (Fig. 13). Slopes of middle and lower Cape Fear weight-length relationships were not significantly different from each other ($P>0.05$).

Mortality   Catch curves used to estimate Atlantic croaker mortality rates were calculated by using ages ≥125 days. All regression slopes were significantly different from zero ($P<0.0001$), although the relationship was more variable for the mid-lower Pamlico area because of the small sample size. Instantaneous mortality rates for Atlantic croaker in the nursery creeks ranged from 0.008 to 0.038 (Fig. 14). Atlantic croaker in the upper and mid-lower Pamlico
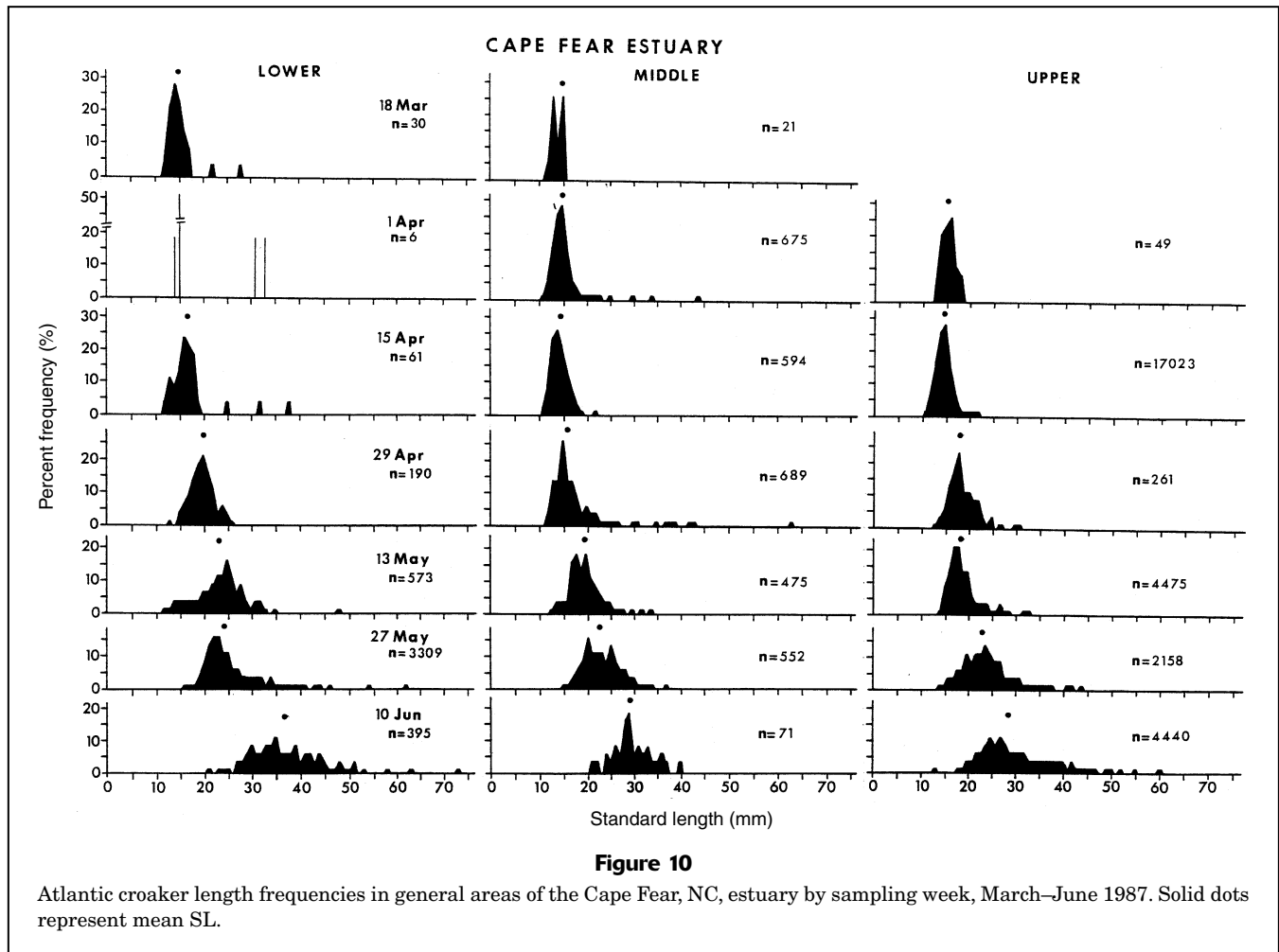
Figure 9

