Abstract.—Factors that affect survival and growth of larvae and influence recruitment variability of striped bass, *Morone saxatilis*, were investigated in the Potomac River and Upper Chesapeake Bay from 1987 to 1989. Ages and growth rates of larvae hatched within 3-day periods (cohorts) were estimated from otolith daily increments. Cohort-specific mortality rates were estimated from declines in cohort abundances over time. Temperature strongly affected larval cohort dynamics and potential to recruit. Storm fronts caused water temperature to drop near to or below 12°C, resulting in episodic mortalities of eggs and newly hatched larvae. Cohort-specific growth rates of larvae were variable, ranging from 0.11 to 0.46 mm·d^{-1} in the Potomac and from 0.18 to 0.36 mm d^{-1} in the Upper Bay, and were positively correlated with mean water temperatures. Cohort instantaneous mortalities (d^{-1}) also ranged widely, from $Z = 0.05$ to 0.92 in the Potomac and from $Z = 0.02$ to 0.28 in the Upper Bay, but were not correlated with temperature, growth rate, or other measured variables. The medians of cohort G/Z ratios (ratios of weight-specific growth rate to instantaneous mortality rate) and productions of 8.0-mm standard length larvae in each year were positively correlated with juvenile recruitment indices. Larval productions at 8.0 mm also were positively correlated with mean water temperatures because temperature strongly affected larval growth and because of the strong selection for survival of cohorts hatched later in the spawning seasons when water temperatures were consistently >17°C.

The influence of temperature on cohort-specific growth, survival, and recruitment of striped bass, *Morone saxatilis*, larvae in Chesapeake Bay

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Landings of anadromous striped bass, *Morone saxatilis*, along the Atlantic Coast of the United States declined sharply in the 1970's and 1980's owing to overfishing and a series of poor recruitments (Boreman and Austin, 1985). Indices of striped bass recruitments in the Chesapeake Bay vary more than 100-fold (Schaefer et al.[1]). Recruitment levels are established by the juvenile stage, when seine-survey indices correlate with subsequent commercial catches of adults (Goodyear, 1985).

Striped bass spawn in Chesapeake Bay tributaries from April to June, when frequent storms and heavy rainfall cause temperature, river flow, and pH levels to fluctuate. Temperatures experienced by eggs and larvae during the two-month spawning season may range from 10 to 29°C and may have dramatic effects on production, survival, and growth of cohorts. Initiation of spawning in Chesapeake Bay tributaries occurs at 12–18°C when temperatures are increasing rapidly (Olney et al., 1991; Setzler-Hamilton and Hall, 1991; Setzler Hamilton et al.[2]). Rapid drops in temperature to below 12°C are lethal to striped bass eggs and larvae (Bar-

[1] Schaefer, R. K., R. H. Bradford, J. L. Markham, and H. T. Hornick. 1991. Characterization of striped bass stocks in Maryland, p.1–74. *In* H. T. Hornick (project leader), Investigation of striped bass in Chesapeake Bay. US Fish and Wildlife Serv. Fed. Aid Proj. F-42-R-3, MD Dep. Natl. Resour., Tidewater Admin., Annapolis, MD. Available: Maryland Department of Natural Resources, Tidewater Administration, Tawes State Office Bldg., Taylor Ave., Annapolis, MD 20688.

[2] Setzler-Hamilton, E. M., J. A. Mihursky, K. V. Wood, W. R. Boynton, D. Shelton, M. Homer, S. King, and W. Caplins. 1980. Potomac estuary fisheries program, ichthyoplankton and juvenile investigations. 1977 Final Rep. to Maryland Dep. Natl. Resour., Power Plant Siting Program. Univ. of Maryland. Ref. No. [UMCEES]CBL 79-202. Available: University of Maryland Center for Environmental and Estuarine Studies, Chesapeake Biological Laboratory, 1 Williams St., Solomons, MD 20688.

kuloo, 1967; Doroshev, 1970; Davies, 1973; Morgan et al., 1981). Temperature also strongly influences the development of striped bass eggs and larvae (Polgar et al., 1976; Rogers et al., 1977; Rogers and Westin, 1981), the generation times and turnover rates of zooplankton prey (Heinle, 1969), and probably the consumption rates of predators.

Previous studies on striped bass recruitment variability averaged larval growth and mortality rates over multiple daily cohorts (Polgar, 1977; Dey, 1981; Kernehan et al., 1981; Uphoff, 1989; Setzler-Hamilton et al.[2]; Low[3]), thereby obscuring relationships with environmental factors. The presence of daily increments on otoliths allows accurate estimates of larval hatchdates, growth, and survival (Methot, 1983; Crecco and Savoy, 1985; Essig and Cole, 1986; Leak and Houde, 1987; Rice et al., 1987, a and b) and can provide valuable information about processes and factors affecting recruitment. Otolith-based estimates of larval growth histories have the potential to detect the subtle changes in growth rate that could cause order-of-magnitude variability in recruitment (Houde, 1987, 1989).

We hypothesize that variable striped bass recruitments are generated by variable growth and survival rates of cohorts of larvae produced during a two-month period of highly variable environmental conditions. In a related paper (Rutherford et al.[4]), results of a 3-year study of striped bass larval dynamics in the Potomac River and Upper Chesapeake Bay indicated that, on an annual basis, mean larval abundances and ratios of weight-specific growth to instantaneous mortality rate (G/Z) are correlated with juvenile recruitment indices, indicating that recruitment level is fixed during the larval stage. In this study, an analysis of daily cohort abundances and vital rates (growth and mortality) of larvae is presented to describe the process of year-class formation in striped bass and to illustrate how a primary variable, temperature, affects cohort-specific growth, survival, and recruitment potential in Chesapeake Bay.

Methods

Striped bass eggs and larvae were sampled every 3 to 7 days from April to June in the Potomac River (1987–89) and in the Upper Bay (1988 and 1989;

Rutherford et al.[4]; Fig.1). Methods of collecting ichthyoplankton and environmental data are described briefly below and in more detail by Houde and Rutherford[5] and Rutherford et al.[4]

Eggs and larvae were collected in duplicated oblique tows of a paired 60-cm bongo sampler, with 333- and 505-μm mesh nets. Larval abundances based upon the 505-μm mesh size, 60-cm bongo net samples were adjusted for extrusion of some small larvae by comparing catches with those in a paired, 333-μm mesh net. Adjustments for gear avoidance by large larvae were made by comparing 60-cm net catches during daylight with a series of night catches made on the same dates, and by comparing the 60-cm net catches with those in a 2-m² Tucker trawl at the same stations and dates. The 2-m² Tucker trawl (700-μm mesh) also provided collections of large larvae in late-season surveys. Riverwide abundances of eggs and larvae were estimated by multiplying mean station densities by the river volume which those stations represented. Egg abundances also were estimated and are reported in Houde and Rutherford (1992).

Densities of zooplankton that were potential prey for striped bass larvae were estimated from pumped water samples taken near-bottom, mid-depth, and at surface and filtered onto a 53-μm screen, or taken by vertical lifts of a 20-cm, 53-μm mesh plankton net. Temperature, pH, and salinity were measured at all stations on each survey. Conductivity was measured in 1988 and 1989, and turbidity and light were measured in 1987 and 1988. In addition, gauges at dams upstream of the spawning grounds provided continuous temperature measurements.

Larval ages, hatch dates, and age-frequency distributions were estimated from an analysis of sagittal otolith increments, which are deposited daily in striped bass (Jones and Brothers, 1987; Secor and Dean, 1989). Otolith increments were counted at least three times and the mean of the last two counts was used to estimate age. Aged larvae were grouped into 3-day periods (cohorts) based upon their hatch dates. Three-day cohorts were designated because 95% confidence intervals around mean ages indicated a 3-day range. Otolith-aged larvae from represented length classes were used to estimate the proportions of unaged larvae in each 0.5-mm length class that fell within each one-day age class. These 'age-length

[3] Low, A. F. 1986. Striped bass egg and larva survey in the Sacramento-San Joaquin estuary. California Dep. Fish and Game. Unreferenced report, November 1986. Available: California Department of Fish and Game, Stockton, CA 95205.

[4] Rutherford, E. S., E. D. Houde, and R. M. Nyman. Relation of larval stage growth and mortality to recruitment of striped bass, *Morone saxatilis*, in the Chesapeake Bay. Unpubl. manuscr.

[5] Houde, E. D., and E. S. Rutherford. 1992. Egg production, spawning biomass and factors influencing recruitment of striped bass in the Potomac River and Upper Chesapeake Bay. Rep. to Maryland Dep. Natl. Resour., Contract No. CB89-C01-003. Univ. Maryland, Center for Environmental and Estuarine Studies, Ref. No. [UMCEES]CBL 92-017, 313 p. Available: University of Maryland Center for Environmental and Estuarine Studies, Chesapeake Biological Laboratory, 1 Williams St., Solomons, MD 20688.

