# Seasonal distribution, abundance, and growth of young-of-the-year Atlantic croaker (*Micropogonias undulatus*) in Delaware Bay and adjacent marshes*

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**Abstract**—We examined the spatial and temporal distribution, abundance, and growth of young-of-the-year (YOY) Atlantic croaker (*Micropogonias undulatus*) in Delaware Bay, one of the northernmost estuaries in which they consistently occur along the east coast of the United States. Sampling in Delaware Bay and in tidal creeks in salt marshes adjacent to the bay with otter trawls, plankton nets and weirs, between April and November 1996–99, collected approximately 85,000 YOY. Ingress of each year class into the bay and tidal creeks consistently occurred in the fall, and the first few YOY appeared in August. Larvae as small as 2–3 mm TL were collected in September and October 1996. Epibenthic individuals <25 mm TL were present each fall and again during spring of each year, but not in 1996 when low water temperatures in January and February apparently caused widespread mortality, resulting in their absence the following spring and summer. In 1998 and 1999, a second size class of smaller YOY entered the bay and tidal creeks in June. When YOY survived the winter, there was no evidence of growth until after April. Then the YOY grew rapidly through the summer in all habitats (0.8–1.4 mm/d from May through August). In the bay, they were most abundant from June to August over mud sediments in oligohaline waters. They were present in both subtidal and intertidal creeks in the marshes where they were most abundant from April to June in the mesohaline portion of the lower bay. The larger YOY began egressing out of the marshes in late summer, and the entire year class left the tidal creeks at lengths of 100–200 mm TL by October or November when the next year class was ingressing. These patterns of seasonal distribution and abundance in Delaware Bay and the adjacent marshes are similar to those observed in more southern estuaries along the east coast; however, growth is faster—in keeping with that in other northern estuaries.

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Atlantic croaker (*Micropogonias undulatus*) is a commercial and sport fishery species that inhabits demersal habitats in estuarine, coastal, and continental shelf systems along the Atlantic coast of North America and in the Gulf of Mexico (Joseph, 1972). They spawn primarily over the continental shelf during a protracted spawning season that, based on the presence of larvae along the Atlantic coast, may extend from early July through March (Lewis and Judy, 1983; Cowan and Birdsong, 1985; Warlen and Burke, 1990; Hettler et al., 1997; Nixon and Jones, 1997; Able and Fahay, 1998). The exact location of spawning in the Middle Atlantic Bight (MAB) may be related to the areal extent of favorable warm bottom waters for spawning (Norcross and Austin, 1988) and may sometimes occur within or close to the mouth of Chesapeake Bay (Barbieri et al., 1994b; Reiss and McConaugha, 1999). The larvae and postlarvae have been observed to be more abundant in deeper layers of water that may facilitate transport into and retention within estuarine nursery areas (Weinstein et al., 1980; Norcross, 1991). The young-of-the-year (YOY) usually begin to enter estuaries and tidal creeks along the Atlantic coast in September, or occasionally August, and they are often common components of the fish fauna in tidal creeks and estuaries until fall of the next year from New Jersey southward along the Atlantic coast and in the Gulf of Mexico (Chao and Musick, 1977; Knudsen and Herke, 1978; Weinstein, 1979; Currin et al., 1984; Ross, 1988; Able and Fahay, 1998). In some years there is a second pulse of small YOY that arrives in estuaries along the Atlantic coast in the spring or summer; this pulse may be the offspring from later spawning (Chao and Musick, 1977; Ross, 1988). In general, the YOY use estuarine habitats with salinities ranging from almost pure freshwater to seawater (Miglarese et al., 1982).

Although YOY Atlantic croaker are present in some Atlantic coast estuarine habitats during the winter (Haven, 1957; Bearden, 1964; Dahlberg, 1972; Chao and Musick, 1977; Shenker and Dean, 1979; Bozeman and Dean, 1980; Able and Fahay, 1998), they appear to experience winter mortality in the MAB in years with unusually cold winters (Massman and Pacheco, 1960; Joseph, 1972; Chao and Musick, 1977; Wojcik, 1978). Recent laboratory studies have found that YOY Atlantic croaker do not survive in sustained water temperatures of 3°C or lower (Lankford and Targett, 2001); therefore extended periods of low winter water temperatures may have drastic effects on their overwinter survival in some estuaries.

Previous studies have indicated that YOY Atlantic croaker reach about 107–187 mm TL after their first year

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of growth in estuaries along the Atlantic coast and 102–250 mm TL in the Gulf of Mexico (Knudsen and Herke, 1978), but only a few studies have reported seasonal growth rates (Hansen, 1969; Knudsen and Herke, 1978). Length-frequency based growth rate estimates for the first year of growth for YOY along the Atlantic coast have ranged from 0.32 to 0.41 mm/d (Knudsen and Herke, 1978). However, these were based on the entire year, including the larval and early juvenile period when analysis of otolith daily growth rings indicates much slower growth rates of 0.18–0.41 mm/d during the fall and winter months (Nixon and Jones, 1997). Length-frequency data from estuarine nursery areas clearly indicate that most growth occurs during the spring and summer months (Haven, 1957; Chao and Musick, 1977; Ross, 1988; Able and Fahay, 1998).

Despite various studies of YOY Atlantic croaker in some areas of the Atlantic and Gulf coasts, there is relatively little known of their early life history near the northern part of their range in the MAB and this is especially true for Delaware Bay. Our four-year study used extensive collections in Delaware Bay and in adjacent tidal marsh creeks to describe the timing of Atlantic croaker ingress, their seasonal abundance and size, growth rates, and the timing of their egress out of the marshes.

## Methods

### Study sites

Delaware Bay is the estuary of the Delaware River and encompasses about 1878 km$^2$ of open water along the southern edge of New Jersey and the northern edge of Delaware (Fig. 1). It has a relatively deep area (10–30 m) in the middle of the lower bay, bordered by narrow shoals and flanked by extensive tidal flats and salt marshes, which contain an additional 85.5 km$^2$ of open water in tidal creeks bordered by approximately 640 km$^2$ of marsh-plain area. Depending on the amount of river discharge, salinities range from 30–31‰ at the mouth of the bay, to 1–10‰ in the lower Delaware River (Table 1; Cronin et al., 1962; Garvine et al., 1992).

### Ichthyoplankton survey

Catch data from an ichthyoplankton survey (Table 2) was used to analyze the distribution, abundance, and size of larval Atlantic croaker in Delaware Bay and the lower Delaware River from April to October 1996. Sampling was performed during daylight hours once a month in April and October and twice a month from May to September. Each sampling period included one tow at 70 randomly selected stations distributed among eight designated sampling zones (Fig. 1). Samples were collected with a 1-m diameter plankton net (0.5-mm mesh) deployed with a depressor in single stepwise oblique tows from the surface to the bottom. Tows were made at a speed of 1.4–1.9 knots for four to six minutes in the direction of the tidal flow. Up to 50 individuals were measured to the nearest millimeter total length (TL) from each sample.

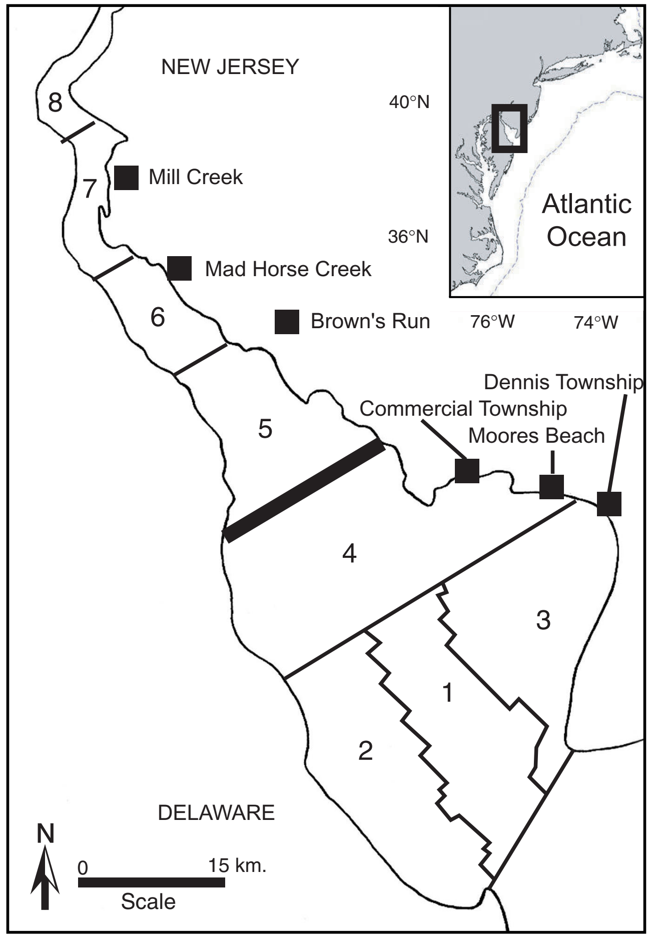


**Figure 1**

Locations of salt marsh tidal creek sampling sites (1996–99) and designated sampling zones (1–8) in the Delaware Bay and in the lower Delaware River for the ichthyoplankton (April–October 1996) survey and the otter trawl (April–October 1996–98) survey. The heavier line across the bay indicates the boundary between the upper (5–8) and lower (1–4) sampling zones and marsh sites.

