Abstract.-Age-0 weakfish *Cyno-scion regalis*, were sampled from the Chesapeake Bay-York River estuary in 1983 and 1984 to test for the existence of multiple cohorts and compare growth rates. In both years juveniles were first collected in the estuary in late July, were significantly more abundant from August to mid-October, but were uncommon by the end of October. Significantly more weakfish were collected in 1983 than in 1984. Daily ages were determined based on scale circuli. Cohorts were separated by local minima in birthdate distributions: cohort 1 hatched before 16 July 1983, cohort 2 (16 July-15 August 1983), cohort 3 (15 August-9 September 1983), cohort 4 (5 May-20 June 1984), and cohort 5 (5 July-1 September 1984). Compared with other cohorts, groups 1 and 4 had significantly slower growth rates (0.83 and 0.84 mm/day, respectively), while cohort 5 had a significantly faster growth rate (1.09 mm/day), and cohorts 2 and 3 were intermediate (both at 0.96 mm/day). Weakfish juveniles were transient and migrated up the estuary as they grew, as indicated by cohort and age distributions over stations and dates. Also, cohorts appeared to partition the estuary; for example, cohort 1 was more common up the estuary compared with other cohorts. The existence of multiple cohorts with significantly different growth rates and apparent differential habitat use suggests that the juvenile stage of weakfish may show high variability in survival, and the presence of multiple cohorts within a single year-class must be considered in the estimation of juvenile recruitment to the adult population.

Differential Growth Among Cohorts of Age-0 Weakfish *Cynoscion regalis* in Chesapeake Bay*

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A common assumption of early-life-history studies of fishes has been that the most critical period for survival occurs during egg and larval stages, thereafter juvenile fish show fairly constant growth and mortality rates (Cushing 1975, Williams 1983, Hewitt et al. 1985, Victor 1986). However, postmetamorphic survival may be highly variable and we may need to extend the critical survival concept to include the juvenile stage of fishes to better understand year-class variability (Walline 1985, Eckert 1987, West and Larkin 1987). The existence of multiple cohorts within age-0 fishes may help explain variable annual survival of juvenile fishes (Buchanan-Wollaston and Hodgson 1929, Cooper 1937, Lambert and Ware 1984). Survival is difficult to estimate without information on residency time, but growth rate can be used as an indicator of potential survival because it is an integrator of most other environmental factors. For example, those individuals that grow the fastest will increase their chances of survival because they grow through the size range vulnerable to predators at a faster rate (Tonn and Paszkowski 1986, Post and Prankevicius 1987, Post and Evans 1989). Faster growth also implies that they are more physically fit, e.g., larger individuals may be able to survive overwinter stress better than smaller individuals (Conover and Ross 1982, Takita et al. 1989).

The key to evaluating variation in growth rates among age-0 fishes is the ability to age young fish. Larval and juvenile fishes have been assigned daily ages by length-frequency analysis, a somewhat imprecise method (MacDonald 1987), or by counting microincrements in otoliths (see reviews: Campana and Neilson 1985, Jones 1986). Daily aging of juvenile weakfish *Cynoscion regalis*, by otolith microincrements was unreliable (Szedlmayer 1988), but a new method of counting circuli in scales appears promising (Szedlmayer et al. In press). The present study uses this new method to test for multiple cohorts within age-0 weakfish, and to estimate growth rates and differential habitat use by fish collected in the Chesapeake Bay-York River estuary, Virginia.