Figure 1

Map of sampling areas and stations on the Potomac River and Upper Chesapeake Bay, 1987–89.
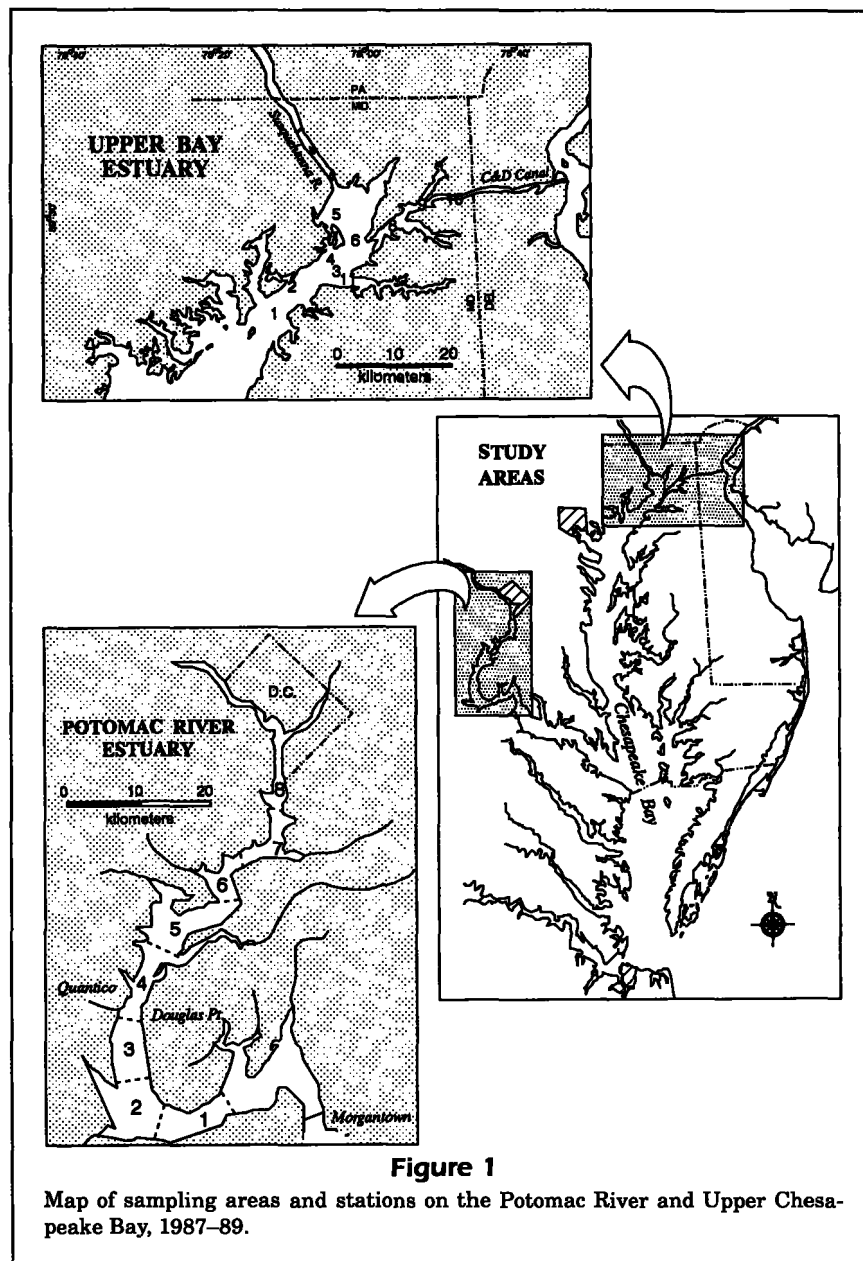
keys' were developed separately for the Potomac River and the Upper Bay in each year, except 1988, from regressions of otolith-derived ages on larval lengths. In 1988, otoliths of the few larvae collected in the Upper Bay were unreadable because of poor preservation; consequently the age-length key for 1988 Potomac River larvae was also applied to Upper Bay larval catches.

Larval growth rates were estimated by using both an "aggregate sample" method and a back-calculation method. In the aggregate sample method, standard lengths and otolith-derived ages of the entire sample of otolith-aged larvae were analyzed for each

cohort in each of the areas. Growth rates of larvae were derived from exponential regressions of larval lengths on ages. Exponential models also were fit to the mean back-calculated length at age of larvae to estimate back-calculated, cohort-specific growth rates.

We backcalculated fish lengths at age by using the "biological intercept" method (Campana, 1990). This method does not assume that larvae from all cohorts or populations have the same body length and otolith-radius relationship; thus it allows reconstruction of individual growth histories, which was desirable for our analysis. This method, and other back-calculation methods that assume a constant proportional-

ity between otolith growth and fish growth (Fraser-Lee, simple regression), will accurately estimate fish length if somatic growth is relatively fast (Secor and Dean, 1989, 1992; Campana, 1990). If somatic growth is slow, otoliths of slow-growing fish may grow relatively fast, causing the relationship between fish and otolith growth to be nonlinear and thus bias back-calculated growth-rates (Geffen, 1982; Reznick et al., 1989; Secor and Dean, 1989, 1992; Campana, 1990). To minimize biased estimates of back-calculated lengths at age for 1988 Potomac River larvae, when growth effects were significant and body size and otolith-size relationships were nonlinear, we followed the recommendation of Campana and Jones (1992) and $\log_e$-transformed fish lengths and otolith radii before applying the biological intercept method.

Larval cohort mortality rates were estimated from the exponential declines in cohort abundances at age obtained from 60-cm sampler catches. In 1989, larval mortality rates in the Potomac River and Upper Bay may have been overestimated when only larvae collected in the 60-cm sampler were considered. Striped bass spawned later in 1989 than in 1987 or 1988, and abundances of cohorts hatched in late May probably were under-represented in 60-cm sampler collections that were completed by 1 June. Better estimates of cohort mortality rates in 1989 were obtained by combining larval collections from the 60-cm sampler with those from the 2-m² Tucker trawl made from late May to mid-June.

A "Pareto" model, which assumes that mortality rate declines in relation to age (Lo, 1986), was compared with the linear model, and the model with the lowest residual sum of squares was selected to estimate each cohort's mortality rate. The ratio of instantaneous growth-in-weight rate to instantaneous mortality rate (G/Z), an index of larval production (biomass), was estimated for each cohort. Instantaneous growth-in-weight rates were derived from back-calculated growth-in-length rates by using a length-weight relationship (Houde and Lubbers, 1986) for striped bass larvae. Abundances of cohorts at 8 mm standard length (SL) were estimated to index their potential contributions to recruitment. At 8–10 mm, striped bass larvae reach the postfinfold larval stage (Fritsche and Johnson, 1980; Olney et al., 1983), when development of fins and increased swimming ability facilitates feeding as well as ability to avoid predators and can result in a decline in mortality rate. Abundances, and growth and mortality rates of larval cohorts were analyzed in relation to environmental variables by using stepwise multiple

regression analysis (SAS, 1988) to identify factors associated with variable recruitments.

Results

Spawning, egg and larval abundances, and zooplankton densities

Striped bass spawned during April and May, generally during periods of rising temperatures (Figs. 2 and 3). The major spawning peak in the Potomac
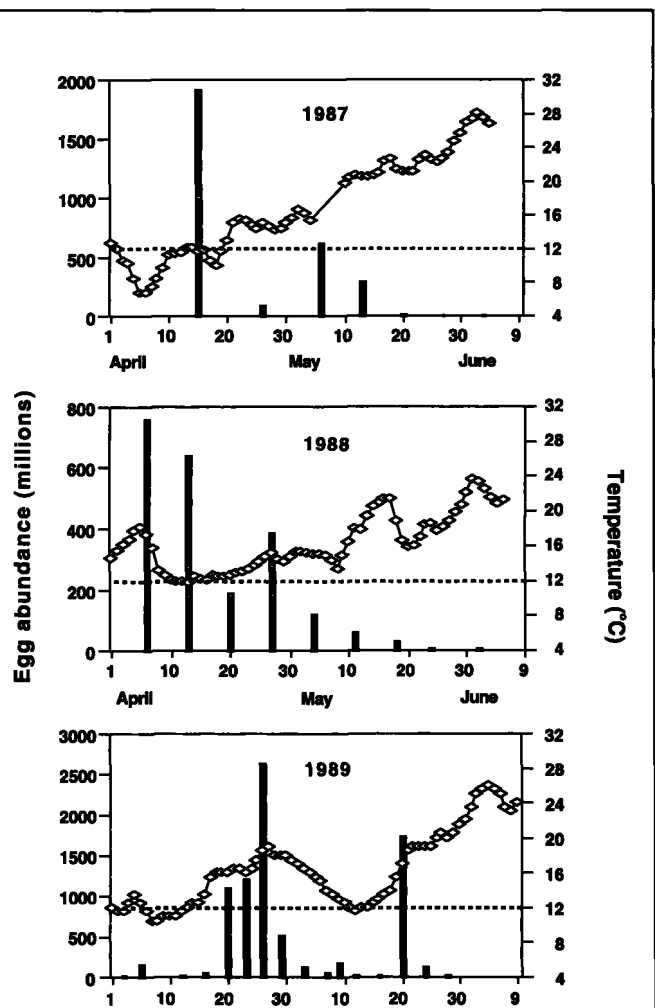

Figure 2

Riverwide egg abundances (millions) of striped bass, *Morone saxatilis*, estimated on each survey date (bars) during the three years of sampling effort in the Potomac River, 1987–89. Water temperatures recorded at Wilson Bridge during the spawning season also are given (open diamonds). The 12°C critical low temperature, at which 100% egg and larval mortality may occur, is indicated by the dotted line. Note that the Y-axis scales change among years.

River occurred in April in each year when temperatures rose to ≥12°C. A secondary spawning peak was evident in mid-May of 1989 (Fig. 2). Peak spawning in the Upper Bay occurred in mid to late May when water temperatures rose to ≥14°C (Fig. 3). Striped bass egg abundances were highest in 1989 and lowest in 1988 (Rutherford et al.[4]). Egg abundances were nearly an order of magnitude higher in the Upper Bay in 1989 (77.9 eggs·m^{-2}) than in 1988 (8.2 eggs·m^{-2}) but did not differ significantly (*P*>0.05) among years in the Potomac (25.1 to 73.5 eggs·m^{-2}).