### Otter trawl survey

We used catch data from a three-year otter trawl survey (Table 2) to analyze the distribution, abundance, and growth of settled YOY Atlantic croaker in Delaware Bay and the lower Delaware River. Sampling was performed during daylight hours twice a month from April to October in 1996 and once a month in 1997 and 1998, at 40 stations divided up among the same eight sampling zones of the ichthyoplankton survey (Fig. 1). Station locations were selected by using a stratified random sampling design from a grid of 1002 stations, excluding the stations over the deepest water near the mouth of the bay in zone 1. There were eight stations sampled each month in zone 3, six in zone 4, and four in all the other zones. Trawling was done with 4.9-m otter trawls (6 mm stretched codend mesh), made against the prevailing direction of the tide at a speed of 1.8 m/sec for 10 minutes. Up to 100 individuals were measured from each sample. For presentation

**Table 1**

Physical characteristics of marsh and adjacent bay study sites located along the New Jersey shore of Delaware Bay, 1996–99. See Figure 1 for locations of individual sites.

| Marsh site | Surface temp. range (°C) | Average surface temp. (°C) | Surface salinity range (‰) | Average surface salinity (‰) | Average surface dissolved oxygen (mg/L) |
|---|---|---|---|---|---|
| Upper bay | | | | | |
| Mill Creek | 5.0–29.0 | 19.5 | 0–8.4 | 2.8 | 7.4 |
| Mad Horse Creek | 0–31.0 | 19.2 | 0.7–23.0 | 9.1 | 6.3 |
| Browns Run | 7.0–31.3 | 20.5 | 0.2–14.0 | 7.0 | 5.4 |
| Bay | 7.0–28.0 | 20.2 | 1.5–17.8 | 10.2 | 6.3 |
| Lower bay | | | | | |
| Commercial Township | 8.0–30.0 | 19.8 | 4.5–22.9 | 17.0 | 6.8 |
| Upper Moores Beach | 2.0–30.0 | 18.7 | 10.0–23.8 | 17.2 | 6.2 |
| Lower Moores Beach | 5.0–29.0 | 19.0 | 4.0–25.0 | 18.9 | 7.0 |
| Dennis Township | 6.0–32.0 | 20.4 | 6.2–24.7 | 17.0 | 5.7 |
| Bay | 6.0–29.1 | 19.6 | 11.1–24.7 | 17.8 | 7.3 |

**Table 2**

Yearly catch per unit of effort (CPUE=number of fish per tow or weir set) for the different types of gear in the marsh creeks or in Delaware Bay and the total number of Atlantic croaker collected by each type of gear. RUMFS = Rutgers University Marine Field Station; EEP = Public Service Enterprise Group Estuary Enhancement Program.

| | 1996 CPUE | 1997 CPUE | 1998 CPUE | 1999 CPUE | Total number of tows/sets | Total number of fish | Source |
|---|---|---|---|---|---|---|---|
| Marsh creeks | | | | | | | |
| Otter trawl (creeks) | 2.4 | 3.8 | 19.1 | 3.9 | 4,654 | 36,295 | RUMFS |
| Otter trawl (bay) | 164.6 | 15.3 | 29.3 | 49.5 | 336 | 12,755 | RUMFS |
| Weir | 1.1 | 41.6 | 46.8 | 98.7 | 443 | 20,714 | RUMFS |
| Delaware Bay | | | | | | | |
| Otter trawl | 4.6 | 2.8 | 19.7 | — | 1,438 | 13,497 | EEP |
| 1-m plankton net | 1.7 | — | — | — | 957 | 1,638 | EEP |
| Total fish | 8,671 | 12,350 | 43,942 | 19,936 | 7,828 | 84,899 | |

and statistical analysis of some aspects of the data of the ichthyoplankton and otter trawl surveys in the bay, the upper four zones were combined into an upper bay region and the lower four combined into a lower bay region (Fig. 1).

## Marsh creek survey

Tidal creek sampling was carried out at six salt marsh sites on the New Jersey side of Delaware Bay (Fig. 1, Table 1). Dennis Township, Commercial Township, and Moores Beach will be referred to collectively as the lower bay sites, and Browns Run, Mill Creek, and Mad Horse Creek will be referred to as the upper bay sites. The average depth of the trawling stations (1.3–2.6 m) and Secchi depth values (0.3–0.4 m) were similar at all sites. The upper bay sites in the mostly oligohaline region of the bay had average salinities of 2.8–9.1‰ and the lower bay sites were in the mesohaline region with average salinities of 17.0–18.9‰ (Table 1).

We sampled each of the marshes (Fig. 1) monthly from April through November 1996–99 (Table 2). Small intertidal marsh creeks were sampled with weirs set at high tide and hauled at low tide, approximately six hours later. Each weir (2.0 m × 1.5 m × 1.5 m, with 5.0 m × 1.5 m wings, 6.0-mm stretched mesh) consisted of a funnel-shaped net stretched across the channel with wings extended back onto the marsh surface from each end of the net. In cases when the creek did not drain completely the area in front of the weir was seined into the weir.

Trawling in larger intertidal to subtidal marsh creeks took place around high tide and consisted of four replicate two-minute tows per station, made against the current with a 4.9-m otter trawl (6-mm stretched codend mesh) towed at a constant engine RPM of 2500. Trawling station locations at each site were designed to sample fishes along the mouth to upper creek gradients (see Able et al., 2000; 2001; Able et al.[1]). Thus, at each of the marshes there were six trawling locations. These locations included two large subtidal creeks and two smaller creeks with lower subtidal and upper subtidal or intertidal sections in each of the latter. Additional trawling locations were established in the bay immediately outside the mouth of the large creek at the Dennis Township, Moores Beach, Commercial Township, and Mad Horse Creek study sites (Fig. 1). The fish collected at these bay stations were used in the length-frequency figures for the bay (exclusive of November when there was no trawl survey sampling in the bay) and for the growth calculations, but not in the catch-per-unit-of-effort (CPUE) calculations for the bay. Atlantic croaker collected in each weir set and in each trawl were enumerated, and up to 50 individuals per weir set and 20 per trawl were measured to the nearest millimeter total length. Abundances (CPUE, number of fish per trawl) were compared between the upper and lower bay sites in Delaware Bay, among the six different marsh sites, and among years, by using the nonparametric Mann-Whitney *U*-test, or the Kruskal-Wallis ANOVA of ranks for multiple comparisons, and when differences were found, the Dunnís test was used (criteria for significance: $P<0.05$) to make pair-wise comparisons.

Physical variables were measured at the end of each weir and otter trawl sample in the marshes and in Delaware Bay (Table 1). Temperature, salinity, and dissolved oxygen concentrations were measured with a hand-held salinity, temperature, and oxygen meter (YSI Model 85), by lowering the probe into the water and recording surface values. Water transparency was measured by lowering a Secchi disc into the water column until it was no longer visible and recording the corresponding depth in 0.1-m increments.