Mean catch per unit of effort for Atlantic croaker in general areas of the Cape Fear and Pamlico Sound, NC, estuaries by sampling week, March–June 1987. Vertical bars represent plus and minus one standard error of the mean. The *x*-axis labels (from left to right) stand for March, April, April, April, May, May, June.

areas had similar instantaneous mortality rates (analysis of covariance, $P>0.05$). Upper Cape Fear Atlantic croaker exhibited significantly lower mortality rates than those in the lower Cape Fear ($P<0.05$). All Atlantic croaker mortality rates in the Cape Fear were significantly higher than those in the Pamlico. Daily mortality rates for Atlantic croaker in the upper and lower Cape Fear were 2.96 %/d and 3.73 %/d, respectively and in the upper and mid-lower Pamlico were 0.90 and 0.80 %/d, respectively.

Discussion

Primary nursery area habitats in two different estuaries were not equally valuable for spot and Atlantic croaker. Considered together, growth, mortality, and distribution data indicated that upstream oligohaline creeks provided

the best environment, followed closely by downstream polyhaline areas. In all regards, the middle reaches of the estuary appeared to be less valuable (or at least less used). These consistent results for both species in the two separate estuarine systems lend support to their general applicability. Other studies were marginally useful in evaluating these results because of their lack of synoptic comparisons across a wide variety of habitats and because of limitations in or lack of growth and mortality data for estuarine juveniles of these species.

The main evidence that oligohaline habitats provided better environments than polyhaline areas was that spot (both systems) and Atlantic croaker (in Cape Fear) exhibited significantly lower mortality in the freshwater PNAs. Miller et al. (1985) reported lower mortality for these species in mesohaline areas compared to high salinity areas of Pamlico Sound. In the Cape Fear River, Weinstein and