Episodic mortalities of striped bass eggs and larvae occurred in the Potomac River in each year after spring storms, which caused flood conditions and sharp declines in river temperatures to or below the 12°C lethal limit. In 1987, a storm on 16–17 April and a subsequent temperature drop caused complete

mortality of all striped bass eggs and larvae, effectively eliminating >50% of the season's egg production (Rutherford et al.[4]). Although no larvae survived that event, relatively minor spawning (Fig. 2) that occurred later, combined with favorable conditions for larval growth and survival, resulted in higher mean larval abundances than those in 1988 or 1989 (Rutherford et al.[4]). After 20 April 1987, Potomac River temperatures increased steadily and were both warmer and less variable than in 1988 or 1989. Temperature profiles in the Upper Bay were similar in both 1988 and 1989 (Fig. 3). In the Upper Bay, the initial order of magnitude difference between years in egg abundance was maintained through the larval stage (Rutherford et al.[4]).

Mean densities of zooplankton that were potential prey for larval striped bass cohorts during the first 5–20 days posthatch were highest in the Potomac River in 1987 and in the Upper Bay in 1989 (Fig. 4). Densities of copepod nauplii, *Eurytemora affinis*, and rotifers (including *Brachionus, Asplanchna, Synchaeta, Polyarthra*), in particular, which are initial prey of striped bass larvae (Takacs, 1992; Beaven and Mihursky[6]), were higher in the Potomac River in mid to late May 1987 than in 1988 or 1989.

Growth

Body length and otolith-radius relationships Larval length was strongly correlated with otolith size in each year (Table 1). The best regression relationships were linear for most cohorts with adequate sample sizes (*n*>4) and ranges in body length. Exponential models provided better fits for some Potomac River cohorts, and age was a significant covariate of otolith size for two cohorts in 1989 (Table 1).

With few exceptions, cohorts hatched early in the season, experienced mean temperatures <17°C during the first 20 days posthatch, and had relatively larger otoliths per unit body length than did cohorts hatched when temperatures were warmer. Differences in body length-otolith radius relationships among Potomac River striped bass cohorts were significant in 1989 (ANCOVA; *P*<0.001), but not in 1987 (ANCOVA; *P*>0.10) or 1988 (ANCOVA; *P*>0.20).

Growth rates Growth rates of striped bass larval cohorts, estimated by both aggregate and back-calculated methods, indicated that growth varied sea-
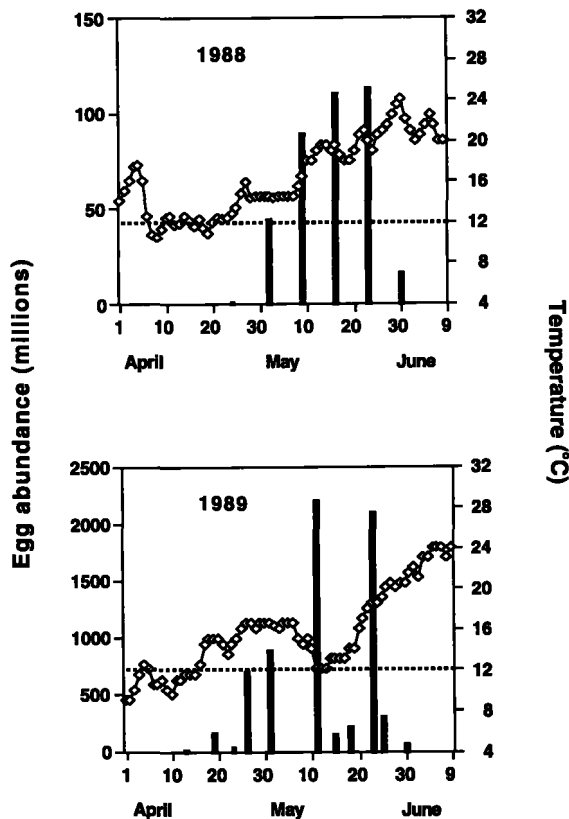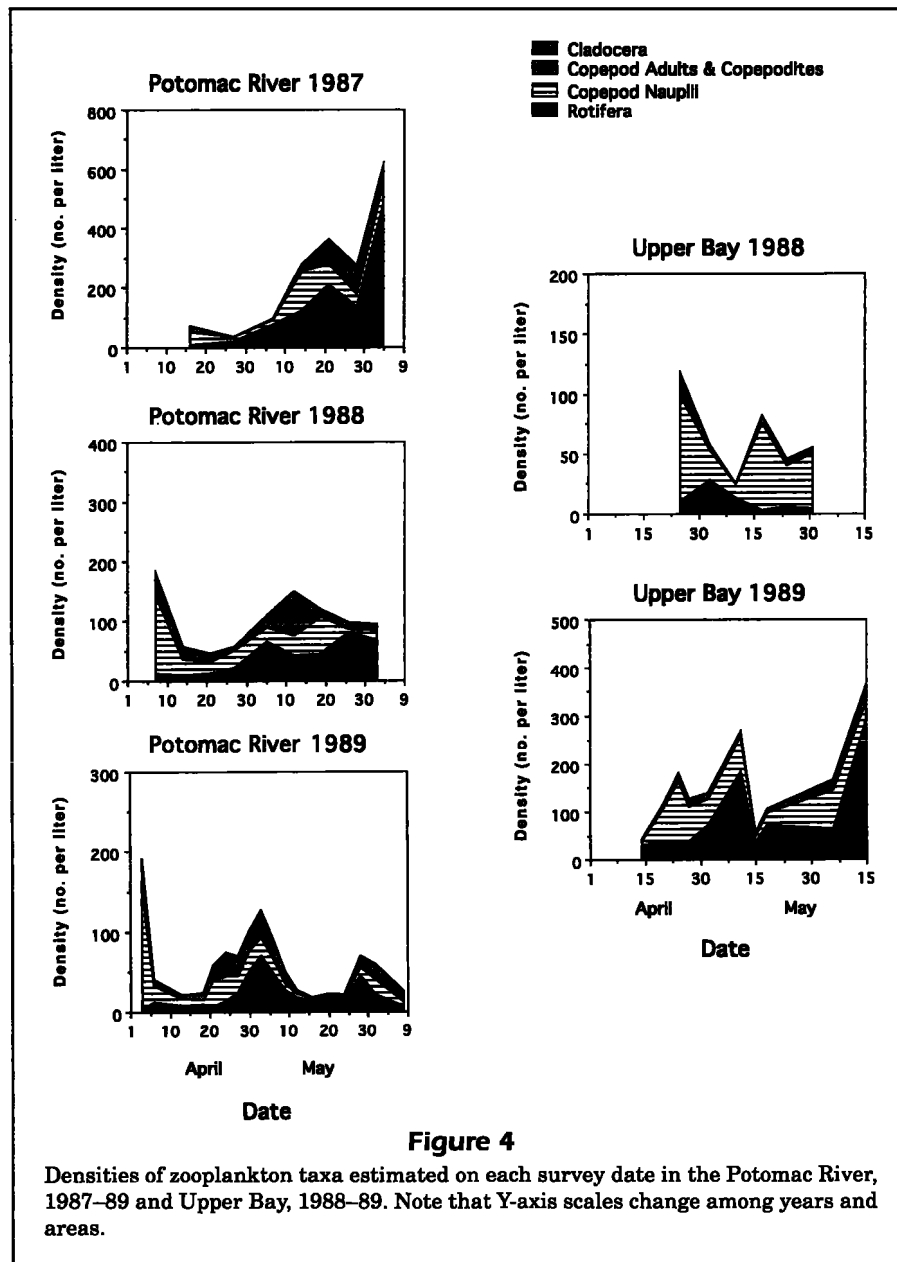

Figure 3

Areawide egg abundances (millions) of striped bass, *Morone saxatilis*, estimated on each survey date (bars) during the two years of sampling effort in the Upper Bay, 1988–89. Water temperatures recorded at Conowingo Dam during the spawning season also are given (open diamonds). The 12°C critical low temperature, at which 100% egg and larval mortality may occur, is indicated by the dotted line. Note that the Y-axis scales change between years.

[6] Beaven, M. S., and J. A. Mihursky. 1979. Food and feeding habits of larval striped bass: an analysis of larval striped bass stomachs from 1976 Potomac estuary collections. Ref. No. [UMCEES]CBL 79-045, Chesapeake Biological Laboratory. Available: University of Maryland Center for Environmental and Estuarine Studies, Chesapeake Biological Laboratory, 1 Williams St., Solomons, MD 20688.

Figure 4

Densities of zooplankton taxa estimated on each survey date in the Potomac River, 1987–89 and Upper Bay, 1988–89. Note that Y-axis scales change among years and areas.

sonally in each year. Cohorts that hatched late in the season grew relatively fast, had shorter stage durations (Fig. 5), and reached larger sizes by 20 days posthatch than did cohorts hatched earlier, which grew in cooler water. Both methods of estimating growth produced similar rates, although estimates from the aggregate method were much less precise (Figs. 5 and 6).

Aggregate-sample growth rates of Potomac River larvae differed significantly among 3-day cohorts in 1987 and 1989. Cohort growth rates, after adjusting for age by analysis of covariance, tended to increase as the season progressed (Fig. 5). They ranged from

0.19 to 0.44 mm·d^{-1} (mean ±95% CI=0.26 ±0.06 mm·d^{-1}) in 1987, from 0.11 to 0.22 mm·d^{-1} (mean=0.18 ±0.04 mm·d^{-1}) in 1988, and from 0.12 to 0.53 mm·d^{-1} (mean=0.24 ±0.07 mm·d^{-1}) in 1989. The regression fits of growth data were poor for some Potomac River cohorts in 1988. The predicted mean lengths at 20 days posthatch of larval cohorts were variable, ranging from 7.7 to 11.7 mm SL in 1987, from 6.9 to 9.0 mm SL in 1988, and from 4.8 to 11.1 mm SL in 1989. Predicted ages at 8.0 mm SL also varied, ranging from 13.2 to 21.2 days in 1987, from 14.2 to 23.8 days in 1988, and from 14.6 to 31.6 days in 1989 (Fig. 5).