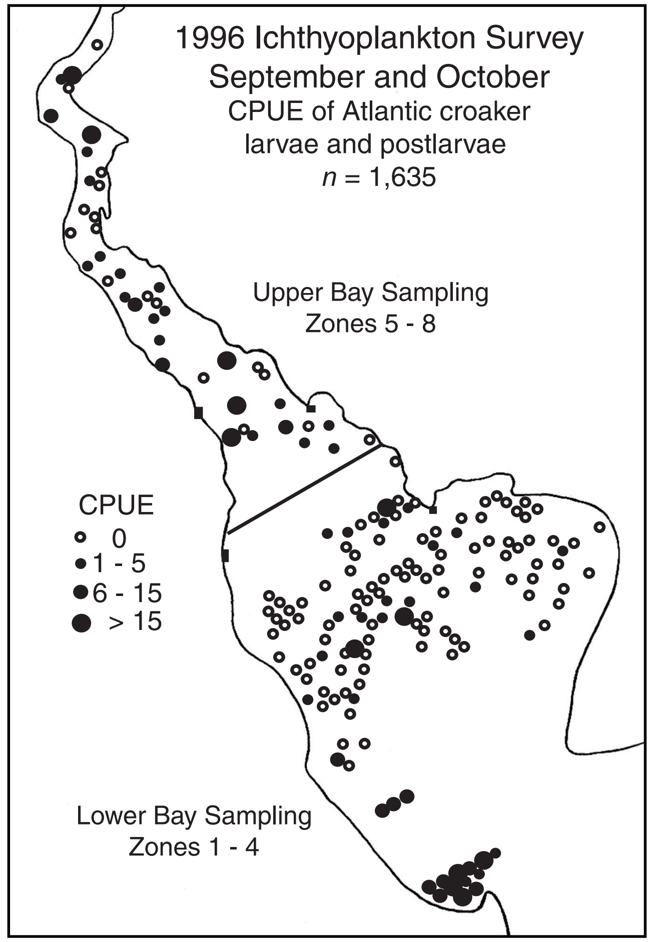


**Figure 2**

Catch per unit of effort (CPUE) of larval and postlarval Atlantic croaker (*Micropogonias undulatus*) collected in the ichthyoplankton survey in September and October 1996.

## Growth

Growth rates for YOY Atlantic croaker were calculated for samples collected during the late spring through fall in the upper and lower regions of the bay in 1997 and 1998 and in the upper and lower bay marsh sites during 1997, 1998, and 1999. We compared growth using the progression of the monthly median lengths in each area by computing the change in the median length of a cohort over a time period divided by the number of days in the period. This method was based on the following assumptions: 1) no new (small) recruits join the population during the calculation interval, and 2) no (large) individuals leave the population over the calculation interval. To best meet these assumptions, median growth rates were calculated by using the monthly length data from May to July when there was a minimum of movement of fish between different areas, and then for longer-term monthly comparisons, from May to August, September, and October when fish were moving out of the marshes into the bay. The smaller-size cohort present in the bay in June and July 1998 and in the marshes in 1999 was excluded from the growth calculations for those years. The linearity of the progression of median lengths was tested by using linear regression, and the resulting lines were compared between the upper and lower bay.

[1] Able, K. W., D . M. Nemerson, and T. M. Grothues. In review. Evaluating salt marsh restoration in Delaware Bay: continued analysis of fish response at former salt hay farms.

## Results

### Distribution, abundance, and size during fall ingress and settlement

Atlantic croaker larvae were collected only in the late summer and fall during the ichthyoplankton survey in Delaware Bay in 1996 (Figs. 2 and 3). A few individuals were first collected in August ($n$=3, CPUE=0.02 fish/tow), and then large numbers of larvae were collected through September ($n$=639, CPUE=3.6) and October ($n$=996, CPUE=9.0), but they were absent from April to July. The overall September–October CPUE was 9.0 fish/tow (range:

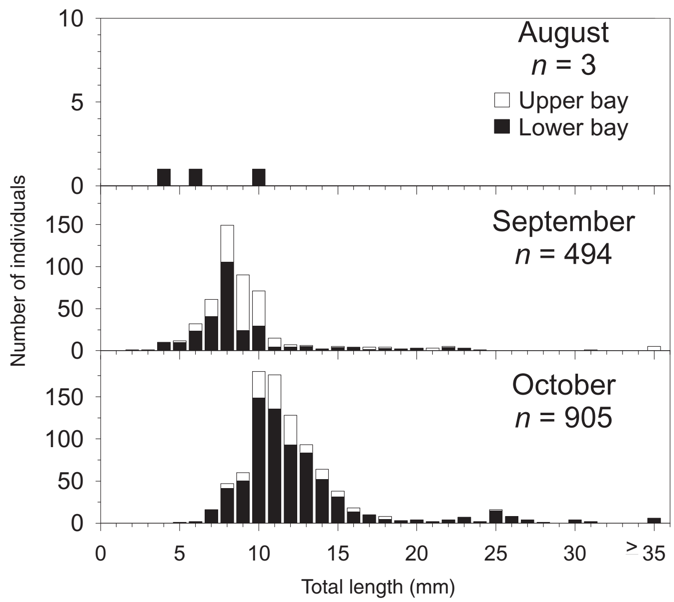


**Figure 3**

Length-frequency distributions of larval and postlarval Atlantic croaker (*Micropogonias undulatus*) collected in the upper and lower regions of Delaware Bay during the ichthyoplankton survey in 1996.

0–56) in the upper bay zones 5–8 and 4.9 (range: 0–36) in the lower bay zones 1–4 (Figs. 1 and 2), and these CPUE values were significantly different between zones ($P$=0.03). At least one individual was collected in each of the eight zones in both September and October; the highest two-month combined CPUE occurred in the uppermost zone 8 (CPUE=13.4), followed by zone 5 (CPUE=9.6), and the lowest occurred in zone 3 (CPUE=0.1). Larvae were 4–10 mm during August (all in zone 2), predominantly 2–24 mm in September, and 5–28 mm in October (Fig. 3)—the smallest individuals being caught in the lower bay.

Benthic YOY Atlantic croaker of a variety of sizes first appeared in substantial numbers in September in the otter trawl surveys in both the bay (Fig. 4) and marshes (Fig. 5) at lengths >5 mm, and with modes of 15–30 mm for the primary cohort. Exceptions occurred in the bay in 1997, when they were not collected by the trawl survey until October and when they were not collected during September at two of the three upper bay marsh sites each year.

The CPUE of benthic YOY Atlantic croaker was usually highest during October in the lower bay marshes (Fig. 6). This pattern of abundance is illustrated by the much higher four-year overall CPUE of recently ingressed YOY, especially at Dennis Township, Commercial Township, and Upper Moores Beach (Fig. 7). The combined four-year CPUE values were significantly different ($P$<0.001) at each of the six sites, and the CPUE values at the Dennis Township site were significantly greater than at all the sites except for Commercial Township. Similarly, Commercial Township was different from all sites except Dennis Township and Upper Moores Beach, and Upper Moores Beach also was different from Browns Run in the upper bay.

Recently settled YOY Atlantic croaker were also caught in the weirs in small intertidal marsh creeks during September, October, and November in all three years; the majority were collected at the Dennis Township marsh in the lower bay (Fig. 8). The monthly CPUE (fish per set) in the weirs at Dennis Township was greatest in October 1997 and November 1999 (the weirs were not in place until October 1996) and the largest total number was collected during 1999. The combined four-year CPUE values for 1996–99 at each of the six sites were significantly different ($P$<0.001), and the CPUE values at the Dennis Township site were significantly greater than those at all the sites, except Commercial Township.

The monthly CPUE values during ingress in the bay also were highest in October, but in contrast to the marsh sites were usually higher in the upper part of the bay (Fig. 6). The combined CPUE values for September and October were significantly different between the upper and lower bay regions in 1998 ($P$<0.001) and 1997 ($P$=0.048), but not in 1996 ($P$=0.51). The combined CPUE values for September and October for each year (1996–98) were significantly different among years ($P$<0.001) and were different between 1996 and 1997, and between 1996 and 1998.