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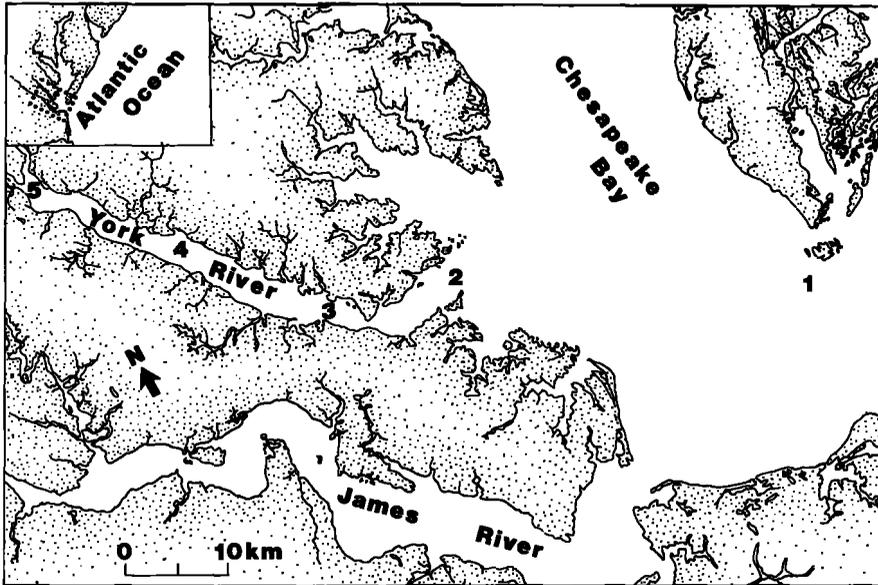
Figure 1
Station locations for age-0 weakfish collections in Chesapeake Bay-York River, VA. Station 1 (0 km, bay entrance), station 2 (30 km up estuary), station 3 (45 km up estuary), station 4 (63 km up estuary), and station 5 (75 km up estuary).

Materials and methods

Juvenile weakfish were collected at night (Leber and Greening 1986) with an otter trawl (4.9 m, 19-mm mesh wings, 1.5-mm codend). In 1983, collections were made weekly at four stations in the York River estuary, Virginia, from 12 July to 26 October: stations 2, 3, 4, and 5; 30, 45, 63, and 75 km up the estuary from the Bay entrance, respectively (Fig. 1). Station 1 was added at the mouth of Chesapeake Bay in 1984, while collections at Station 4 were discontinued (Fig. 1). In 1984, collections were made every 2 weeks from 21 June to 16 November. Repetitive, 2-minute trawls were made at each station until 30 fish were captured or until 6 tows were completed. Salinity and temperature were recorded with a Beckman conductivity meter at the bottom at each station.

Weakfish were stored in 70% ethanol. Standard lengths of preserved fish were recorded with calipers to the nearest 0.1 mm. At least three scales were taken from just below the midbody lateral line curve (usually five) and circuli were counted according to Szedlmayer et al. (In press). When three scales could not be taken, the fish was not used. The highest scale circuli counts from individual weakfish were used for age estimations. Age was estimated, based on daily scale circuli counts, plus a 26-day estimate of the time delay from hatching to first circulus formation. Also, if fish were <14 mm SL (prior to scale formation), age was estimated by quadratic regression of size on age based

on laboratory-reared fish (for validation of daily circuli deposition and further details of this method, see Szedlmayer et al. In press). Subsequently, birthdates were backcalculated by subtraction of estimated age from date of capture. Birthdate frequency distributions were smoothed with a 3-day moving average. Cohorts within a year-class were identified by local minima in the birthdate frequency distributions (Graham and Townsend 1985). After separation of fish into their respective cohorts, growth rates were estimated by linear regression of standard length on age. Migration patterns within the estuary and differential habitat use by cohorts were suggested by abundance modes over stations and collection dates, mean ages by stations, and cohort-specific age-frequency distributions over stations and collection dates.

A 0.05 level of significance was used for analysis of variance and covariance. Nonparametric analysis of variance by ranks of main effects (year, station, date) was used to test for abundance differences (catch-per-unit-effort = number/2-minute trawl tow). Analysis of covariance was used to test for significant differences in growth rates among cohorts. Analysis of variance was used to test for age differences among stations, pooled over dates. After significance was determined, Student-Newman-Keuls test was used to show specific differences at a 0.05 level of significance or a 0.10 level if a type II error resulted at the former level (Zar 1984).