Table 1

Body length (SL mm)-otolith radius (R, μm) regressions for larval cohorts of striped bass, *Morone saxatilis*, larvae, collected from the Potomac River, 1987–89 and the Upper Bay, 1989. "A" = Age (days posthatch); SE = standard error, *n* = sample size.

Cohort Hatch Date	Regression	SE (slope)	r^2	n	$P <$
Potomac River 1987					
22 April	SL = 6.220 + 0.029R			2	
25 April	Ln(SL) = 1.907 + 0.003R	<0.001	0.99	7	0.001
28 April	SL = 6.025 + 0.022R	0.004	0.99	3	0.010
1 May	SL = 5.160 + 0.033R	0.001	1.00	5	0.001
4 May	SL = 5.922 + 0.024R	0.004	0.95	4	0.050
7 May	SL = 5.221 + 0.024R	0.002	0.98	8	0.001
10 May	SL = 5.235 + 0.033R	0.003	0.96	9	0.001
13 May	SL = 5.057 + 0.032R	0.002	0.95	25	0.001
16 May	SL = 4.900 + 0.031R	0.002	0.94	21	0.001
19 May	SL = 4.856 + 0.036R	0.002	0.97	20	0.001
Potomac River, 1988					
12 April – 3 May	SL = 4.491 + 0.035R	0.002	0.92	32	0.001
6 May	SL = 3.233 + 0.045R	0.003	0.94	9	0.001
9 May	SL = 5.919 + 0.026R	0.004	0.88	10	0.001
12 May	SL = 4.658 + 0.036R	0.005	0.86	11	0.001
15 May	SL = 5.683 + 0.029R	0.012	0.37	12	0.050
18 May	SL = 5.693 + 0.030R	0.008	0.51	16	0.001
Potomac River, 1989					
17–26 April	SL = 6.068 + 0.021R	0.002	0.97	9	0.001
29–April	SL = 5.976 + 0.024R	0.002	0.94	10	0.001
2 May	SL = 6.531 + 0.021R	0.006	0.76	11	0.001
5 MayS	SL = 3.13 + 0.18A + 0.01R	0.058, 0.004	0.78	27	0.001
8 May	SL = 3.69 + 0.02A + 0.13R	0.002, 0.034	0.97	19	0.001
11 May	SL = 5.331 + 0.031R	0.003	0.90	19	0.001
14 May	Ln(SL) = 1.914 + 0.003(R)	<0.001	0.80	14	0.001
17 May	SL = 4.513 + 0.034R	0.003	0.83	25	0.001
20 May	SL = 5.027 + 0.029R	0.003	0.77	28	0.001
23–26 May	SL = 6.606 + 0.015R	0.005	0.44	14	0.01
Upper Bay, 1989					
8 May	SL = 3.890 + 0.037R	0.002	0.97	6	0.001
11 May	SL = 4.400 + 0.035R	0.001	0.99	6	0.001
14 May	SL = 5.058 + 0.031R	0.003	0.95	11	0.001
17 May	SL = 5.058 + 0.032R	0.000	0.97	34	0.001
20 May	SL = 5.402 + 0.027R	0.002	0.92	50	0.001
23 May	SL = 5.146 + 0.028R	0.003	0.91	47	0.001
26 May	SL = 4.507 + 0.032R	0.003	0.90	17	0.001
29 May	SL = 4.750 + 0.029R	0.003	0.93	14	0.001
1 June	SL = 4.211 + 0.038R	0.005	0.97	4	0.050
4 June	SL = 3.393 + 0.056R			2	

The larval growth rate estimates of Upper Bay cohorts in 1989 did not differ significantly ($P>0.25$) and ranged from 0.21 mm·d^{-1} for larvae hatched on 8 May to 0.32 mm·d^{-1} for larvae hatched on 1 June (Fig. 5). The mean cohort growth rate was 0.25 ±0.03 mm·d^{-1}. Predicted mean lengths at 20 days posthatch of the 9 cohorts ranged from 7.4 to 10.0 mm. Predicted ages at 8.0 mm SL ranged from 14.8 to 22.1 days (Fig. 5).

Back-calculated growth rates of 5–20 days posthatch larval cohorts from the Potomac River ranged from 0.19 to 0.46 mm·d^{-1} in 1987 (mean=0.27 ±0.05 mm·d^{-1}), from 0.18 to 0.34 mm·d^{-1} in 1988 (mean=0.23 ±0.04 mm·d^{-1}), and from 0.11 to 0.36 mm·d^{-1} in 1989 (mean=0.23 ±0.04 mm·d^{-1}) (Fig. 6). Back-calculated growth rates of Upper Bay larvae, available only for 1989, ranged from 0.18 to 0.36 mm·d^{-1} (mean=0.26 ±0.03 mm·d^{-1}) (Fig. 6).

The differences in back-calculated growth rates among cohorts in each year resulted in different predicted lengths at 20 days posthatch. There were
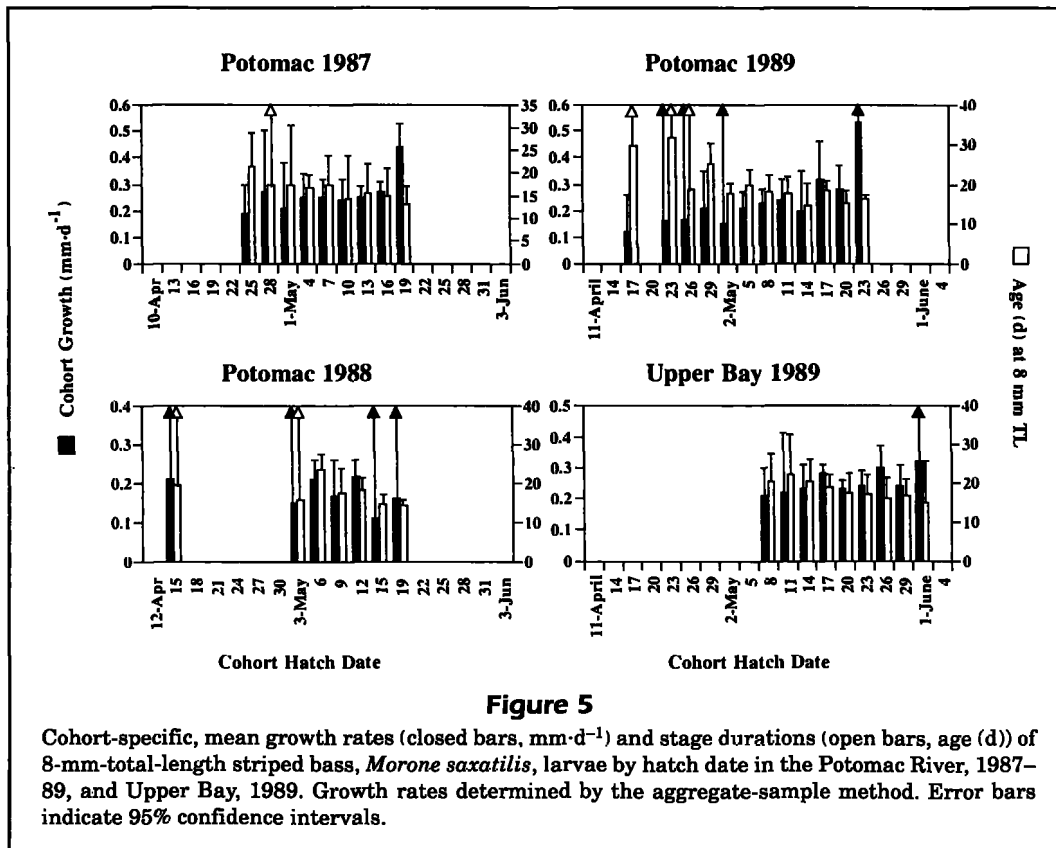
Figure 5

Cohort-specific, mean growth rates (closed bars, mm·d⁻¹) and stage durations (open bars, age (d)) of 8-mm-total-length striped bass, *Morone saxatilis*, larvae by hatch date in the Potomac River, 1987–89, and Upper Bay, 1989. Growth rates determined by the aggregate-sample method. Error bars indicate 95% confidence intervals.
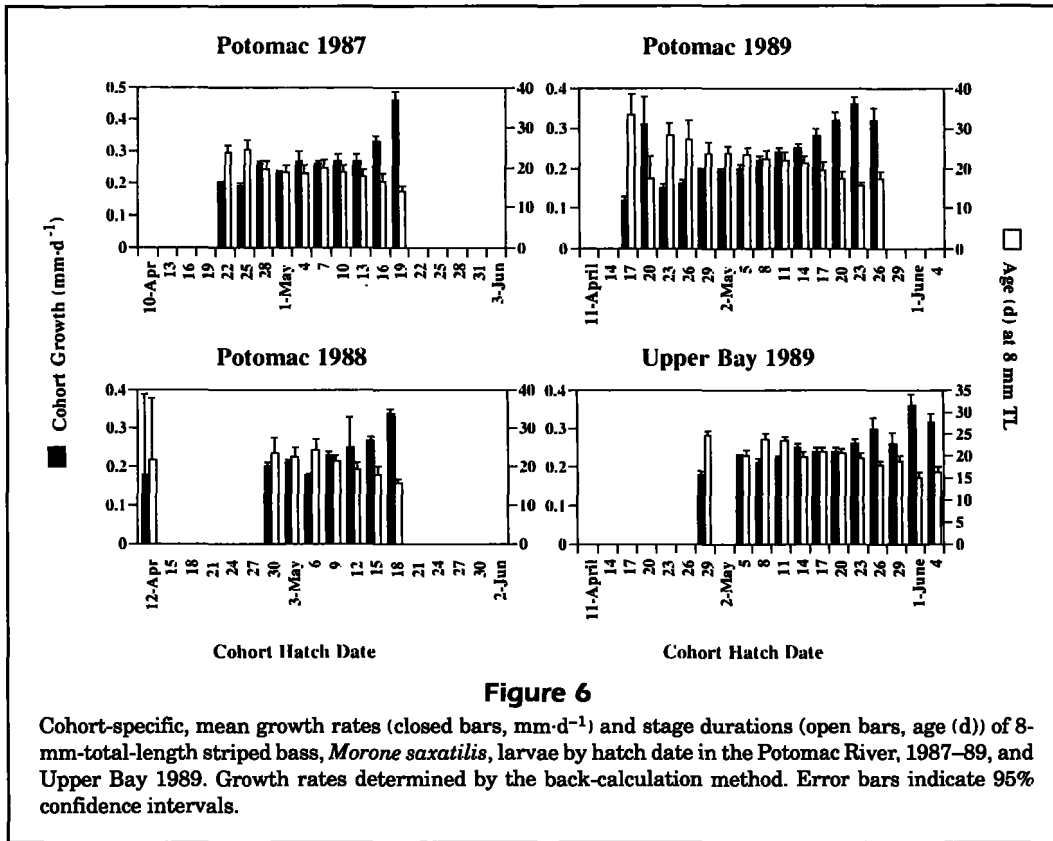
among-cohort differences of up to 4.8 mm, 3.0 mm, and 4.6 mm in the Potomac in 1987, 1988, and 1989, respectively, and differences of 3.4 mm in the Upper Bay. Maximum among-cohort differences in predicted ages at 8.0 mm were 11, 9, and 21 days in the Potomac River in 1987, 1988, and 1989, respectively, and 10 days in the Upper Bay (Fig. 6).

