Growth, mortality, and recruitment of larval *Morone* spp. in relation to food availability and temperature in the Hudson River

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Abstract.–We measured age and growth of larval striped bass (*Morone saxatilis*) and white perch (*M. americana*) and tested whether growth and survival were enhanced in relation to a seasonal pulse ("bloom") of high zooplankton abundance. Growth rates were lowest before the zooplankton bloom and highest afterwards for both fish species. An index of recruitment potential (instantaneous growth rate, *G*, divided by instantaneous mortality rate, *Z*) did not relate clearly to either water temperature or to zooplankton abundance in the case of striped bass but did relate to both factors for white perch. Retrospective analysis of hatch dates in recruited juvenile striped bass from the same year class indicated that later, faster growing cohorts were under-represented when compared to the larval cohort distribution, and that cohorts that co-occurred with high densities of the cladoceran zooplankton *Bosmina freyi* were over-represented. Comparison of these results with similar analyses from other systems suggests that biotic controls on year-class strength may predominate in estuarine systems where physical factors are relatively damped (Hudson) but may play relatively minor roles in those systems with high physical variability.

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Survival during the first year of life determines the year-class strength of many fish. The degree to which biotic or physical factors regulate recruitment of fish from larval to juvenile stages varies from one aquatic system to another, and even temporally within systems (Leggett and DeBlois, 1994). The factors promoting or inhibiting recruitment are a subject of intense interest both in theoretical analysis and practical management of fish populations (cf. Hilborn and Walters, 1992). Mortality of young fish below harvestable size is difficult to observe and difficult to measure by means of standard approaches to population assessment (e.g. mark and recapture).

The age and growth rates of young fish, however, can be precisely quantified with otolith analysis (cf. Campana and Neilson, 1985; Secor et al., 1995). This technique has permitted the determination of hatching dates, age, and growth rates of both larvae and juveniles of many species. Comparisons of hatching dates and growth between life stages (e.g. larvae vs. juveniles) allow inferences about the fates of larvae. For example, if larval survival is particularly high during a specific time period, analysis of juvenile hatch dates should reflect the differential survival (assuming adequate sampling). These measures can also be used with repeated samplings of the population to track the growth and mortality of specific age classes (e.g. weekly cohorts) over time. Relationships between these cohort-based rates can be analyzed with respect to variables such as food availability, predation, and the physicochemical environment.

We previously documented that larval striped bass (*Morone saxatilis*) and white perch (*M. americana*), which co-occurred with increases in crustacean zooplankton in the tidal Hudson River, showed a potential energetic advantage compared with larvae that preceded the zooplankton increase (Limburg et al., 1997). A major increase ("bloom") in zooplankton in early summer is a key feature of the Hudson estuary. Larvae occurring before the bloom are exposed to sparse zooplankton densities and low temperature, both of which are associated with mortality risks (Rogers and Westin, 1981; Chesney, 1989; Margulies, 1989; Uphoff, 1989; Tsai, 1991; Cowan et al., 1993). Larvae occurring during and after the bloom have high consump-

tion rates and are at lower risk of exposure to suboptimal or lethal temperatures.

Do these temperature and food conditions translate into differential survival conditions for larval *Morone* spp. in the Hudson River? We addressed this question using methods of otolith age and growth-rate reconstruction. Specifically, we tested if periods of high food availability (zooplankton bloom conditions) were also periods of high larval growth rates. Further, by analyzing the otoliths of juveniles of the same year class (i.e. successful recruits from the larval stage), we also assessed whether or not fish that survived the larval period had high larval growth rates and hatching dates associated with the zooplankton bloom.