Results

Salinity variation was associated with station, while temperature variation was associated with season. As
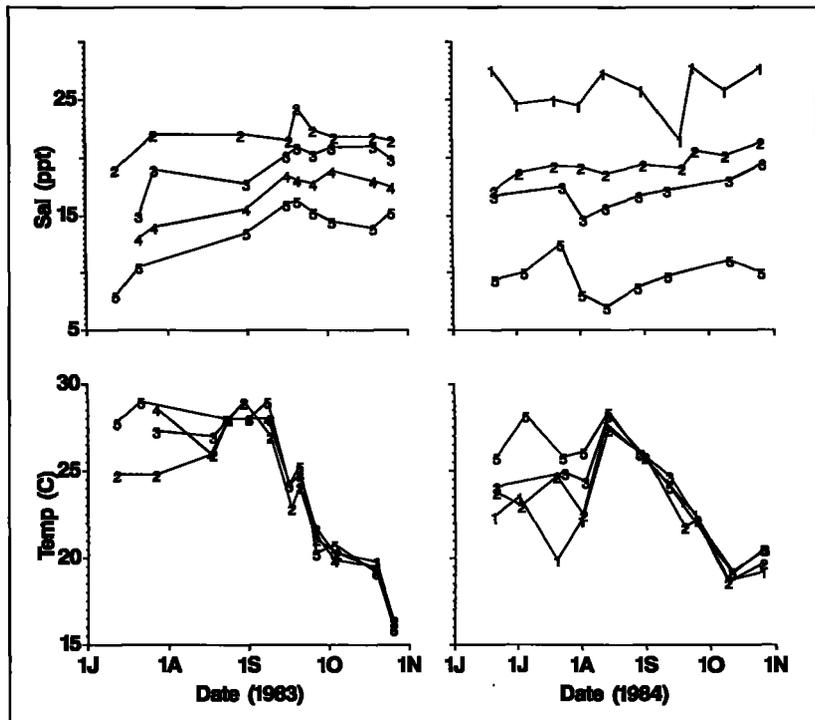
Figure 2
Salinity and temperature in Chesapeake Bay-York River, VA, from all collections, 1983 and 1984. Numbers on each line refer to station and mark data points.

expected, salinity was highest at station 1, and decreased up the estuary. Salinity was slightly higher at stations 2 through 5 in 1983 compared with 1984 (Fig. 2). Little difference was detected in temperature among stations, except in June and July 1984, where temperatures were 4–5°C warmer at the upper estuary stations. Seasonally, temperature ranged 16–29°C in 1983, and 18–29°C in 1984 (Fig. 2).

Weakfish catch-per-unit-effort was significantly greater in 1983 than in 1984 (Table 1; Fig. 3). Seasonally, fish were uncommon in July samples, significantly more abundant in samples taken from mid-August to mid-October, but by the end of October were few in number. No significant differences in catch-per-unit-effort were detected among stations. Lack of replication in some cells (i.e., one 2-minute tow resulted in >30 weakfish) prevented testing for interaction effects between station and date. However, although not statistically significant, there was an apparent pattern: in both years fish were first abundant down estuary, and as the season progressed became more abundant further up the estuary (Fig. 3).

In 1983, 845 fish were aged out of 993 collected, and in 1984, 361 fish were aged out of 571 collected, by the scale circuli method. An additional 98 fish were <14 mm SL (prior to scale formation), and ages were estimated by applying a quadratic regression of known age on standard length from laboratory-reared weakfish (Szedlmayer et al. In press).

Table 1

Juvenile weakfish CPUE (no./2-minute tow) from the Chesapeake Bay and York River, VA, based on three-factor (main effects only) nonparametric ANOVA by rank abundance. Student Newman Keuls test (SNK) was used to show specific differences, denoted by different letters (0.05 level).

Source of variation	df	MS	F	$P>F$
Year	1	5138.7	16.90	0.0001
Station	4	389.4	1.28	0.2870
Date	7	1216.4	4.00	0.0012
Error	61	303.7		