Back-calculated (r^2=0.67; Fig. 7) and aggregate-sample (r^2=0.62) cohort growth rates were strongly and positively related to the mean water temperatures in which larvae grew. A stepwise multiple regression analysis indicated that densities of copepod nauplii, a probable prey of first-feeding striped bass larvae, were negatively correlated with larval growth rate, presumably because nauplii densities were higher near the beginning of the spawning season (Fig. 4) when growth rates were lowest. No other environmental variable, including densities of other zooplankton taxa or densities of striped bass eggs, larvae, or *Morone* spp. larvae (striped bass plus white perch, *M. americana*), explained a significant proportion of the variance in larval growth rates.

Individual growth rate variability Growth histories of larvae *within* each cohort that presumably had experienced the same suite of environmental

conditions indicated that some individuals grew much faster than average. Within a cohort, individual larvae differed by as much as 5.0 mm in length at 20 days posthatch (Upper Bay 1989, cohort hatched 23 May), and by up to 0.33 mm·d⁻¹ in growth rate (Upper Bay 1989, cohort hatched 23 May). The maximum individual growth rate of a 3-day cohort was 68% higher than the mean. Variance (%CV) in larval growth rate or lengths at 20 days posthatch within-cohorts did not differ significantly (Kruskal-Wallis; P>0.10) among years. There was no significant relationship between variance in growth rate within-cohorts and the mean (P>0.20) or variance (P>0.50) in daily temperatures experienced by cohorts.

Evidence for size-selective mortality operating on larger individuals was detected in back-calculated growth histories of striped bass larval cohorts examined from the Potomac River, 1987 and 1989, and Upper Bay, 1989. To detect evidence of size-selective mortality, lengths at capture of larval cohorts collected early in the spawning season were compared with back-calculated lengths at age of older larvae in the same cohort collected later in the season. For 10 of the 11 cohorts examined from the Potomac River 1987 (n=5), 1989 (n=4), and the Upper Bay 1989 (n=2), mean back-calculated lengths at 10 and 20

Figure 6

Cohort-specific, mean growth rates (closed bars, mm·d⁻¹) and stage durations (open bars, age (d)) of 8-mm-total-length striped bass, *Morone saxatilis*, larvae by hatch date in the Potomac River, 1987–89, and Upper Bay 1989. Growth rates determined by the back-calculation method. Error bars indicate 95% confidence intervals.

days posthatch of surviving larvae collected late in the season were significantly smaller (*t*-test; *P*<0.001) than lengths at capture of larvae collected earlier, suggesting that within-cohort mortality had acted selectively against larger individuals. There was no significant difference (*P*>0.50) in mean lengths at age between early and late-captured larvae in the eleventh cohort.

Analysis of back-calculated larval growth histories suggested that in most Potomac River and Upper Bay cohorts in each year, small larvae are able to compensate for slow initial growth and obtain the same length at >20 days posthatch as larvae with large initial lengths. Lengths at capture were compared with back-calculated growth rates in the period 5–20 days posthatch and with calculated lengths at 5, 10, 15, and 20 days posthatch. For all cohorts (*n*=38) in all years, there either was no significant relationship between length at capture and their back-calculated lengths at 5 and 10 days posthatch, or the relationship was negative, i.e. within a cohort, some of the smallest-sized larvae at capture had relatively large back-calculated lengths at 5 and 10 days posthatch.

For individuals hatched early in the spawning season (in 14 of 15 cohorts), there also was no relationship between lengths at capture and back-calculated

lengths at 15 and 20 days posthatch. However, larvae that hatched later in the season (in 20 of 23

Figure 7
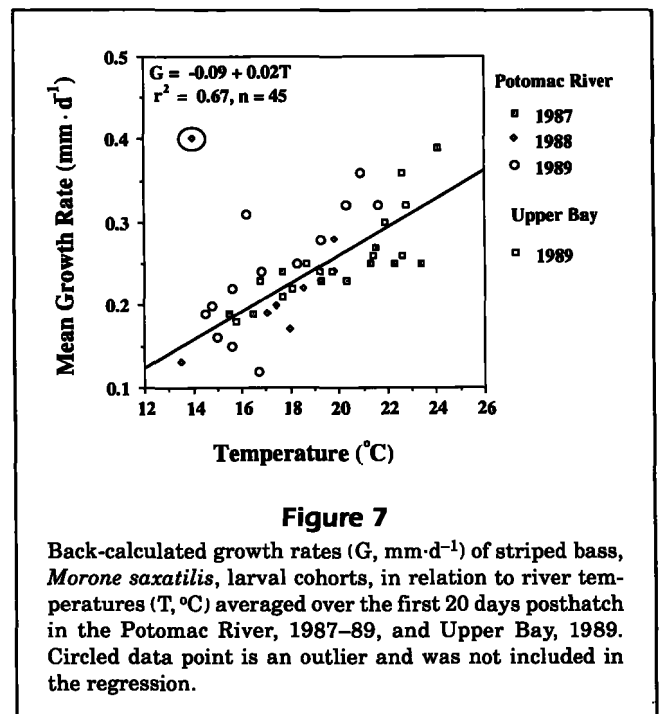
Back-calculated growth rates (G, mm·d⁻¹) of striped bass, *Morone saxatilis*, larval cohorts, in relation to river temperatures (T, °C) averaged over the first 20 days posthatch in the Potomac River, 1987–89, and Upper Bay, 1989. Circled data point is an outlier and was not included in the regression.

cohorts), when mean water temperatures were relatively warm, had within-cohort growth rates and back-calculated lengths at 15 and 20 days posthatch that were positively related to lengths at capture. For example, individual growth rates of Upper Bay larvae hatched on 14 May 1989 were not correlated with their lengths at capture, suggesting that there had been compensation for slow (or fast) growth at earlier ages (Fig. 8). Growth rates of Upper Bay larvae hatched on 23 May were positively related to their

lengths at capture, indicating that initial growth rate differences had been maintained (Fig. 8).

Mortality rates

Mortality rates of larval cohorts, which were highly variable, were not correlated with initial cohort abundance, growth rate, growth rate variability, stage duration, or with any measured environmental factor. Mean mortalities of cohorts from the Potomac River ranged from 21.9 to 23.9% d^{-1} in 1987–89. Cohort-specific mortality rates of Potomac River larvae ranged from Z = 0.05 to 0.92·d^{-1} in 1987, from Z = 0.05 to 0.46·d^{-1} in 1988, and from Z = 0.07 to 0.60·d^{-1} in 1989 (Fig. 9). Temporal trends indicated that mortality rates of Potomac River larvae were high in April, lowest in early May, and apparently highest in late May (Fig. 9). Larval cohort mortality rates in the Upper Bay during 1989 ranged from Z = 0.02 to 0.28·d^{-1}, averaging 11% d^{-1}. There was no obvious temporal trend in Upper Bay larval mortality rates (Fig. 9).
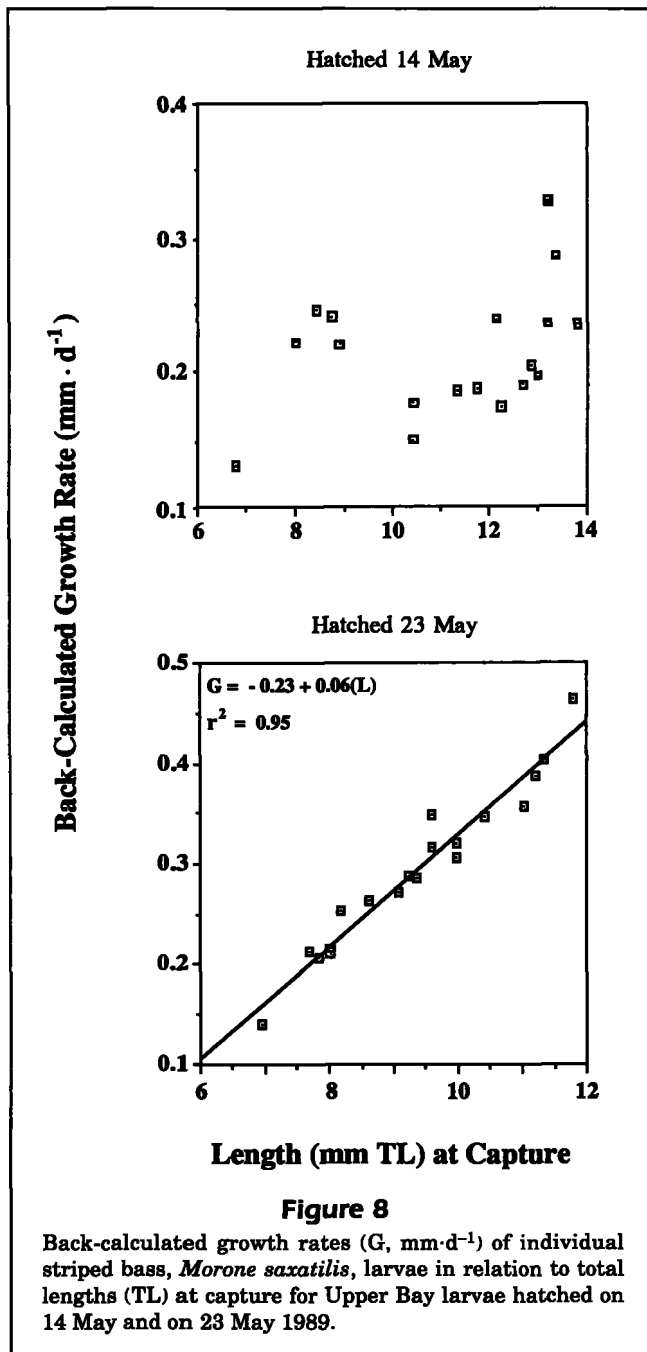
G/Z ratio