Studies of *Morone saxatilis* in Chesapeake Bay tributaries have used both interannual variations in larval abundance (Uphoff, 1989) and cohort analysis methods (Rutherford and Houde, 1995; Secor and Houde, 1995; Rutherford et al., 1997) to establish that rapid drops in water temperature below 12°C virtually eliminate larval cohorts. These studies concluded that the frequency of low temperature events can be an important factor in the recruitment of striped bass in those systems. In contrast, Pace et al. (1993) found no evidence that temperature affected interannual variation of *Morone* spp. recruitment in the Hudson River, although Dey (1981) presented evidence for temperature-induced mortality in Hudson River striped bass in 1976 (temperature dropped suddenly from 15° to 12°C in late May). Thus temperature effects, although not detectable among years, might still manifest themselves as seasonal variability. In this paper we examine the 1994 year classes of striped bass and white perch, including an appraisal of the relation of zooplankton abundance and temperature to growth and mortality of individual cohorts. With this information, we can make tentative comparisons between analyses for the Hudson River and Chesapeake Bay.

Materials and methods

The Hudson River, a partially stratified estuarine-river system in New York State, is tidal up to the Green Island dam, 245 river kilometers (rkm) from the mouth. All life stages of white perch are found throughout the oligohaline and freshwater sections of the estuary (Klauda et al., 1988). Striped bass adults migrate into the estuary in spring to spawn. Larvae are found in both freshwater and oligohaline sections (Boreman and Klauda, 1988). Juveniles spread throughout the estuary and move seaward during late summer and fall (Dovel, 1992).

Larval collections and preparation

Field collections of larval *Morone* spp. were undertaken in the spring and early summer of 1994. Sampling details are described in Limburg et al. (1997). Briefly, three sites, in the upper (Kingston, rkm 148), middle (New Hamburg, rkm 105), and lower (Haverstraw Bay, rkm 65–70) portions of the estuary were sampled between 18 May and 6 July; all sites overlapped with spawning areas. Sampling frequency was designed to examine larval and zooplankton dynamics before, during, and after the intensive bloom of the cladoceran zooplankton *Bosmina freyi* (=*Bosmina longirostris* with older nomenclature). Fish were collected during the daytime with 5-min oblique tows of 0.5-m diameter bongo nets (500-mm mesh). Five replicate tows were conducted at each site on each date. Samples were preserved in 100% ethanol which, when diluted with the sample, reached a final concentration of no less than 75%. Care was taken not to over-dilute the samples below this concentration because of risk of otolith erosion (Brothers, 1987).

In the laboratory, fish were sorted by family and stored in fresh 100% ethanol. Three replicates were chosen at random from the five available at individual stations for each sampling date, and up to twenty *Morone* individuals were arbitrarily selected from each replicate; more replicates were used when larval abundances were low. The larvae were rehydrated, soaked for 15 min in sodium borate buffer solution (30% saturated sodium borate), and then cleared by adding a small quantity of trypsin to the buffer solution. *Morone* larvae were measured to 0.1 mm notochord length (NL) and identified to species by a combination of internal and external characters (Limburg et al., 1997). Lengths were not corrected for preservation shrinkage, but rehydration and clearing fully relaxed constricted musculature so that lengths were readily measured. Otoliths were visible under 25× magnification on a stereomicroscope. Fine insect pins, the tips of which were sharpened further, were used to dissect the sagittal otoliths. Otoliths of fish less than 5 mm NL were cleaned in deionized water and placed directly in mineral oil for later viewing. Following the suggestion of Rutherford (1992), otoliths of larger (>5 mm NL) fish were embedded in Spurr's epoxy, then ground and polished with a series of increasingly fine grinding papers (down to 3 mm).

Juvenile fish collection and preparation

In order to make comparisons between recruited juveniles and larvae, we obtained a total of 218 juve-

nile striped bass from five sites along the Hudson River (at river kilometers (rkm) 40, 63, 95, 114, and 201) during July (n=37), August (n=88), and September (n=93) from state-run fishery surveys. Fish were collected either with a 30.5-m (100-ft) beach seine with 6.1-m bag, 0.64-cm mesh, or with a 61-m (200-ft) beach seine with 1.27-cm stretch mesh (0.64 cm square). Fish were held on ice in the field, then stored frozen.