	CPUE	Trawls	SNK-test
Date			
16–29 July	1.2	20	C
30 July–12 Aug.	0.8	16	C
13–26 Aug.	5.0	60	A B
27 Aug.–9 Sept.	7.1	51	A
10–23 Sept.	8.5	37.5	A
24 Sept–7 Oct.	5.1	52	A
8–21 Oct.	4.4	46	A B
22 Oct.–4 Nov.	1.6	49	B C
Year			
1983	6.5	152.5	A
1984	3.2	179	B
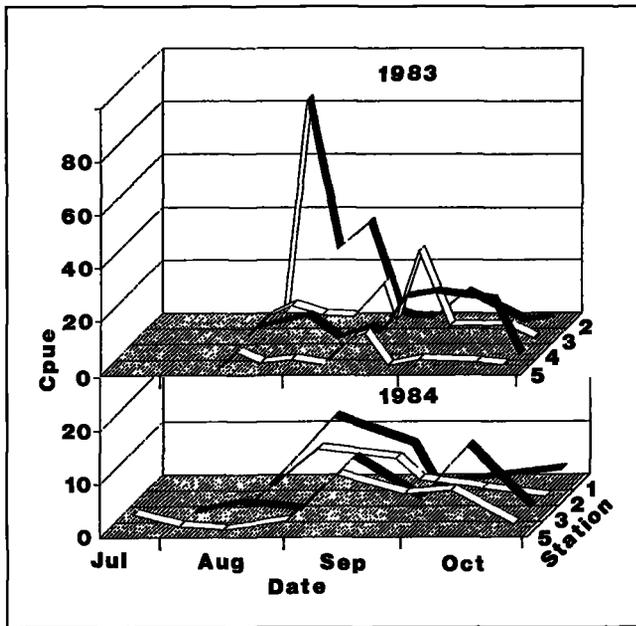
Figure 3

Standardized abundance of age-0 weakfish (CPUE = number/ 2-minute tow) by station and date in Chesapeake Bay–York River, VA.

Figure 4

Birthdate frequency distribution of age-0 weakfish cohorts in Chesapeake Bay–York River, VA, based on a 3-day moving average. Numbers at the peaks of the distributions refer to cohorts (separated by open and shaded bars).

Multiple cohorts were apparent in both years. The birthdate frequency distributions showed three cohorts in 1983, and two cohorts in 1984 (Fig. 4). Cohorts were defined in 1983 as follows: cohort 1 hatched before 16 July, cohort 2 between 16 July and 15 August, and cohort 3 after 15 August. Another cohort may have been present in 1983 before 18 June, but these fish were relatively few in number and subsequently pooled with cohort 1. In 1984 two cohorts 4 and 5 were defined as those that hatched before 30 June and those after, respectively (Fig. 4).

Weakfish growth rates were significantly different among cohorts within years, and between years (Table 2). Cohorts 1 and 4, both early-season cohorts, had the lowest growth rates and were not significantly different from each other. Cohorts 2 and 3 had intermediate growth rates, and cohort 5 had the fastest growth rate compared with all other cohorts (Table 2).

After separation of individual weakfish into their respective cohorts, a similar pattern of movement by each cohort was apparent: up the estuary with age and season (Figs. 5, 6). For example, the youngest fish in cohort 2 were first most abundant in the lower estuary (stations 2 and 3), and as the season progressed older fish from this cohort were more abundant up the estuary at the same location where few individuals of this cohort were collected earlier (station 4 in August vs station 4 in September 1983; Fig. 5). Cohort 4 showed the only difference from the above migration pattern.

Table 2

Growth rates (mm/day) of individual age-0 weakfish cohorts. Analysis of covariance of standard length on age with cohort as the covariate (0.05 level). Student Newman Keuls test (SNK-test) was used to show specific differences, denoted by different letters (0.10 level).

Source of variation	df	MS	F	$P>F$
Cohort	4	20178.39	1597.8	0.0
Age	1	448840.88	35540.4	0.0
Age * Cohort	4	1686.94	133.6	0.0
Error	1294	12.63		