A second, smaller cohort of YOY Atlantic croaker appeared in the bay in June and July 1998 and in the tidal

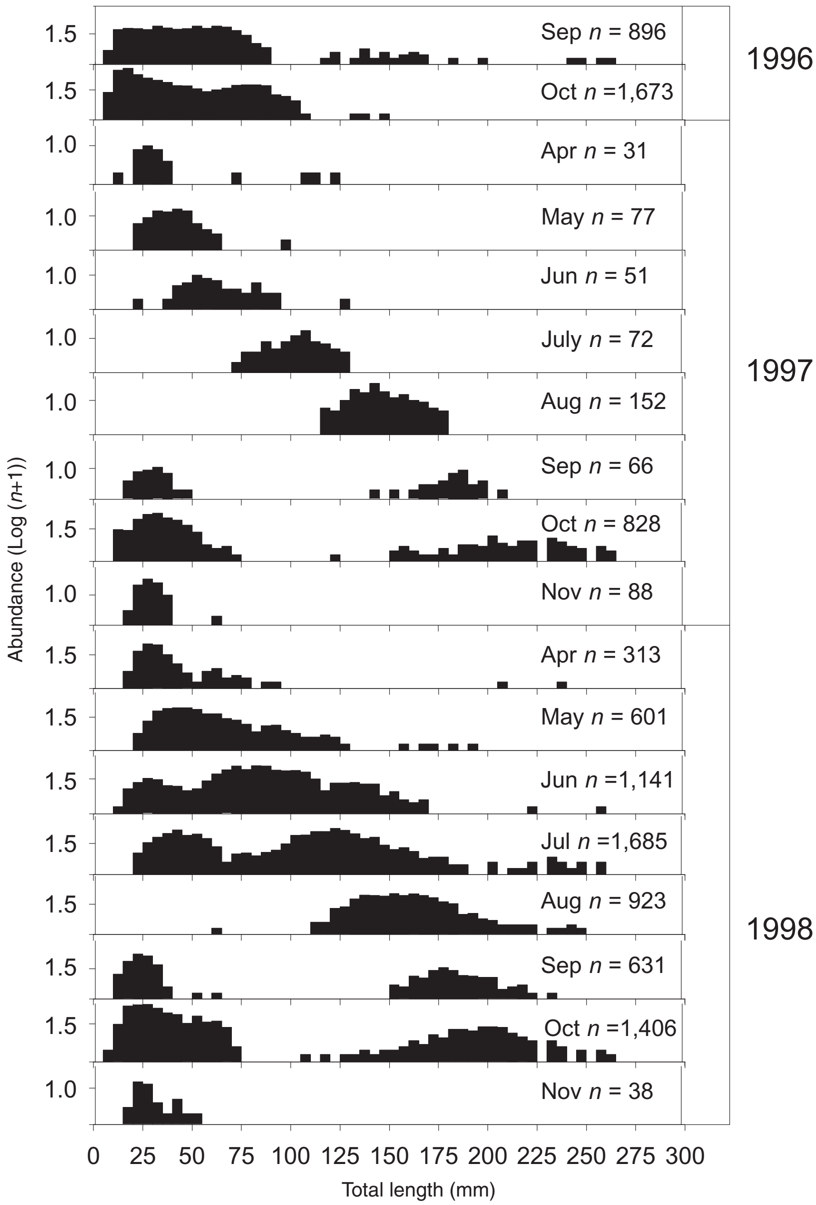


**Figure 4**

Length-frequency distributions of log ($n$+1) transformed numbers of Atlantic croaker (*Micropogonias undulatus*) collected by otter trawl between April and November in Delaware Bay from 1996 to 1998. None were collected in the bay from April to August of 1996.

creeks in June 1999 (Fig 4). In the bay these were as small as 15 mm in June 1998 and had a mode of 26–30 mm. They were even more abundant in the bay during July 1998 and had a mode of 41–45 mm. Individuals of this cohort were collected at five of the eight zones in the bay during June and July but were rare in subsequent months (Fig. 4). A smaller size cohort of YOY ($n$=69 fish) also appeared in the marshes (Fig. 5) and in the associated bay stations in June 1999.

## Distribution, abundance, and habitat use during summer residency

Young-of-the-year Atlantic croaker were abundant in Delaware Bay and in the adjacent marsh creeks from April through the fall egress of each year, except in 1996, when trawling in both the marshes and the bay caught no YOY until 26 individuals (115–200 mm) were collected in the bay in September and October (Fig. 4). In contrast, the

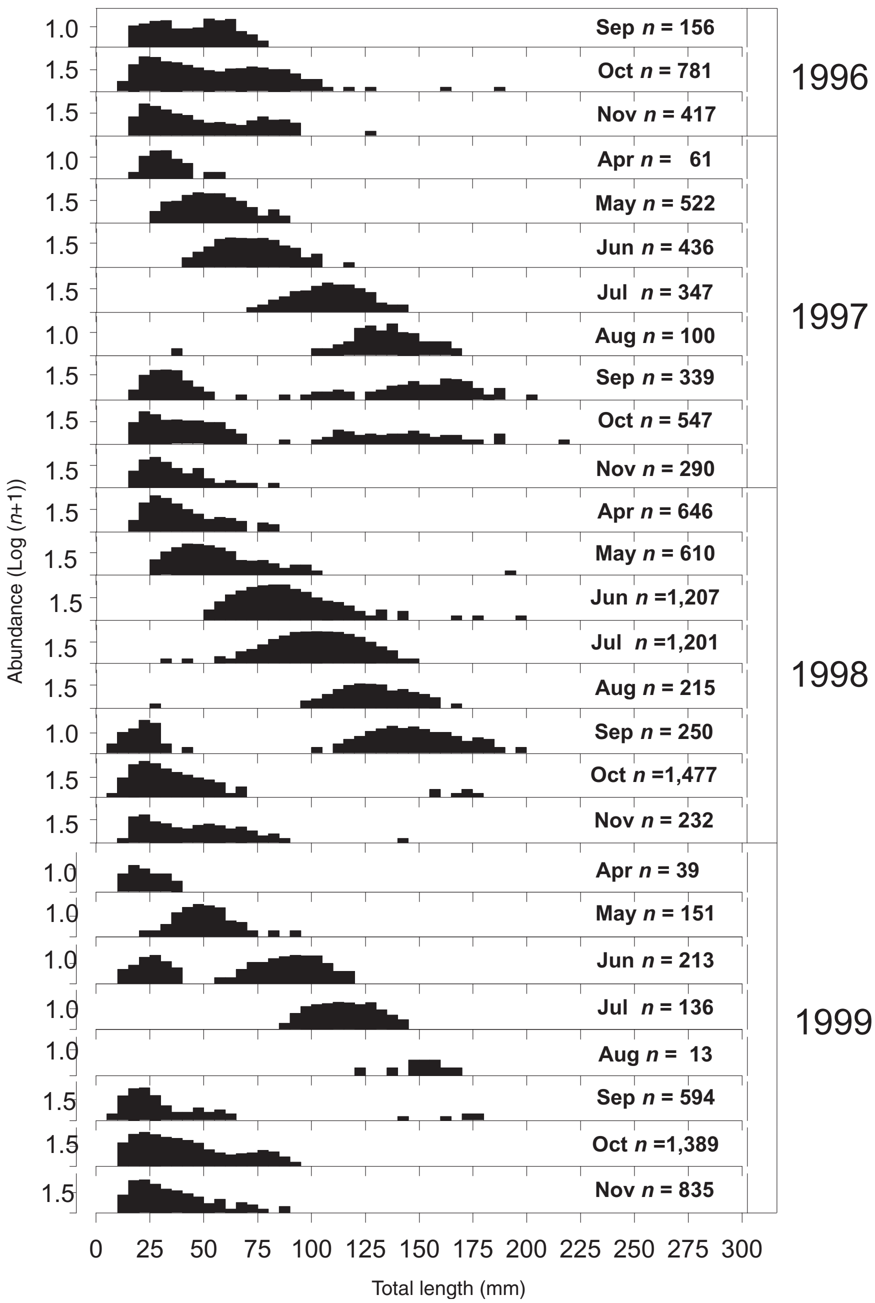


**Figure 5**

Length-frequency distributions of log ($n$+1) transformed numbers of Atlantic croaker (*Micropogonias undulatus*) collected by otter trawl (April to November) in salt marsh creeks along the northern shore of Delaware Bay from 1996 to 1999. None were collected in the marshes from April to August of 1996.

marsh creek surveys found YOY in both the large and small creeks from April to September during 1997, 1998, and 1999. Typically in the years after 1996, the CPUE was greatest from April to June at the lower bay marsh sites and then decreased after July to an almost total absence of fish toward the end of the fall egress out of the marshes in November (Fig. 6). The overall CPUE at each marsh site for all three year classes combined (April to November in 1997, 1998 and 1999) was highest at Dennis Township and Commercial Township and at Upper Moores Beach in the lower bay and lowest at Lower Moores Beach and at the upper bay sites (Fig. 7). As a result, the monthly