Figure 10

Atlantic croaker length frequencies in general areas of the Cape Fear, NC, estuary by sampling week, March–June 1987. Solid dots represent mean SL.
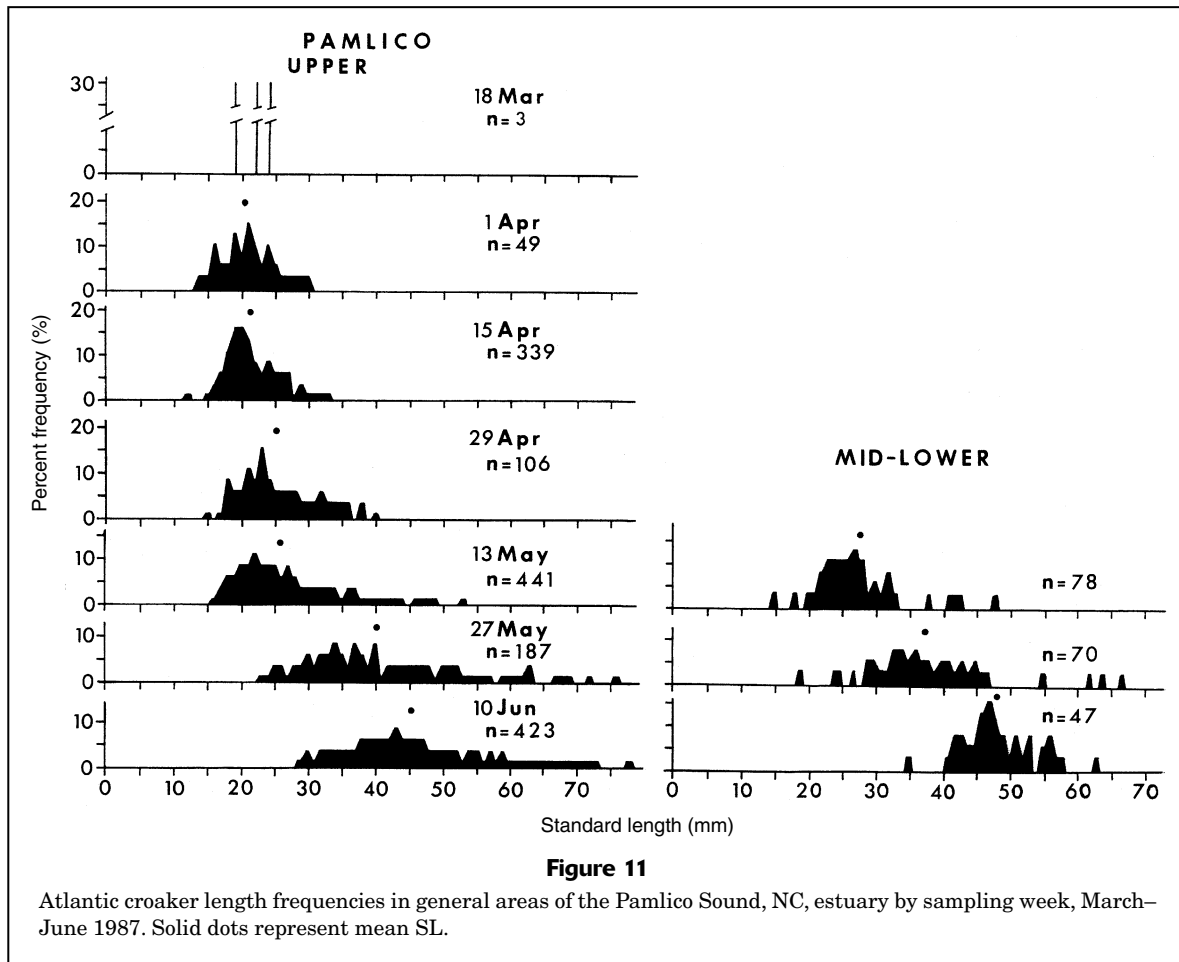
Walters (1981) found consistently high mortality for spot in polyhaline creeks during two years, but variable mortality between years (one year higher, one year lower) in low salinity regions. Mortality rates reported in the present study may not be affected by fish density (Ross, 1992), and it is unlikely that starvation (Currin et al., 1984) played a major mortality role. Predation may cause most of the PNA natural mortality; it was previously proposed that predation rates were lowest in oligohaline habitats because these areas contained relatively fewer predators (Weinstein and Walters, 1981; Currin et al., 1984; Miller et al., 1985). This hypothesis continues to lack direct, convincing evidence. Predators in oligohaline habitats (e.g. southern flounder, catfishes, gar, striped bass, etc.) may, in fact, be just as numerous near the upriver nurseries (author's pers. obs.; Patrick and Moser, 2001; Moser[4]) as marine predators are around polyhaline creeks. Also, because water levels in the upriver creeks, especially in the Pamlico, do not vary as much as in polyhaline areas, predators may have more opportunity to use these creeks (Currin et al., 1984).

One alternative explanation for lower mortality estimates in upriver PNAs is that mortality could be related, perhaps indirectly, to ambient salinity. Although freshwater conditions probably do not increase mortalities of these fishes (Moser and Hettler, 1989), there may be negative effects of high salinity on survival that have not been investigated. Moser and Hettler (1989) reported that spot exhibited the highest respiration rates in high salinity conditions, which suggest increased stress.