Cohort	Growth rate	R^2	N	SNK-test
1	0.83	0.95	383	A
2	0.96	0.96	405	B
3	0.96	0.94	57	B
4	0.84	0.96	75	A
5	1.09	0.98	384	C
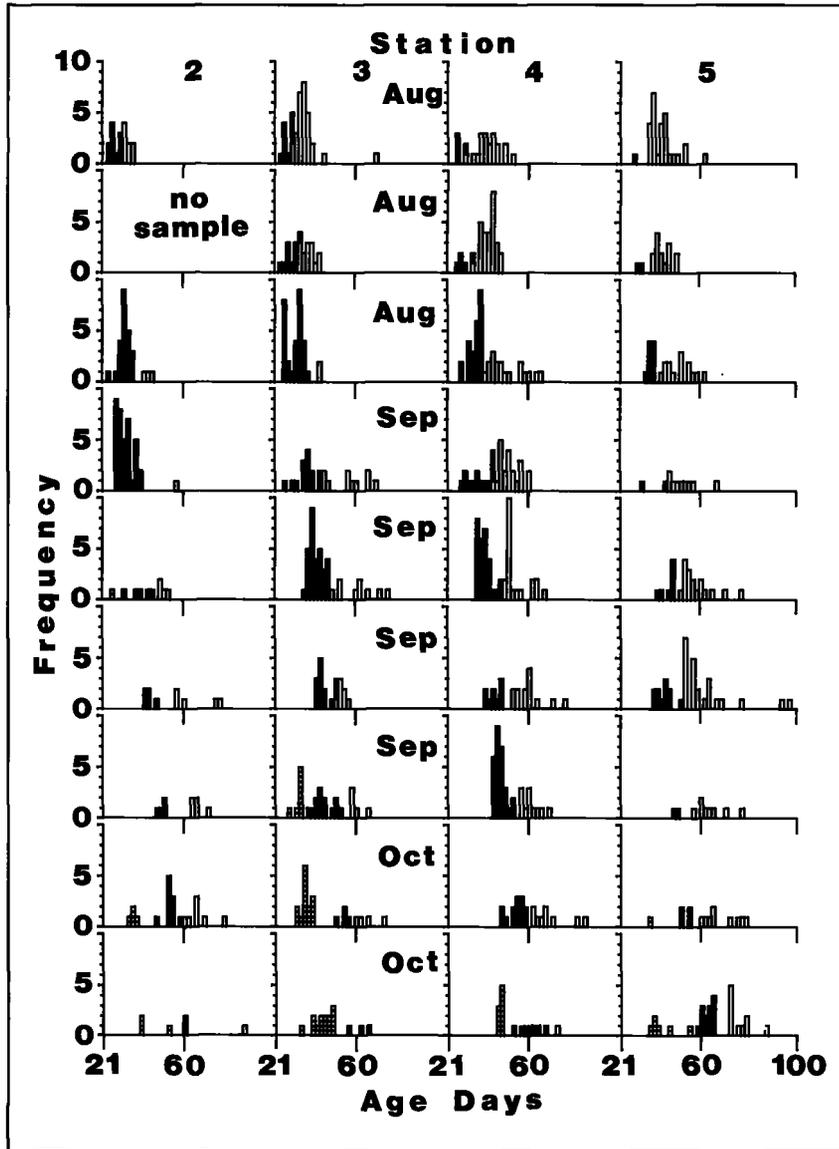
Figure 5
Age of weakfish estimated from scale circuli for 1983, versus frequency (number/2-minute tow), by station, date, and cohort in Chesapeake Bay-York River, VA. Cohort 1 = open bars, cohort 2 = solid bars, and cohort 3 = cross-hatched bars.

The earliest recruits in cohort 4 were first collected at the upper estuary station (5), then appeared to spread down the estuary in subsequent collections (Fig. 6). An up-the-estuary movement with age pattern was also supported by the mean ages associated with each station, because weakfish were significantly older as the distance from the Bay mouth station (1) increased (Table 3), and by an increase in total catch-per-unit-effort up the estuary with season (Fig. 3). Different cohorts appeared to segregate habitats. In 1983, cohort 1 was more common further up the estuary compared with other cohorts, while cohort 2 dominated the middle habitats (Fig. 5). Cohorts 3 and 4 were lower in abundance and it is difficult to suggest a pattern, while cohort 5 appeared dominant at all stations after August 1984 (Fig. 6).