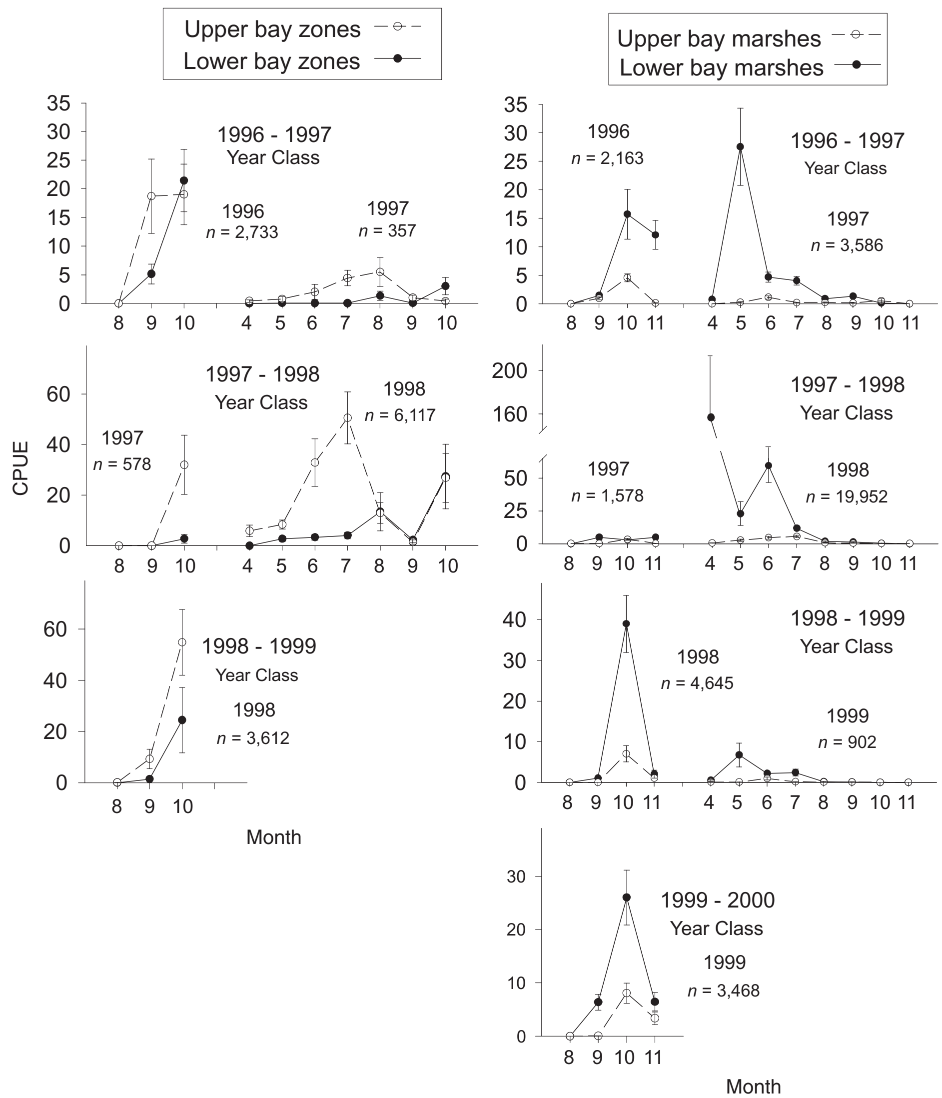


**Figure 6**

Monthly average catch per unit of effort (CPUE ±SEM) of young-of-the-year Atlantic croaker *(Micropogonias undulatus)* collected by otter trawl during the fall ingress and from April to November for three year classes in the upper and lower regions of Delaware Bay (left panels: CPUE=fish/10 min. tow) and of four year classes in tidal creeks at the upper and lower bay marsh sites (right panels: CPUE=fish/2 min. tow). No data are presented from April to July of 1996 because Atlantic croaker were absent from the bay and marshes until October.

CPUE at the lower bay marshes was consistently more than twice as high as that in the upper bay (Fig. 6). The combined four-year CPUE values for YOY caught during April–October 1997–99, at each of the six sites were significantly different ($P<0.001$), and the CPUE values at the Dennis Township site were significantly greater than at each of the other sites. The CPUE values at Commercial Township and Upper Moores Beach in the lower bay also were greater than those at all the upper bay sites.

Young-of-the-year Atlantic croaker also used small intertidal creeks in the marshes from April to August, where they were collected in weirs. They were most abundant at the Dennis Township site in the lower bay in all three years where they were present from May to July in 1997 and from April to August in 1998, 1999 (Fig. 8). The monthly CPUE (fish per set) in the weirs at Dennis Township was greatest in June of both 1997 and 1998. Compared to the total catch in the weirs at Dennis Township in all three years ($n$=3994), far fewer were caught in the weirs at the other sites in the lower bay during all three years ($n$=152) and fewer still at the sites in the upper bay ($n$=9). The CPUE of YOY Atlantic croaker in Delaware

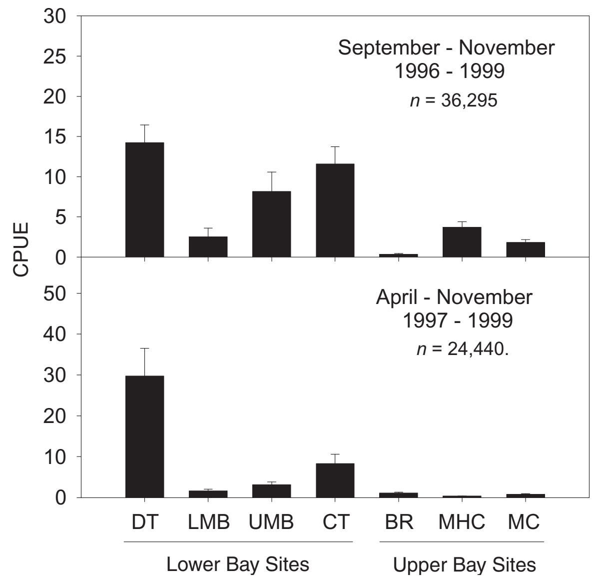


**Figure 7**

Combined overall average catch per unit of effort (CPUE= fish/2 min. tow [±SEM]) of young-of-the-year Atlantic croaker (*Micropogonias undulatus*) collected by otter trawl at the Dennis Township (DT), Lower Moores Beach (LMB), Upper Moores Beach (UMB), Commercial Township (CT), Browns Run (BR), Mad Horse Creek (MHC) and Mill Creek (MC) marsh sites during the fall ingress of four years (1996–99) and of post-ingress croaker (April to November 1997–99).

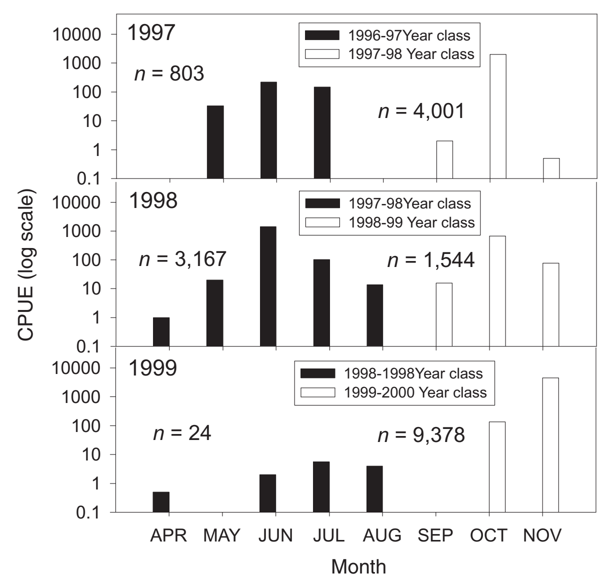


**Figure 8**

Catch per unit of effort (CPUE, fish/set) of four year classes of young-of-the-year Atlantic croaker *(Micropogonias undulatus)* caught each year in the two monthly weir sets across small intertidal creeks at the Dennis Township marsh site in the lower bay during the fall ingress (white bars) and during spring and summer of the following year (black bars).

Bay was higher in the upper bay, which has mud sediments in most areas, and was much higher in 1998 than in 1997. The monthly CPUE in the upper bay peaked in July or August, but in the lower bay it peaked in October of both years (Fig. 6). The combined CPUE values in the upper and lower bay zones were different between the two regions in both 1997 and 1998 ($P<0.001$) and the catches within each region were different between the two years ($P<0.001$).

During the summer most YOY were collected in areas of Delaware Bay that had muddy sediments (Fig. 9). In the upper bay zones 7 and 8, which likely have mostly pure mud sediments, YOY were collected at 82% of the stations. In contrast, they were absent in the deeper, large central area of the lower bay that has predominantly sandy and gravelly sediments. However, in the shallow portion of the lower bay, sandy mud, muddy sand, and gravelly mud sediments appear to be distributed on both sides of the bay, and YOY were almost exclusively collected over or near these substrates from April to August.