Another potential explanation is that fishes may leave high salinity areas more rapidly than freshwater areas. Although I attempted to minimize effects of emigration on mortality estimates by limiting the analyses to the period before mid-June, the mortality rates I calculated could have contained an unknown effect of emigration. Other studies (Weinstein, 1983; Weinstein and O'Neil, 1986; Miller and Able, 2002; author's pers. obs.) supported my assumption that emigration of spot and Atlantic croaker from PNAs was negligible at least through June. Such early habitat fidelity seems to be a common trait among juvenile fishes (Rountree and Able, 1992; Ross and Lancaster, 2002). Many individuals of OWS juvenile fishes leave PNAs by July (Ross, 1988; NC Division of Marine Fisheries[1]); therefore,

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[4] Moser, M. L. 1998. Personal commun. NW Fisheries Science Center, NMFS, 2725 Montlake Blvd., Seattle, WA 98112.

Figure 11

Atlantic croaker length frequencies in general areas of the Pamlico Sound, NC, estuary by sampling week, March–June 1987. Solid dots represent mean SL.
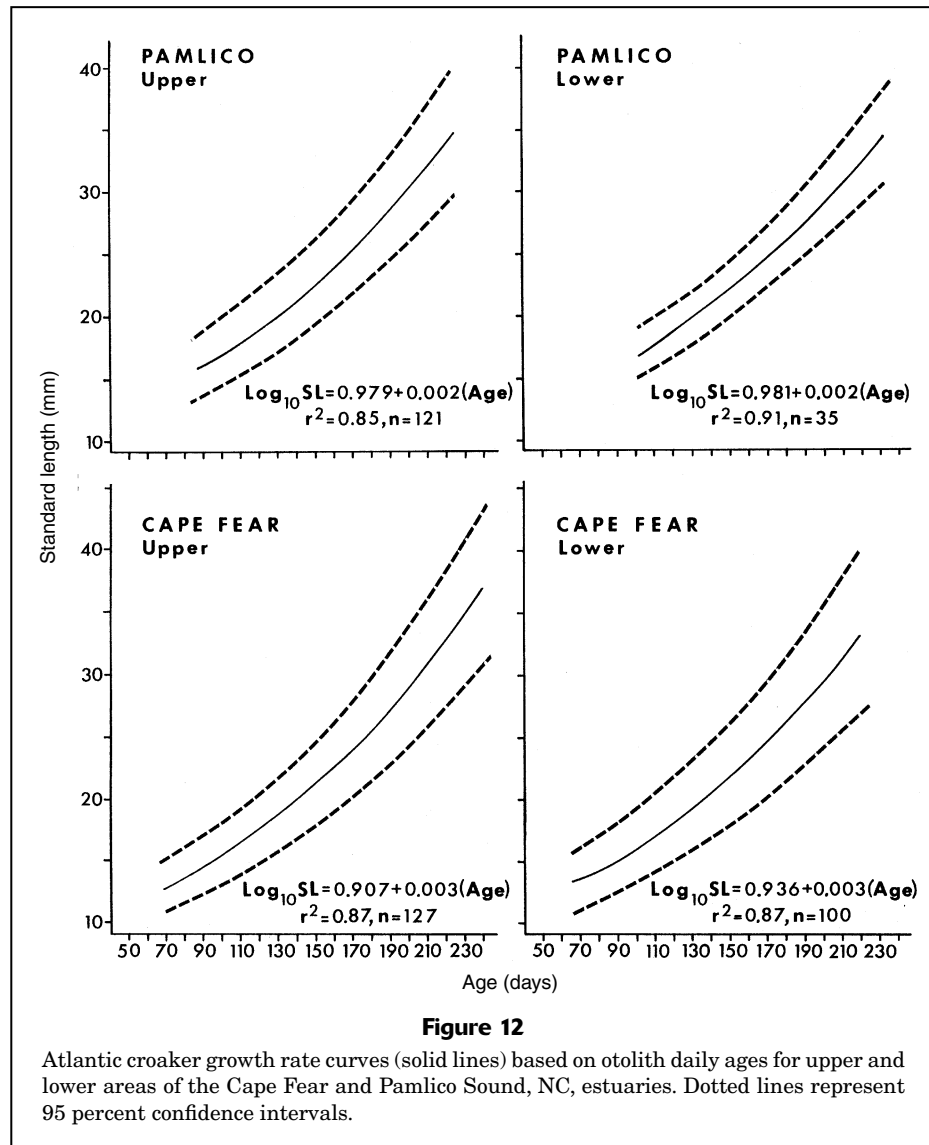
previous mortality estimates are likely confounded by emigration because measures of declining fish numbers were extended longer into the nursery season (through August, Weinstein and Walters, 1981; through October, Currin et al., 1984; through July, Miller et al., 1985).