Discussion

To our knowledge this is the first clear identification of multiple age-0 weakfish cohorts, and they showed significantly different growth rates and appeared to partition habitats. Earlier, Massmann (1963) suggested the existence of age-0 multiple cohorts from bimodal length-frequency distributions, but did not examine growth rates or differential habitat use. Except for two early studies (Buchanan-Wollaston and Hodgson 1929, Cooper 1937) reports of multiple cohorts in the juvenile stage of fishes are few (Shlossman and Chittenden 1981, DeVries and Chittenden 1982, Crecco and Savoy 1985, Kumagai et al. 1985, Eckert 1987, Isely et al. 1987, Wicker and Johnson 1987). This may be because of the difficulty of aging juvenile fishes (Geffen 1986,
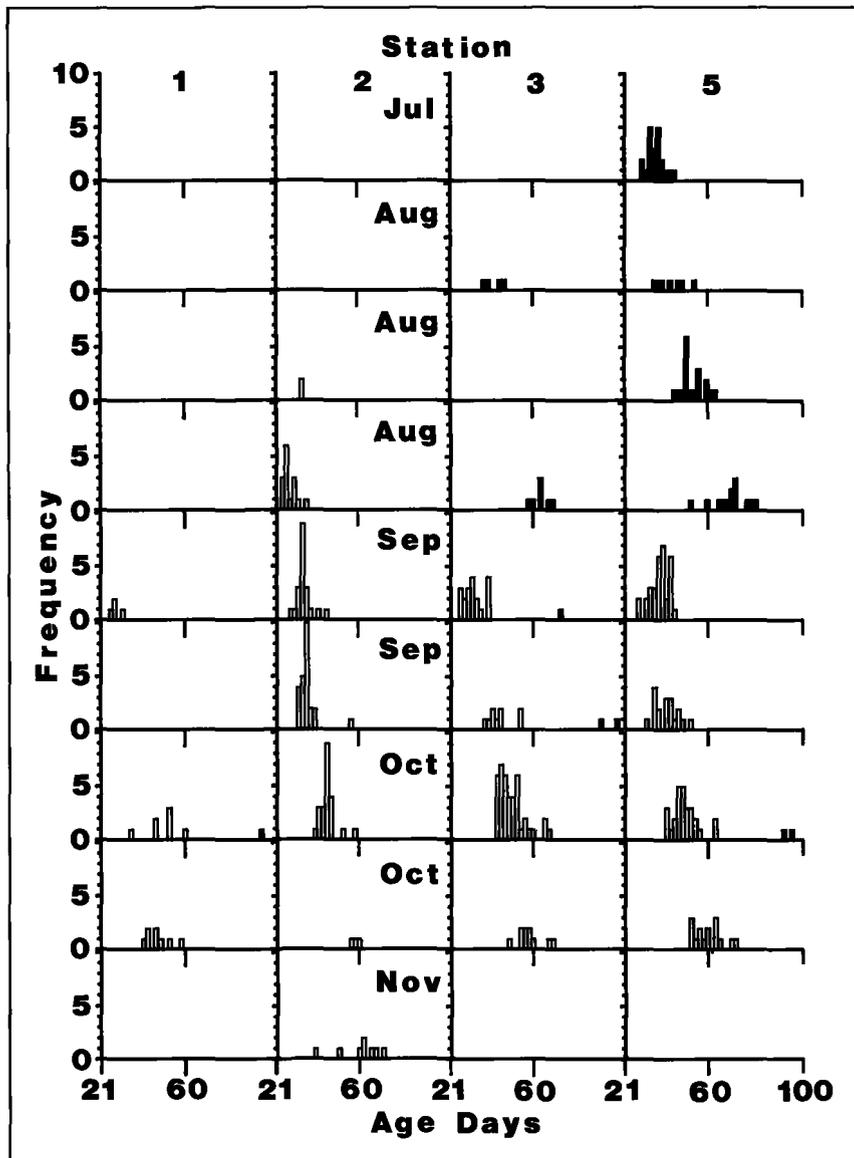
Figure 6
Age of weakfish estimated from scale circuli for 1984, versus frequency (number/2-minute tow), by station, date, and cohort in Chesapeake Bay-York River, VA. Cohort 4 = solid bars, cohort 5 = open bars.

Table 3
Comparison of weakfish age by station, pooled over dates, based on ANOVA (0.05 level). Student Newman Keuls test (SNK-test) was used to show specific differences, denoted by different letters (0.05 level).