The cohort-specific G/Z ratios were variable, but the median values in each year were positively related to apparent year-class strength in the Potomac River. The median ratios were 1.03 in 1987, 0.41 in 1988, and 0.94 in 1989 (Fig. 9). The Upper Bay median G/Z ratio in 1989 was 1.70, a value higher than the Potomac River median ratios because cohort mortality rates generally were lower in the Upper Bay. In the Potomac River, the cohort-specific G/Z ratios in each year were generally highest for cohorts hatched during the last week of April and the first 10 days of May, when growth rates were increasing and mortality rates were lowest (Fig. 9).

Productions of late-stage larvae

Summed cohort productions of 8-mm-SL larvae were correlated with juvenile recruitment indices in the Potomac River, suggesting that recruitment is essentially fixed during the larval stage. Summed cohort productions were 190 million in 1987, 23 million in 1988, and 109 million in 1989. Potomac River indices of juvenile recruitment for those years were 6.4, 0.4, and 2.2, respectively (Schaefer et al.[1]). Summed production of Upper Bay larval cohorts at 8 mm SL was 47 million in 1989. The Upper Bay's juvenile recruitment index in 1989 was 19.4, a value 1.6 times higher than the long-term mean (Schaefer et al[1]).

Most cohorts with larvae surviving to 8 mm SL were hatched late in the spawning season when egg production was low or declining (Fig. 10). In the Potomac River, cohort productions of 8-mm-SL larvae were positively
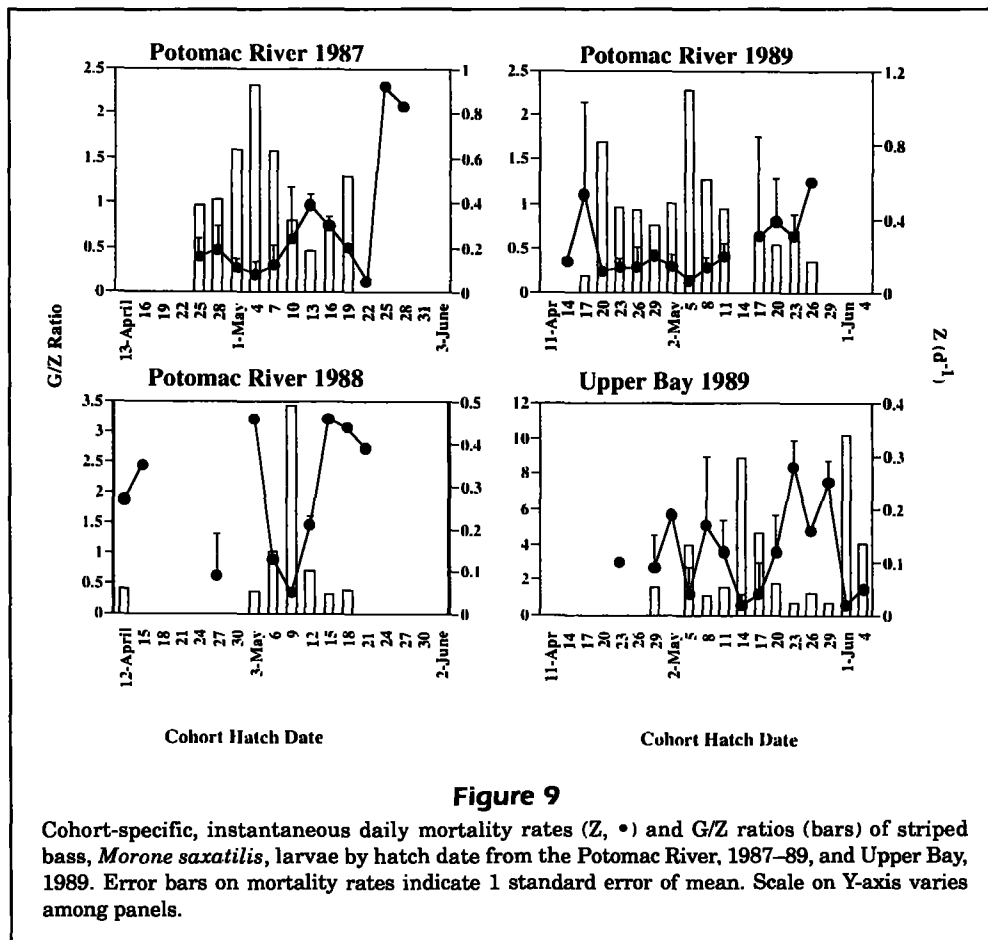

Figure 8
Back-calculated growth rates (G, mm·d^{-1}) of individual striped bass, *Morone saxatilis*, larvae in relation to total lengths (TL) at capture for Upper Bay larvae hatched on 14 May and on 23 May 1989.

Figure 9

Cohort-specific, instantaneous daily mortality rates (Z, •) and G/Z ratios (bars) of striped bass, *Morone saxatilis*, larvae by hatch date from the Potomac River, 1987–89, and Upper Bay, 1989. Error bars on mortality rates indicate 1 standard error of mean. Scale on Y-axis varies among panels.

related to cohort growth rates, and in the Upper Bay to water temperature. The relationships are

for the Potomac River,

$$Ln(N_8) = 6.43 + 31.43 \ (G); \ (r^2=0.22, P<0.01, n=28)$$
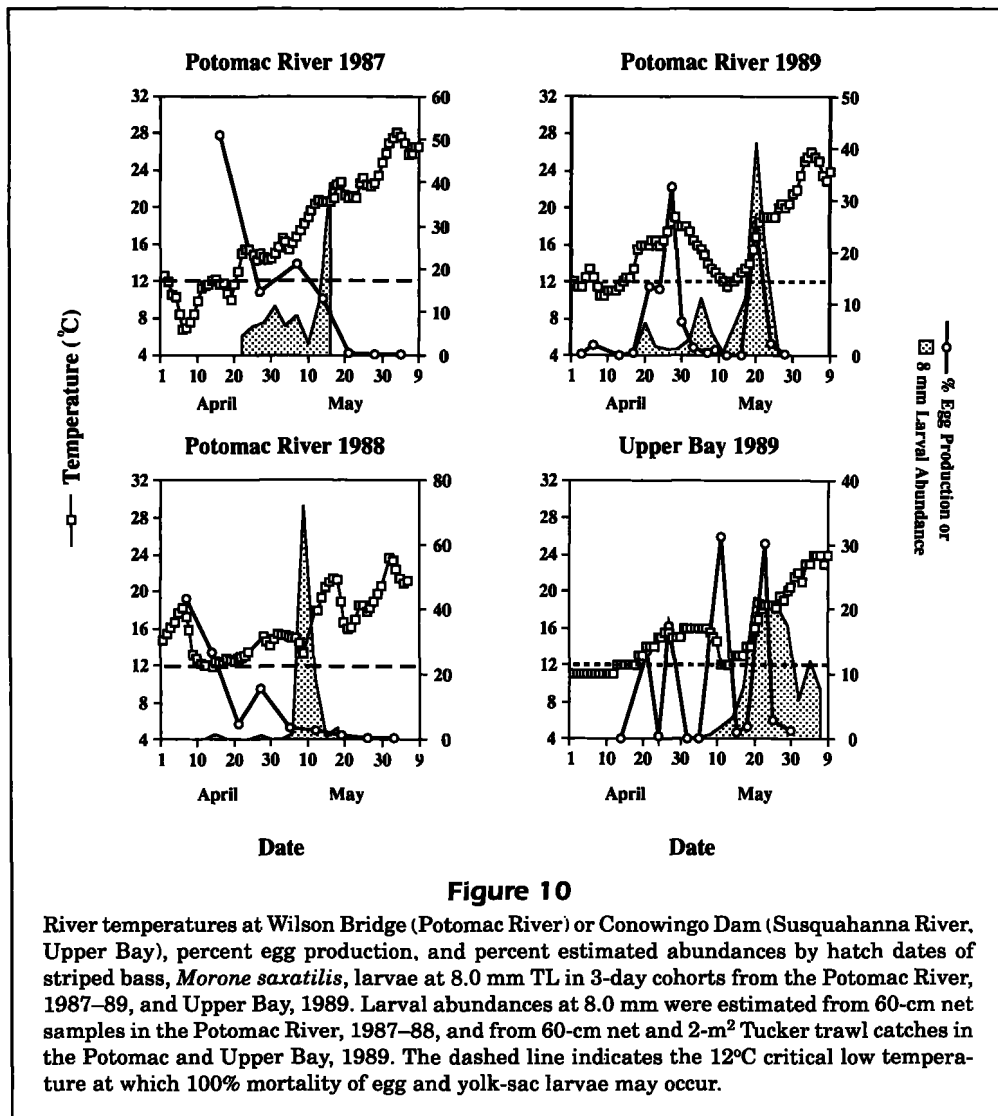
for the Upper Bay,