Growth in weight (weight-length relationships) also indicated advantages of oligohaline habitats for these fishes. Higher weights per length have been equated with greater fitness (Friedland et al., 1988; Bolger and Connolly, 1989). Improved fitness was suggested by a consistent trend for individuals of both spot and Atlantic croaker in both systems to be heavier per length in the oligohaline creeks. Laboratory experiments on spot (Moser, 1987) resulted in heavier fish per length in freshwater, and the weight difference was attributed to a higher feeding rate in freshwater, rather than water absorption because of osmotic imbalance. Spot from oligohaline areas of the James River, VA, were heavier per length compared to those from several other estuaries (McCambridge and Alden, 1984), but the role of salinity in these differences was unclear. Peterson et al. (1999) indicated that reduced salinity itself caused higher growth rates (in weight) for Atlantic croaker in oligohaline conditions.

Growth (in length) rates and size distributions indicated that PNA habitats at extreme ends of estuaries were equally valuable to both species (with one exception). The exception—depressed spot growth rates in the upper Pamlico area—did not appear to be correlated with lower salinities or temperatures because spot from other areas with low salinity and similar or lower temperatures exhibited higher growth rates. The most obvious difference between upper Pamlico creeks and all other areas was the extremely long (often >100 km) estuarine migration required to reach them. Potential costs involved in such migrations should be examined as should the degree to which the lower spot growth rates persisted into later life. General lack of growth rate variation between oligohaline and polyhaline habitats suggested that salinity (and probably tidal influence) did not affect growth to a degree detectable in the present study. This conclusion is supported by previous studies (Moser and Gerry, 1989; Moser and Hettler, 1989; Miller et al., 2000) despite a general prediction that fish growth rates should be higher in brackish waters (Boeuf and Payan, 2001). The lack of evidence for negative effects of fish density on growth (Ross, 1992) indicated that resources in oligohaline or polyhaline PNAs may not limit these fishes. Currin et al. (1984) also suggested that food resources did not limit spot production in middle areas of Pamlico Sound.

Lack of spatial variation in early estuarine growth rates was also found in the few relevant studies available. Wein-

Figure 12

Atlantic croaker growth rate curves (solid lines) based on otolith daily ages for upper and lower areas of the Cape Fear and Pamlico Sound, NC, estuaries. Dotted lines represent 95 percent confidence intervals.

stein and Walters (1981) and O'Neil and Weinstein (1987) reported no consistent differences in spot growth rates between oligohaline and polyhaline creeks in the Cape Fear River and York River, VA, estuaries, respectively. Miller et al. (1985) indicated that spot and Atlantic croaker growth rates were probably not different between Pamlico Sound mesohaline and polyhaline areas. Similarly, Beckman and Dean (1984) found no significant differences in spot growth rates among localities in a small, polyhaline South Carolina estuary. Necaise (2000) failed to find growth differences among juvenile summer flounder caged (and fed *ad libitum*) over a wide range of abiotic habitats in southern North Carolina. Guindon and Miller (1995), however, did find growth rate differences among caged (not fed) southern flounder across abiotically similar oligohaline habitats in the Pamlico River. Differences in fish growth rates among estuarine habitats (e.g. Sogard, 1992) indicate that there are different species-specific responses to habitats, responses related to zoogeography, or responses related to

habitat structure or food availability. My data and most of the above studies, covering different years and a variety of estuaries, suggest that variation in growth rates, especially for spot, between PNAs is generally lacking or at least difficult to detect. Such results are consistent with the view that these fishes are hardy, omnivorous, opportunistic colonizers of an undersaturated environment.