Source of variation	df	MS	F	P>F
Station	4	37126.0	123.6	0.0001
Error	1299	300.3		

Station	Age	N	SNK-test
1	26.1	104	A
2	50.2	248	B
3	57.1	346	C
4	61.8	279	D
5	66.8	327	E

Essig and Cole 1986, Jenkins 1987, Post and Pranke-vicius 1987), or that fewer studies have examined postmetamorphic life stages because juvenile survival after metamorphosis was considered relatively constant compared with larval stages (Cushing 1975, Victor 1986). Constant growth and mortality in postmetamorphic juveniles have been questioned; for example, Wicker and Johnson (1987) showed a large increase in the rate of mortality in age-0 largemouth bass *Micropterus salmoides* when juveniles shift from an invertebrate to fish diet. Van der Veer and Bergman (1987) suggested that mortality due to predation by shrimp *Crangon crangon* on newly settled juvenile plaice *Pleuronectes platessa* may be significant and thus account for the difficulty of predicting year-class abundance based on egg and larval surveys. However,

studies of American shad *Alosa sapidissima* suggested that year-class strength is established before the juvenile stage (Crecco et al. 1983, Crecco and Savoy 1984, Crecco and Savoy 1985). Consequently, the importance of critical periods during the juvenile stage may be species-specific. Because several age-0 cohorts of weakfish showed variable growth rates and distribution, survival of the juvenile stage of this species should not be assumed to have a constant rate.

Different population parameters among cohorts are difficult to relate to salinity and/or temperature differences observed among stations. First, juvenile weakfish are transient, as observed over the present study area and in earlier studies (Harmic 1958, Massman 1963, Chao and Musick 1977, Shepherd and Grimes 1983), and until accurate residency times can be estimated it may be ineffective to ascribe cohort differences to particular habitat parameters. Second, other factors not measured in the present study, e.g., prey abundance, turbidity, currents, and predation may also be linked to cohort differences.

In comparison with other juvenile fish, age-0 weakfish appear to grow at an average rate. Juvenile growth rates derived from length frequencies for other sciaenid fishes were similar to our estimates for weakfish: *C. arenarius* (~1 mm/day, Shlossman and Chittenden 1981), *C. nothus* (0.8–1.3 mm/day, DeVries and Chittenden 1982). Shenker and Olla (1986) provide estimates of juvenile fish growth rates ranging from a low of 0.26 mm/day (*Sebastes melanops*) to a high of 4.7 mm/day (*Coryphaena hippurus*). Other growth rate estimates of juvenile fishes include: 1.5 mm/day for *Anoplopoma fimbria* (Boehlert and Yoklavich 1985), 1.0–1.3 mm/day for *Chanos chanos* (Kumagai et al. 1985), and 1.1 mm/day for *Alosa sapidissima* (Crecco and Savoy 1985).

The ecological advantage of extended spawnings that result in multiple cohorts within a single age-0 year-class can be thought of as a "hedged bet" strategy that spreads age-0 production over time to take advantage of a variable environment (Lambert and Ware 1984). However, distinct cohorts within age-0 fish can also result from environmental factors acting on a single spawning effort; for example, through variation in prey availability (Timmons et al. 1980, Keast and Eadie 1985, Wicker and Johnson 1987), or a combination of biotic and abiotic factors (Lambert 1984, Crecco and Savoy 1985). However, previously published information indicates that the multiple cohorts observed in the present study probably resulted from multiple spawnings. Shepherd and Grimes (1984) showed that large weakfish "tiderunners" 55–80 cm enter the Delaware Bay estuary in the spring and spawn. In the summer these were replaced by 25–35 cm gravid weakfish. Harmic (1958) showed a repeating pattern of multiple

spawning over 3 years, where a peak of egg abundance occurred in mid-June, followed by a conspicuous gap, and another peak in mid-July.

In summary, the present study showed that multiple cohorts exist within the age-0 year-class of Chesapeake Bay-York River weakfish. These cohorts showed significant differences in growth rates and appeared to partition habitats. Consequently, population studies directed at predicting year-class strength from juvenile surveys need to consider the potential for age-0 cohort variability.

Acknowledgments

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