$$Ln(N_8) = -36.65 + 4.75 \ (T) - 0.11 \ (T^2); \ (r^2=0.91, P<.001, n=12)$$

where $ln(N_8)$ is the log_e-transformed cohort production of 8-mm-SL larvae, G=cohort growth rate (mm·d^{-1}) and T=mean temperature experienced by the cohort from 5–20 days posthatch. In the Potomac River, cohort larval productions at 8 mm SL also tended to be positively correlated with water temperature, but the correlation was not significant ($P>0.10$). In the Upper Bay, cohort production at 8 mm SL was not correlated with cohort growth rate ($P>0.50$).

The relative cohort abundances of larvae collected in the 2-m^2 Tucker trawl on the last day of the sam-

pling season, standardized to 8-mm-SL productions from cohort-specific stage durations and survival rates, provided another indicator of larval survival and potential recruitment. Tucker trawl catches in the Potomac River on 4–5 June 1987 indicated that surviving cohorts, which potentially contributed to recruitment, were hatched from 22 April to 19 May and that most survivors hatched in the 22–25 April and 4–10 May periods (Fig. 11A). In 1988, Tucker trawl catches on 2–3 June indicated that surviving 8-mm larvae were hatched from 3 May to 30 May and that most hatched during the 18–24 May period (Fig. 11B). The 1989 Tucker trawl index of 8-mm larvae on 8–9 June suggested that, while some potential recruits were hatched in every 3-day period from 20 April to 23 May (Fig. 11C), cohorts hatched on 20 April and 14 and 17 May accounted for >80% of the total numbers represented on 8 June.

Relative cohort abundances of 8-mm larvae in the Upper Bay on the last sampling day in 1989 (14 June) indicated that potential recruits were hatched from 5 May to 4 June (Fig. 11D). More than 80% of these larvae were hatched between 14 May and 1 June.
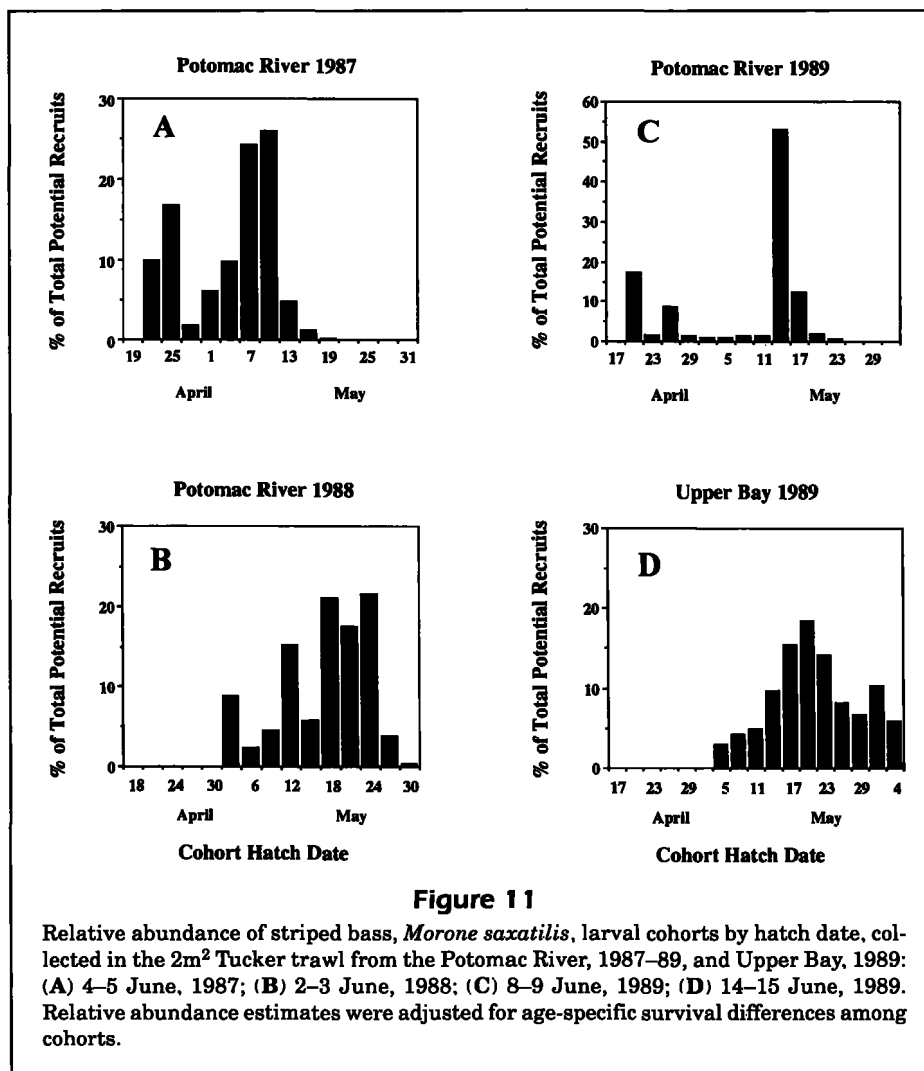
Figure 10

River temperatures at Wilson Bridge (Potomac River) or Conowingo Dam (Susquahanna River, Upper Bay), percent egg production, and percent estimated abundances by hatch dates of striped bass, *Morone saxatilis*, larvae at 8.0 mm TL in 3-day cohorts from the Potomac River, 1987–89, and Upper Bay, 1989. Larval abundances at 8.0 mm were estimated from 60-cm net samples in the Potomac River, 1987–88, and from 60-cm net and 2-m² Tucker trawl catches in the Potomac and Upper Bay, 1989. The dashed line indicates the 12°C critical low temperature at which 100% mortality of egg and yolk-sac larvae may occur.

Discussion

Temperature, larval survival, and growth

Estuarine nurseries of anadromous fishes are dynamic environments, subject to fluctuating and sometimes unpredictable conditions for survival and growth. Striped bass spawn in the freshwater, tidal regions of mid-Atlantic estuaries during the spring months, a transitional season when average temperatures are increasing rapidly, but erratically, from 10 to 25°C. Frequent storms and flood conditions can cause temperatures to drop quickly to lethal or near-lethal levels. The unusually wide range of temperatures to which striped bass eggs and larvae may be exposed suggest that temperature may be a factor controlling growth rate, stage duration, and survival rate.

Our results confirmed that temperature affects larval growth rates and stage durations. Except for observed episodic mortalities associated with temperature drops to or below the 12°C lethal limit, more subtle, direct effects of temperature on mortality rates could not be demonstrated. Despite episodic mortalities which impacted early-spawned cohorts, favorable temperatures during the latter half of spawning seasons resulted in significant potential recruitment from small cohorts of late-spawned eggs. The relatively good potential recruitments in the Potomac River, 1987, and Upper Bay, 1989, were derived from modest, late-season spawning that produced fast-growing larvae in environments where water temperatures were steadily increasing.

The application of otolith-ageing to identify 3-day cohorts and to derive cohort-specific growth and

Figure 11

Relative abundance of striped bass, *Morone saxatilis*, larval cohorts by hatch date, collected in the 2m² Tucker trawl from the Potomac River, 1987–89, and Upper Bay, 1989: (A) 4–5 June, 1987; (B) 2–3 June, 1988; (C) 8–9 June, 1989; (D) 14–15 June, 1989. Relative abundance estimates were adjusted for age-specific survival differences among cohorts.

mortality rates of striped bass larvae allowed us to examine the larval stage dynamics of a species that develops over a broad temperature range. Past research on survival and growth of striped bass larvae has depended upon modal-length analyses, assumed hatch dates, and assumptions about developmental stages and stage-durations to make inferences about early-life dynamics and recruitment potential (Polgar, 1977; Dey, 1981; Uphoff, 1989; Low[3]). Our otolith microstructure analysis demonstrated that in 1987–89, only a few cohorts contributed significantly to Potomac River and Upper Bay recruitments and that successful cohorts were hatched late in the season, grew relatively fast, and had short larval-stage durations.

The critical role of temperature, particularly its potential to cause episodic mortalities and its effect on growth, has been identified in previous research on striped bass. For example, Dey (1981) and Kernehan et al. (1981) argued that year-class fail-

ures in the Hudson River and Upper Chesapeake Bay, respectively, were caused by low-temperature events. Positive relationships between mean growth rates of larval striped bass year classes and temperatures have been reported for the Potomac River (Setzler-Hamilton et al., 1980; Martin and Setzler-Hamilton[7]), the Choptank River (Uphoff, 1989), the Hudson River (Dey, 1981), and the Sacramento-San Joaquin Rivers (Low[3]).