Increasing evidence suggests that oligohaline or freshwater habitats in the southeastern United States are important nurseries for the OWS juvenile fishes (Rogers et al., 1984; Rozas and Hackney, 1984; Moser and Gerry, 1989; Moser and Hettler, 1989; Peterson and Ross, 1991). In fact, they may be the most valuable habitats, particularly for maximizing survival of some species. The nursery creeks I sampled supported similar growth rates for two species; however, fitness may be most improved upriver, where both growth (in weight) and survival are optimized. Anderson (1988) predicted that juvenile temperate fishes generally choose to maximize growth over reducing mortality,
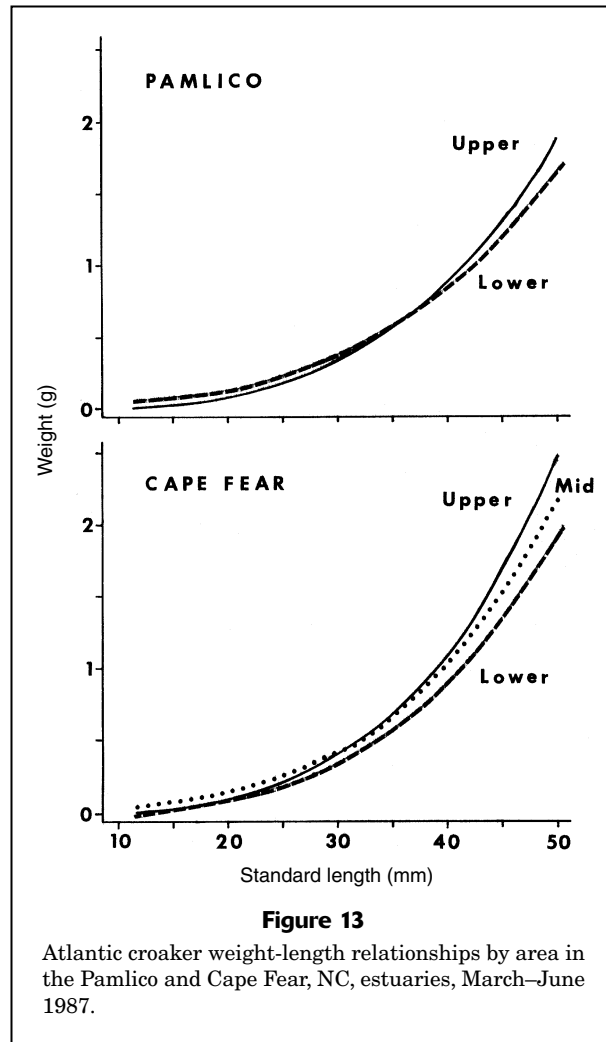
Table 4

Predicted age-specific mean standard lengths (SL), absolute (mm/d), and relative (%/d SL) growth rates for Atlantic croaker from the upper and lower Cape Fear combined (CFR) and the upper and mid-lower Pamlico combined (PAM).