## Growth

Although YOY Atlantic croaker showed rapid growth during the summer, there was no evidence of growth during the winter. The median growth rates for YOY Atlantic croaker calculated for two- to five-month periods beginning in May were fast and ranged from 0.5 to 1.5 mm/d (Table 3). They were slightly higher in the bay than in the marshes (avg.=1.2 mm/d in the bay and 0.9 mm/d in the marshes) and were lowest in 1998 when Atlantic croaker were most abundant. The growth rates dropped off in the marshes when calculated from May to September or October (Table 3). The lowest early summer growth rates occurred in the tidal creeks in the lower bay in 1998 when the CPUE was the highest. The growth rates in the upper and lower regions of Delaware Bay were similar in each year, but as in the lower bay marshes, the values were lower in 1998 when YOY were much more abundant. Linear regressions of the median lengths used to calculate these growth rates showed that median length was strongly correlated to date ($P$=0.02–0.001) and illustrated the slightly slower growth rates at the lower bay sites in both 1997 and 1998 (Fig. 10). These pairs of regression lines were not significantly different (ANCOVA) for upper and lower bay regions of either the marsh sites in 1997 ($P$=0.1), or in the bay in 1998 ($P$=0.6), except in 1998, when a lower growth rate was indicated at the lower bay marsh sites ($P$=0.03). In 1999, a similar linear progression of median lengths was observed in the lower bay marshes ($r^2$=0.98), but sample sizes were too small in the upper bay for growth-rate calculations. Although there was no sampling in the winter, the length-frequency distributions indicated that most fish collected in April in the bay and marshes were the same

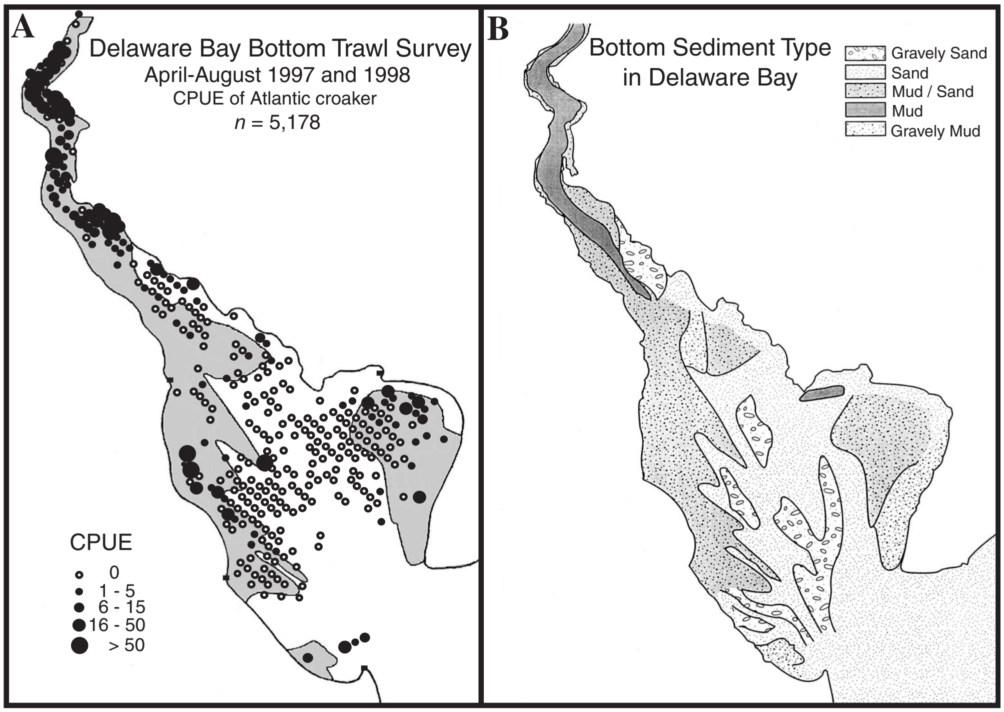


**Figure 9**

(**A**) Catch per unit of effort (CPUE=fish/10 min. tow) of young-of-the-year Atlantic croaker *(Micropogonias undulatus*) collected by otter trawl (April to August in 1997 and 1998). Sediments containing mud are indicated by shading. (**B**) The distribution of specific bottom sediment types in Delaware Bay is modified from Sharp (personal commun. [J. H. Sharp. Marine Studies, Univ. Delaware, Lewes, DE.]).

size or smaller than the ingressed fish collected during the previous fall of all three years (Figs. 4 and 5).

Consistent with the above fast growth rates, YOY Atlantic croaker reached lengths of about 70–140 mm by July and lengths ranging from 90 to 170 mm by August in the marshes and slightly larger in the bay (Figs. 4 and 5). As a result of these fast growth rates, the YOY attained a size of approximately 125–250 mm by September, approximately 12 months after ingress into the bay and adjacent marshes, and were distinctly larger than the next year class that began ingressing during September of each year.

### Egress

Young-of-the-year Atlantic croaker showed a relatively consistent pattern of egress out of the marsh creeks in the late summer and fall of each year, and as a result, there was an increase in CPUE in the bay during October of both years. The monthly CPUE in both upper and lower bay marshes declined during the summer and were low by August in all three years (Fig. 6), but the number of fish present appeared to drop off more rapidly from August to October in 1999 than in other years (Figs. 5 and 6). In the bay, CPUE began to decrease somewhat later, after July or August, but then increased to the yearly maximum for the lower bay in October 1997 and 1998. By November of each year, almost all YOY appeared to move out of the marshes at sizes <200 mm, but in the bay there were large individuals >250 mm caught in October 1997 and 1998. The baywide trawling survey did not provide samples in November, so it was impossible to determine the timing of egress of the remaining YOY out of the bay, but very few age-1 fish were present in the bay or marshes by spring of the next year.

## Discussion

### Ingress and settlement

Young-of-the-year Atlantic croaker ingress into bay and marsh nursery areas starting in the fall of each year in Delaware Bay and in other estuaries along the Atlantic coast. The majority appeared in September, October, and November during our study and in previous collections in Delaware Bay (Able and Fahay, 1998), Chesapeake Bay (Haven, 1957; Chao and Musick, 1977), and North Carolina (Ross, 1988). However, the fall ingress of this cohort was not evident until October in Georgia (Dahlberg, 1972) and December in South Carolina (Bearden, 1964). The sudden appearance of significant numbers of larger fish (50–75 mm) in September 1996 in both the bay and marshes and to some extent in the marshes in 1999 suggests that individuals that experienced different growth rates or came from different spawning events sometimes occurred simultaneously in Delaware Bay.

**Table 3**

Estimated daily growth rates of young-of-the-year Atlantic croaker *(Micropogonias undulatus)* based on the monthly progression of median lengths in the upper and lower regions of Delaware Bay in 1997 and 1998 (see Fig. 1) and in tidal creeks in the marsh sites adjacent to the upper and lower bay in 1997, 1998, and 1999. Growth rate calculations were made for periods of two to five months, with each period starting in May. Calculations for locations with sample sizes <10 fish were excluded.