In our study, it was clear that estimated productions of cohorts at 8 mm SL were positively correlated with cohort-specific growth rates. Growth rates, in turn, were strongly and positively correlated with

[7] Martin, F. D., and E. M. Setzler-Hamilton. 1983. Assessment of larval striped bass stock in the Potomac estuary. Final report to U.S. National Marine Fisheries Service. Ref. No. [UMCEES]CBL83-55, 37 p. Available: University of Maryland Center for Environmental and Estuarine Studies, Chesapeake Biological Laboratory, 1 Williams St., Solomons, MD 20688.

temperature, supporting the conclusion that late-hatched cohorts, which grew faster than average, were the principal contributors to striped bass recruitments in 1987–89. Although cohort-specific mortality rates were not significantly related to cohort growth rates or to any measured variable, the annual median G/Z ratios (i.e. for combined cohorts) were positively correlated with the juvenile recruitment index (Rutherford et al.[4]). This result indicated that, while the relationships between growth and survival of individual cohorts are complex and difficult to demonstrate, the effect of reduced stage duration on larval production and on potential recruitment did occur and could be discerned when cohorts were aggregated. Chesney's (1993) simulation model of Potomac River striped bass larval dynamics in 1987 predicted good growth and survival of cohorts hatched late in the season when temperatures and prey densities were high. Research on other species of temperate estuarine and freshwater fishes also has demonstrated that survival and recruitment are highest for fast-growing cohorts (Rice et al., 1987a; Crecco and Savoy, 1985; Jennings et al., 1991), supporting Cushing's (1973) "single-process" concept, in which fast larval-stage growth enhances recruitment success through shortened stage durations.

Differences in mean temperatures between 1987, 1988, and 1989 in the Potomac River may have led to significant differences in production of 8.0-mm-SL larvae, owing solely to effects on stage duration. Egg productions in the Potomac River were approximately 10 billion in 1987 and 1989, and 6.7 billion in 1988 (Houde and Rutherford, 1992). If larval mortality rate had been equal in all years (e.g. Z=0.25), then the mean effect on larval growth and stage duration of the observed 4.0°C higher mean temperature in 1987, compared with 1988 or 1989, could have accounted for a 3.7-fold greater production of 8.0-mm-SL larvae in 1987 than in 1988, and a 2.6-fold greater production in 1987 than in 1989. Our estimated production of 8.0-mm-SL larvae in 1987 was 7.8 and 1.7 times higher, while the juvenile recruitment index (Schaefer et al.[1]) was 16.0 and 2.9 times higher in 1987 than in 1988 or 1989, respectively. Although our results point to temperature as a critical factor and Chesney's (1993) simulation supports this view, other simulation models of major factors thought to influence year-class strengths of Potomac River striped bass suggest that temperature may be less important than maternal size or zooplankton prey abundance (Cowan et al., 1993), or, under special circumstances, than contaminant levels (Rose et al., 1993).

Previous studies of striped bass larval growth have suggested that growth rates are correlated with temperatures in the spawning areas (Dey, 1981; Uphoff,

1989; Low[3]). However, most growth estimates were based upon modal analysis of larval lengths and, consequently, may have been inaccurate. Without benefit of otolith-increment analysis, among-cohort variability in growth rates was unevaluated. In the Choptank River of the Chesapeake Bay, Uphoff (1989) estimated annual mean growth rates of striped bass larvae to be 0.37–0.56 mm·d^{-1} from 1981 to 1986, on the basis of length-frequency distributions. These rates were higher than our mean estimates in the Potomac and Upper Bay and were higher than growth rates of all except 4 of the 46 cohorts that we analyzed, although temperature ranges and prey densities are similar in these Chesapeake Bay tributaries. Larval cohort growth rates that were backcalculated from otolith-aged, juvenile striped bass from South Carolina also were higher (0.35 to 0.68 mm·d^{-1}; Secor, 1990) than most of our estimates. However, larvae from South Carolina experience mean temperatures during spawning and larval development that are 3–5°C higher than temperatures encountered by Chesapeake Bay striped bass (Secor, 1990). Growth rates of Hudson River larvae in 1973–76, estimated from the weekly seasonal increases in larval mean lengths from a designated, arbitrary hatch date until 15 July, were 0.10 to 0.20 mm·d^{-1} (Dey, 1981). Those rates were lower than our mean rates and generally lower than our individual cohort growth rates, even though mean temperatures encountered by larvae in the Hudson and Chesapeake estuaries are similar. Mean annual growth rates of larvae in the Sacramento-San Joaquin River system, estimated for the 1968–86 period from modes in length-frequency distributions, ranged from 0.29 to 0.46 mm·d^{-1} (Low[3]). These rates are higher, on average, than our mean rates, although many cohorts of Chesapeake Bay larvae grew at rates in this range.

Individual growth rate variability

Our analysis of individual larval growth histories to detect evidence of growth compensation and size-selective mortality may have been compromised somewhat by the back-calculation method. Campana's (1990) biological intercept method will provide accurate estimates of mean back-calculated growth rate even in the presence of a "growth effect" but will tend to linearize individual growth rates and mask growth inflections (Campana, 1990; Secor and Dean, 1992). Campana (1990) demonstrated through simulation analysis that time-varying changes in the body length-otolith radius relationship caused by increasing somatic growth rate could result in underestimated lengths at earlier ages and overestimated lengths of older larvae, giving the appearance of com-

pensatory growth by slow-growing individuals and selective mortality against larger individuals within cohorts.

If our analysis of size-selective mortality against larger individuals is correct, it may be that larger individuals experienced higher mortality because their faster swimming speeds increased contact rates with predators. Recent experimental studies (Litvak and Leggett, 1992; Monteleone and Houde, 1992; Pepin et al., 1992; Cowan and Houde, 1993) indicate that as larvae grow and encounter different predator fields, their probability of being encountered and eaten by some predators may increase, resulting in a higher mortality rate for larger individuals than for smaller individuals. Effects of selective mortality against smaller individuals may not become apparent until later in the larval stage (e.g. Post and Prankevicius, 1987), because it takes time for differences in growth rate to result in significant differences in size that would lower vulnerability to predation (Rice et al., 1993).

We had hypothesized that mortality would select against smaller individuals within cohorts, and that cohorts with higher mean growth rates and highly variable growth rates would contribute more potential recruits than cohorts with lower and less variable growth rates (Pepin, 1989; DeAngelis et al., 1991; Rice et al., 1993). In our study, although mortality rates may have been highest for the largest or fastest-growing individuals, cohorts contributing most to recruitment in each year were those hatched near the end of the spawning season and which had higher but not more variable growth rates than those hatched earlier. For example, in the Potomac River, 1989, late-hatched cohorts grew, on average, nearly twice as fast from 5–20 days posthatch as did early-hatched cohorts. The high productions of late-hatched, fast-growing cohorts suggest that stage duration, by reducing the time that larvae experience high mortalities, is more important than body size alone in determining potential recruitment of striped bass.

Prey densities and growth

The failure to detect any significant influence of prey density on cohort-specific growth, survival, or abundance at 8.0 mm SL was surprising, because mean zooplankton densities were highest in the Potomac River and Upper Bay in years when mean growth rates, G/Z ratios and recruitment indices were highest (Rutherford et al.[4]). Laboratory, pond, and model-simulation studies have demonstrated repeatedly that growth and survival of striped bass larvae increase as prey density increases (Miller, 1976;

Eldridge et al., 1981; Rogers and Westin, 1981; Houde and Lubbers, 1986; Tsai, 1991; Chesney, 1989, 1993; Daniel[8]). The strong and dominant effect of temperature upon larval growth rate may have obscured effects of prey density at the cohort-specific level. In the Potomac River, 1987, and in the Upper Bay, 1989, when highest growth rates were observed, zooplankton densities were highest, increased as the season progressed, and were correlated positively with temperature. In the Potomac River, 1988 and 1989, zooplankton densities were lower and not significantly correlated with temperature, yet growth rates of striped bass cohorts at similar temperatures did not differ significantly from the cohort rates in 1987, indicating that the temperature effect dominated.

It is possible that the failure to demonstrate a relationship between temperature-adjusted, cohort-specific growth rates and prey densities was an artifact that resulted from backcalculating growth rates from mostly older larval survivors. Growth rates of these larvae conceivably may have been higher than growth rates of larvae that died (Miller et al, 1988; Pepin, 1989) and may have obscured impacts of low prey densities on growth. Although for most cohorts, back-calculated growth rates and lengths at age of larvae collected early in the season were not significantly lower than rates and lengths at age of larvae caught later, this result might be artifactual, because of the potential bias on back-calculated growth histories caused by nonlinear changes in the otolith-body size relationship.

We believe that recruitment level of striped bass in Chesapeake Bay is essentially set by the abundances of cohorts that survive to 8.0 mm SL. Relative productions at 8.0 mm SL and abundances in the juvenile surveys conducted 50 to 100 days later were strongly correlated in the Potomac River and Upper Bay (Rutherford et al.[4]). Other evidence that striped bass recruitment is fixed during the early postlarval stage (8.0–10.0 mm TL) has resulted from research on striped bass in the Choptank River (Uphoff, 1989) and from the Sacramento-San Joaquin system (Low[3]). Our results demonstrate that not only is recruitment potential fixed by 8.0 m SL but that relatively few daily cohorts contribute significantly to recruitment in most years. The success of particular cohorts is strongly dependent upon the temperature regime that larvae experience between hatch and 8.0 mm SL. Examination of intraseasonal differences in cohort-specific growth, survival, and pro-

[8] Daniel, D. A. 1976. A laboratory study to define the relationship between survival of young striped bass (*Morone saxatilis*) and their food supply. Calif. Dep. Fish and Game, Anadromous Fisheries Branch, Admin. Rep. 76-1, Sacramento, CA, 13 p. Available: California Department of Fish and Game, Anadromous Fisheries Branch, Sacramento, CA.

duction has provided a clearer picture of the processes influencing striped bass recruitment than could have been obtained solely from analysis of interannual differences in larval vital rates and abundances.

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