Age (days)	CFR Mean SL	CFR Absolute growth rate	CFR Relative growth rate	PAM Mean SL	PAM Absolute growth rate	PAM Relative growth rate
60	11.94			13.61		
65	12.32	0.08	0.63	14.00	0.08	0.57
70	12.71			14.39		
75	13.11	0.08	0.62	14.79	0.08	0.56
80	13.52			15.21		
85	13.95	0.09	0.63	15.63	0.08	0.55
90	14.39			16.07		
95	14.84	0.09	0.63	16.52	0.09	0.56
100	15.31			16.98		
105	15.79	0.10	0.63	17.45	0.10	0.56
110	16.29			17.95		
115	16.81	0.01	0.64	18.45	0.10	0.56
120	17.34			18.97		
125	17.89	0.11	0.63	19.50	0.11	0.56
130	18.45			20.04		
135	19.03	0.12	0.63	20.61	0.11	0.57
140	19.63			21.18		
145	20.25	0.12	0.64	21.78	0.12	0.56
150	20.89			22.39		
155	21.55	0.13	0.63	23.01	0.13	0.56
160	22.23			23.66		
165	22.94	0.14	0.63	24.32	0.13	0.56
170	23.66			25.00		
175	24.41	0.15	0.63	27.70	0.14	0.56
180	25.18			26.42		
185	25.97	0.16	0.63	27.16	0.15	0.56
190	26.79			27.93		
195	27.64	0.17	0.63	28.71	0.16	0.56
200	28.51			29.51		
205	29.41	0.18	0.63	30.34	0.17	0.56
210	30.34			31.19		
215	31.30	0.19	0.63	32.06	0.18	0.56

although the two are intimately related (Werner and Gilliam, 1984). Selecting for optimized growth, however, appears not to be an issue for these two estuarine generalists. If upstream PNAs are better nurseries (i.e. provide better conditions for survival and perhaps growth), delayed PNA recruitment (longer estuarine migrations), especially for Atlantic croaker, may maximize ultimate fitness (Miller et al., 1985; Shapiro, 1987). Factors affecting transport of young to upstream areas may, therefore, be an important determinant of population fitness.

Unexpected patterns of recruitment into middle region creeks suggested that their function or recruitment potential as fish nursery areas may differ significantly from other regions. Even though these creeks were physically similar to creeks on either end of the estuarine transects, lower abundances of spot and Atlantic croaker in middle areas suggested that they either avoided (bypassed) middle areas or endured higher initial mortalities there. Higher initial mortality in middle regions seems unlikely because catches were generally low throughout the sampling period. Relatively poor habitat quality could explain the low densities of fishes in these creeks. This hypothesis was supported by the fact that most fishes settling in middle regions of both systems exhibited significantly smaller mean lengths and were lighter per length. The same pattern was observed for Atlantic menhaden in these systems (Ross, 1992). Szedlmeyer (1991) also found lower abundances and species richness in middle reaches of a Florida estuary and suggested that either less diverse habitat or greater salinity variation (or both) influenced this result. Ross and Epperly (1985) found stations close to the periphery of Pamlico Sound (including the middle area of this study)

Figure 13

Atlantic croaker weight-length relationships by area in the Pamlico and Cape Fear, NC, estuaries, March–June 1987.

to be the most productive, but their study lacked stations near the inlets and in freshwater areas. Weinstein et al.'s (1980) uppermost Cape Fear stations were the same as my middle area and generally produced lower densities of spot than polyhaline areas, but lacking upriver stations, the meaning of this in the present context is inconclusive. These fishes seem to opt either for rapid settlement in polyhaline environments or delayed settlement in oligohaline areas—mesohaline settlement being less "preferred."

The conclusion that PNAs were not equally valuable and the observation that spot were not most abundant in the best habitats, indicated that variation in estuarine distribution could control or at least regulate (fine tune) year-class strength. If movement to general regions of the estuary is largely passive (Pietrafesa et al., 1986b; Pietrafesa and Janowitz, 1988), then my results predict that year-class strength of these species would be decreased when transport conditions force the majority of the recruits toward middle or lower region PNAs. Alternatively, year class strength would be enhanced by conditions favoring greater upstream transport, assuming carrying capacities of the habitats were not exceeded. Ross (1992) proposed that these systems were recruitment limited, that post-