| Habitat | Year | Location in bay | Average collection date | Sample size | Median length (mm TL) | Median growth rate (mm/d) |
|---|---|---|---|---|---|---|
| Delaware Bay | 1997 | Upper bay | 17 May | 25 | 33 | — |
| | | | 7 July | 71 | 103 | 1.37 |
| | | | 5 Aug | 88 | 143 | 1.38 |
| | | | 2 Sep | 16 | 183 | 1.39 |
| | | | 2 Oct | 10 | 190 | 1.14 |
| | | Lower bay | 26 May | 52 | 43 | — |
| | | | 16 Aug | 64 | 154 | 1.35 |
| | | | 20 Sep | 14 | 187 | 1.23 |
| | | | 4 Oct | 96 | 218 | 1.34 |
| | 1998 | Upper Bay | 13 May | 275 | 41 | — |
| | | | 15 Jul | 873 | 121 | 1.27 |
| | | | 10 Aug | 433 | 144 | 1.16 |
| | | | 6 Sep | 45 | 177 | 1.17 |
| | | Lower Bay | 15 May | 326 | 57 | — |
| | | | 19 Jul | 220 | 140 | 1.28 |
| | | | 16 Aug | 490 | 164 | 1.15 |
| | | | 10 Sep | 131 | 182 | 1.06 |
| Marsh Creeks | 1997 | Upper Bay | 21 May | 17 | 46 | — |
| | | | 17 Jul | 13 | 115 | 1.21 |
| | | | 20 Aug | 16 | 154 | 1.19 |
| | | | 14 Oct | 33 | 120 | 0.51 |
| | | Lower Bay | 26 May | 505 | 52 | — |
| | | | 23 Jul | 334 | 110 | 1.00 |
| | | | 26 Aug | 84 | 132 | 0.87 |
| | | | 21 Sep | 99 | 161 | 0.92 |
| | | | 19 Oct | 13 | 150 | 0.67 |
| | 1998 | Upper Bay | 8 May | 142 | 41 | — |
| | | | 8 Jul | 348 | 115 | 1.21 |
| | | | 5 Aug | 41 | 143 | 1.15 |
| | | | 2 Sep | 23 | 153 | 0.96 |
| | | Lower Bay | 13 May | 467 | 50 | — |
| | | | 14 Jul | 851 | 100 | 0.81 |
| | | | 11 Aug | 174 | 125 | 0.83 |
| | | | 9 Sep | 126 | 142 | 0.77 |
| | 1999 | Lower Bay | 18 May | 148 | 49 | — |
| | | | 18 Jul | 128 | 114 | 1.07 |
| | | | 15 Aug | 12 | 151 | 1.15 |

According to the sizes of individuals captured by plankton net in the water column, versus those collected by otter trawl on the bottom, settlement may occur over a broad size range, i.e. approximately 10–40 mm TL. Scale formation in Atlantic croaker begins at 14–16 mm SL and is completed at 31–38 mm SL during this time (Bridges, 1971) and is an indicator of transformation between larval and juvenile stages. Alternatively, collection of overlapping sizes in water column and bottom samples may imply frequent vertical movements as could occur during tidal stream transport (see Weinstein et al., 1980, for recent examples). These movements would provide an appropriate mechanism for small YOY to reach the bay and the lower Delaware River as has been suggested for larval Atlantic croaker in Chesapeake Bay (Norcross, 1991).

The length-frequency data from our study and from previous studies along the Atlantic coast indicate that a second, less-abundant cohort of YOY Atlantic croaker often enter nursery areas during the spring and summer. This second cohort (between 10 and 45 mm) was observed in June 1998 and 1999 during our study and in May or August (20–30 mm) in the York River of the Chesapeake Bay (Chao and Musick, 1977). Similarly, a second mode was usually apparent from April through August during three years in North Carolina creeks and bays (Ross, 1988), and in May in Georgia (Dahlberg, 1972). In South Carolina, a second smaller cohort began appearing in March and subsequently became the dominant mode in June and July (Bearden, 1964). In addition, the larger-size individuals that have appeared during the fall months simultaneously with the ingressing fall cohort during our study and in the Chesapeake Bay (Haven, 1957; Chao and Musick, 1977), may be individuals of this late-arriving second cohort that did not enter the Chesapeake and Delaware bays until fall.

These late arrivals to nursery areas in the Chesapeake and Delaware bays may be individuals that were spawned close to or south of Cape Hatteras in late winter because there is no evidence of spawning in late winter or spring north of Cape Hatteras in the MAB. Atlantic croaker larvae were caught only from August to January 1977–1987 over the continental shelf in the MAB and while entering estuaries in central New Jersey (Able and Fahay, 1998), or from November to February in coastal Virginia (Cowan and Birdsong, 1985). In contrast, just south of Cape Hatteras, larvae as small as 5.2 mm SL were present in collections made from October through mid-April within and offshore of the Newport River estuary in North Carolina in both 1972–73 and 1973–74 (Lewis and Judy, 1983). Small larvae also were collected in the same estuary from November through mid-April in 1985–1986 (Warlen and Burke, 1990) and 1991–92 (Hettler et al., 1997) and in the Cape Fear estuary from mid-March to Mid-April in 1978 (Weinstein et al., 1980). Together, these studies indicate that late winter spawning occurs and suggests that it takes place south of Cape Hatteras. Analysis of otolith microstructure of larval and juvenile Atlantic croaker from the MAB indicates that later spawned larvae and juveniles have slower growth rates (Warlen, 1982; Nixon and Jones, 1997), which may account for the much smaller size of the later-arriving cohort when it enters the Chesapeake and Delaware bays during the late spring and early summer.

Ross (1988) suggested that there may be two groups of Atlantic croaker that overlap and mix in North Carolina. The first group, occurring from North Carolina southward through the northern Gulf of Mexico, with a tendency toward high mortality, lower longevity, early maturation, results from winter spawning (White and Chittenden, 1977; Barger, 1985) and mostly spring recruitment to estuaries. The second group ranges from North Carolina to about New Jersey and may exhibit lower mortality, higher longevity, greater size at age, late summer–fall spawning, mostly fall recruitment, and greater size at maturity (Wallace, 1940; Morse, 1980; Barbieri et al., 1994a). However, the group of larger, older Atlantic croaker observed by Ross (1988) apparently has been absent in Chesapeake Bay in recent years (Barbieri et al., 1994b). Lankford et al. (1999) did not find statistically significant genetic differences between fall-spawned YOY Atlantic croaker from north of Cape Hatteras and spring-spawned YOY from south of Cape Hatteras, but YOY from the Gulf of Mexico were genetically discrete from those from the Atlantic coast. This lack of marked genetic differences north and south of Cape Hatteras is not surprising if there is southward migration of adults from the MAB during winter as has been suggested (Haven, 1957). Although, spawning and recruitment to nursery areas does appear to occur later in the South Atlantic Bight (Bearden, 1964) and in the Gulf of Mexico (Pearson, 1929; Suttkus, 1955; Hansen, 1969), more research is needed to determine if there are significant biological differences between adults in these two areas and if the late arriving YOY in the north originate from spawning at or south of Cape Hatteras.

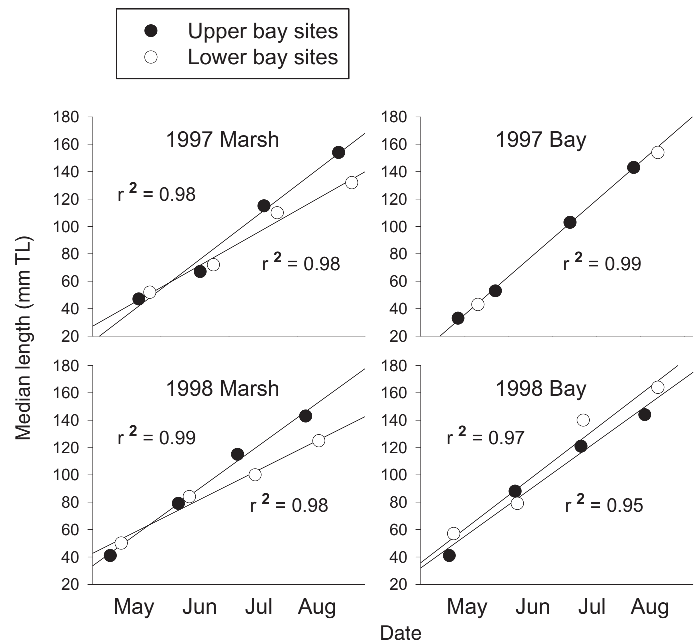


**Figure 10**

Linear regressions and goodness-of-fit measures of the monthly median total lengths of young-of-the-year Atlantic croaker (*Micropogonias undulatus*) caught at the upper bay (open circles) and lower bay (black circles) marsh sites and regions of Delaware Bay from May to August in 1997 and 1998 (see Table 3). The coefficient of determination is shown in the upper left for the upper bay regression lines and in the lower right for the lower bay. There is no regression for the lower bay because sample sizes in this region during June and July of 1997 were too small.

## Habitat use

Young-of-the-year Atlantic croaker in this study used the entire range of marsh creek habitats, i.e. small intertidal creeks and large subtidal creeks within the study area. Intensive tag and recapture studies in marsh creeks at the Dennis Township site found that YOY were resident for periods of up to 78 days from July through October 1998 (Miller and Able, 2002). As a result, our interpretations of habitat use and growth may be representative for much of the summer and fall in Delaware Bay marsh creeks.