settlement mortality was less important in controlling year-class strength than early life history events prior to settlement. If true, factors affecting variation in estuarine distribution may indirectly adjust year-class strength, not control it. Additional data on mortality rate variation in relation to density during the estuarine and oceanic early life history is required to validate this hypothesis.
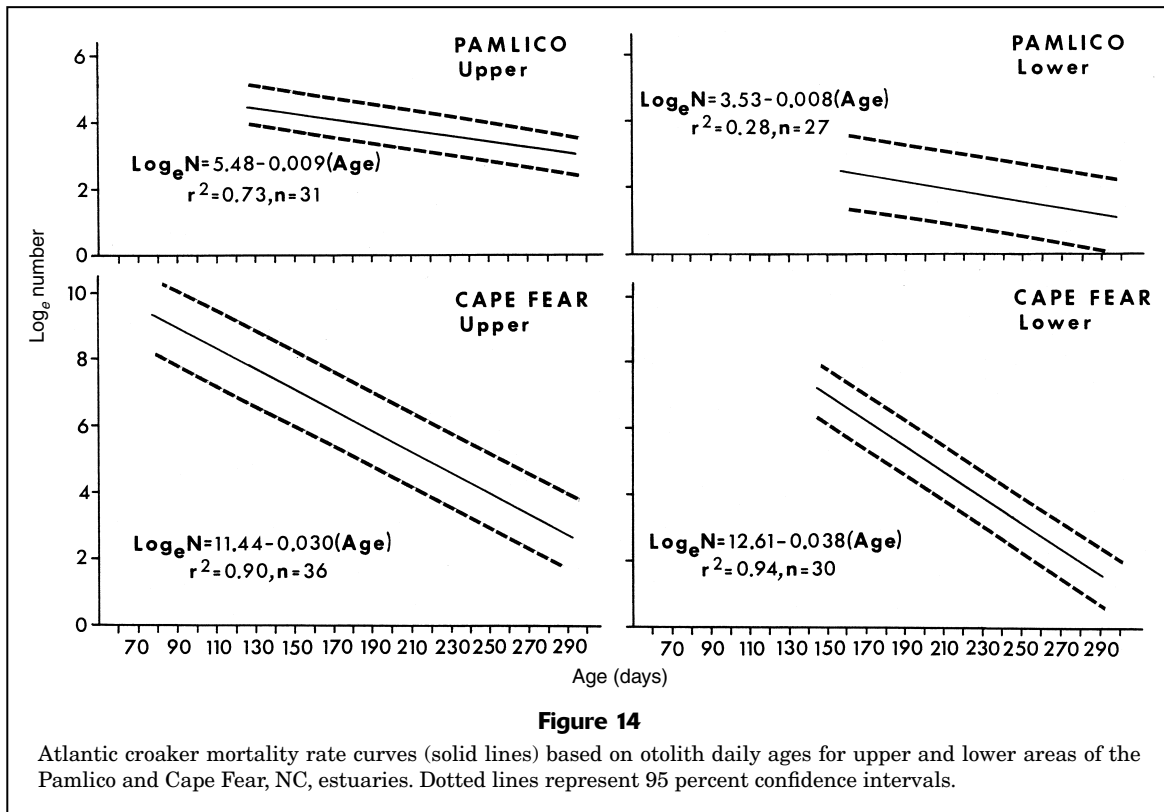
Acknowledgments

Figure 14

Atlantic croaker mortality rate curves (solid lines) based on otolith daily ages for upper and lower areas of the Pamlico and Cape Fear, NC, estuaries. Dotted lines represent 95 percent confidence intervals.

ratory (National Marine Fisheries Service) and the Biology Laboratory of Carolina Power and Light Company for providing space. David Colby made valuable contributions to this research. I appreciate Jeff Isely's advice and help in analyzing fish otoliths. I thank Ernie Aschenbach for sorting samples and mounting otoliths. And lastly I thank Mary L. Moser for help and support during all stages of this work from field sampling to reading numerous manuscript drafts.

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