In the deeper water of the bay, YOY were collected throughout the whole range of salinities but were most abundant over the predominantly pure mud sediments in the lower Delaware River and over areas with mud sediments elsewhere in the lower bay. This pattern is evident elsewhere because YOY have been reported to be most abundant over soft mud sediments in Apalachicola Bay in the Gulf of Mexico (Kobylinski and Sheridan, 1979). As in Delaware Bay, YOY have been collected over the full range of salinities in South Carolina (Bearden, 1964; Miglarese et al., 1982) and Georgia (Dahlberg, 1972). However, laboratory experiments suggest that lower salinities are metabolically less costly for YOY (Moser and Gerry, 1989; Peterson et al., 1999) and that in some areas of Chesapeake Bay, YOY are most abundant in regions with low salinities (<18‰) (Haven, 1957).

Habitat use and survival in the winter may vary between estuaries. Young-of-the-year Atlantic croaker appear to overwinter in estuaries in the Gulf of Mexico (Pearson, 1929; Suttkus, 1955; Hansen, 1969; Knudsen and Herke, 1978) and in the South Atlantic Bight (Bearden, 1964; Dahlberg, 1972; Bozeman and Dean, 1980), but in the MAB there is probably significant overwinter mortality in years with particularly cold winters. The YOY appear to overwinter in some estuarine habitats in the York River region of Chesapeake Bay in most years (Haven, 1957; Chao and Musick, 1977) and in deeper areas of the bay (Welsh and Breder, 1923), but in some years YOY have been observed to experience winter mortality based on their subsequent disappearance after a cold period (Massman and Pacheco, 1960) and on direct observations of mass mortalities and collections of dead YOY in years with unusually cold winters (Joseph, 1972; Chao and Musick, 1977, Wojcik, 1978). Further, analysis of long-term recruitment indices for Atlantic croaker from 1979 to 1993 indicates that the YOY of this species may have experienced winter mortality due to low water temperatures in 30% of the years in Chesapeake Bay and 74% of the years in Delaware Bay (Lankford and Targett, 2001).

Overwintering mortality apparently occurred in Delaware Bay in 1996 when water temperatures in the region dropped below 3°C and remained below 4°C for an extended period of time. The NOAA Buoy 4409, located in the ocean just south of the mouth of Delaware Bay, recorded water temperatures at about 2–4°C for 18 days during January and February 1996, which is at or below the approximate survival temperature of 3°C determined in laboratory experiments (Lankford and Targett, 2001). This apparently resulted in a total absence of YOY throughout the bay and in marsh creeks during the spring and summer, which is not surprising because temperatures in the estuary were likely cooler than in the ocean. In contrast, during the winters preceding the relatively high catch years of 1997 and 1998, water temperatures at the same location never dropped below 4.4°C during the winter of 1996–97 or below 5.6°C during 1997–98.

## Growth

Growth rates that we calculated in both upper and lower regions of the Delaware Bay (two years) and in the marshes (three years) ranged from about 0.8 to 1.4 mm/d from May to July. The strong linear correlation between median length and date suggested that the average growth rates were relatively constant during the summer from May to August before egress from marshes. Seasonal growth rates of YOY Atlantic croaker in other estuaries along the Atlantic coast may be similar to those in Delaware Bay, but the way in which they were calculated influences the values. Knudsen and Herke (1978) reviewed the apparent growth rates of YOY Atlantic croaker from a variety of sources but presented growth rates only for the entire first year of growth, which were all less than 0.5 mm/d for studies along the Atlantic coast and in the Gulf of Mexico. However, these estimates included both larval and overwintering periods; therefore they probably underestimated the growth rates during the summer when growth rates are highest. Monthly modal progression in published lengths indicate relatively fast growth rates during the summer in estuarine areas south of Delaware Bay. Our calculation of modal progression in lengths from May to July in various parts of the York and Pamunkey rivers of Chesapeake Bay suggested growth rates of approximately 1.3 and 0.7 mm/d in 1952 and 1953, respectively (Haven, 1957) and of 0.9 mm/d in 1972 (Chao and Musick, 1977). Similarly, calculated values for May to July for fish from shallow creeks in North Carolina indicated growth rates of 0.6, 0.8, and 0.9 mm/d in 1979, 1980, and 1981, but the 1979 estimate is likely to be an underestimate because many of the larger fish appeared to be moving into deeper habitats during that time period (Ross, 1988). In our study, the growth rates remained relatively high when calculated through October (1.1–1.3 mm/d) in the bay but dropped off in the marshes (0.5–0.7 mm/d), potentially reflecting the egress of larger YOY out of the marshes into the bay.

Data from the Gulf of Mexico suggest slower growth rates of YOY Atlantic croaker in some areas but egress of larger fish out of the sampling area may also bias these estimates. Hansen (1969) used length-frequency data to determine growth rate estimates of 0.3 mm/d from January through August in the Pensacola Estuary on the Florida gulf coast in both 1964 and 1965 but noted the highest growth rates were in July (0.6 mm/d). Knudsen and Herke (1978) estimated growth of YOY in a semi-impounded marsh in Louisiana using recaptured individuals sprayed with fluorescent pigment during winter and spring and found rates of 0.4–0.5 mm/d for fish marked in late January and early February and recaptured into March. Rates for those marked mid-February to late March and recaptured into May were 0.8–0.92 mm/d. A previous study at the same location, using the same techniques, estimated that fish marked from December to March and recaptured into June grew at about 0.47 mm/d (Arnoldi et al., 1974). The monthly length-frequency data from Lake Pontchartrain, Louisiana (Suttkus, 1955), indicated a constant but slow growth rate of 0.3 mm/d from February to September 1954, and no increase in growth rate during the summer. As a result of the above, it appears that growth rates may be faster, and thus countergradient in more northern populations, as suggested for *Menidia* (Conover and Present, 1990), but care should be taken in interpreting growth rates from the literature, especially those based on modal progression.

### Egress

Young-of-the-year Atlantic croaker have a regular pattern of egress out of tidal creeks and estuaries in the MAB during the late summer and fall after reaching lengths of about 100–250 mm. As we observed in the Delaware Bay system, the majority left the marsh creeks from August to October at lengths <200 mm. The larger individuals appeared to leave the marshes first, as has been observed elsewhere (Haven, 1957; Yakupzack et al., 1977), and almost all had left by November. However, the CPUE increased in Delaware Bay in October of both years, and this may have been caused by fish egressing out of the marshes into the bay. Large individuals remained in Delaware Bay longer than in the marshes and substantial numbers of fish 150–300 mm were present in the bay in September and October. This finding suggests that egress from the tidal creeks caused the disappearance of Atlantic croaker there, and not gear avoidance, because large fish continued to be caught in the bay. The exact timing of egress of the majority of Atlantic croaker out of the bay is unclear due to lack of sampling throughout the bay after October. However, previous collections in Delaware Bay have shown no evidence of any individual >100 mm from November to March (Able and Fahay, 1998), suggesting that egress out of the bay is finished by November in some years. The same pattern of egress out of nursery habitats in the fall has been observed in Chesapeake Bay (Haven, 1957), but in some years there were substantial numbers of fish present into November (Chao and Musick, 1977). Very few of each year class reappear in collections during the spring and summer of the next year in either Chesapeake or Delaware bays (Haven, 1957; Chao and Musick, 1977; Able and Fahay, 1998) and therefore the fate of these individuals is unknown.

Fall egress also occurs out of estuaries in the South Atlantic Bight and the Gulf of Mexico, but in contrast to the Chesapeake and Delaware bays, more Atlantic croaker appear to either remain through the winter or re-enter these habitats in some areas in late winter or early spring. In North Carolina, egress out of tidal creeks was mostly completed by November, but this same year class was present again as age-1 fish in the bays in March, April, and May when sampling resumed (Ross, 1988). A similar pattern of egress from estuaries was observed in South Carolina, but the reappearance of age-1 fish in February was even more prominent and they continued to be collected until fall (Bearden, 1964). In the Gulf of Mexico, some age-1 fish have been observed to remain in estuarine habitats for an additional year in Lake Pontchartrain, Louisiana (Suttkus, 1955), or reappear from January to April after leaving the study area in December in coastal Texas (Pearson, 1929).

In summary, this study presents the first comprehensive examination of YOY Atlantic croaker seasonality and habitat use in Delaware Bay and the adjacent marshes. Although patterns of habitat use and seasonality are similar along the east coast, some divergence from the seasonal patterns in Delaware Bay are evident in estuaries in the South Atlantic Bight and the Gulf of Mexico. Growth estimates appear to be the most divergent of any characteristics examined—faster growth rates occurring in the more northern estuaries such as Delaware Bay.

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