In the laboratory, juvenile striped bass were defrosted, and standard, fork, and total lengths (SL, FL, and TL respectively) were measured. Sagittal otoliths were removed from each fish, cleaned in 10% sodium hypochlorite (bleach), and embedded in Spurr's epoxy. One otolith from each pair was subsequently sectioned along the transverse axis and prepared in thin section according to the method of Secor et al. (1991). A total of 63 juvenile otoliths were successfully prepared and read.

Otolith microstructure analysis

Otolith microstructure was examined with a light microscope with a video attachment connected to an image analysis system. Specimens were viewed in the sagittal plane by using the digital image for projection. Most specimens were viewed at magnifications of 500–750×, but 1250× (100× objective) was used to resolve the finest increments. Increments were counted several times and averaged. Larval otoliths were examined by one reader, and two independent readers were used to cross-check the consistency of increment counts for juvenile striped bass otoliths.

Ages were estimated by correcting for the effect of temperature on the timing of first increment deposition (Houde and Morin[1]). Age at first increment deposition was estimated as (11.56–0.45 T) for striped bass and (9.05–0.32T) for white perch, where T is water temperature (Houde and Morin[1]). From our measurements of water temperature (n=30) from 14 April to 19 July 1994, we estimated a linear increase in river temperatures over the study period with the regression

$$Water\ temperature = -17.6 + 0.23 \times (day\ of\ year) \quad [r^2=0.98,\ P<10^{-4}].$$

We used this equation to estimate water temperatures on the day of the first increment and assumed little change in temperature back to the hatching day. Ages were estimated as number of increments + temperature adjustment; hatching dates were then backcalculated from the date of capture.

Image analysis was used to measure increment widths. For larvae, widths of the total number of increments on an otolith were measured and averaged to obtain an average daily increment width (in mm). In addition, when possible, widths of the first five increments (I1–I5) and of the sixth and seventh increments (I6–I7) were measured to obtain two standardized estimates of early growth. Increments I1–I5 exhibited slower average growth than did increments I6–I7. In all, otoliths of 248 larval striped bass and 526 larval white perch were examined.

Somatic growth rates were calculated for larvae and juveniles by the equation

$$(L_t - L_{t_0})/Age,$$

where L_t = length at capture; and
L_{t_0} = length at hatch.

L_{t_0} is assumed to be 3.0 mm for white perch and 4.0 mm for striped bass (Mansueti, 1958; Lippson and Moran, 1974). In addition, "standardized" growth rates were calculated for 7-day-old larvae so that comparisons of growth could be made before, during, and after the zooplankton bloom. This was done by determining the number of increments deposited by age 7 (typically <5), multiplying that number by the mean increment width of I1–I5, adding the result to the otolith core radius, and then by using the following regressions to calculate standard lengths at age 7 days:

$$SL_{SB} = -0.37 + 1.95\ (\text{natural log of otolith width}) \quad [r^2= 0.83,\ n=210,\ P<10^{-4}],$$

$$SL_{WP} = -1.67 + 2.18\ (\text{natural log of otolith width}) \quad [r^2= 0.88,\ n=522,\ P<10^{-4}].$$

The same procedure was used to backcalculate age 7-d somatic growth rates for juvenile striped bass.

Mortality and recruitment potential

For purposes of comparison with Chesapeake Bay studies, mortality rates were estimated for fish larvae collected at New Hamburg (rkm 105) by using a method similar to that described in Secor and Houde (1995). Cohort analyses were confined to the New Hamburg station because we were able to collect both species consistently in large numbers. All larvae in these samples were counted, and lengths of at least

[1] Houde, E. D., and L. G. Morin. 1990. Temperature effects on otolith daily increment deposition in striped bass and white perch larvae. International Council for the Exploration of the Sea, Copenhagen, Denmark, Council Meeting 1990/M:5.

100 individuals were measured unless fewer than 100 occurred in the sample. Densities (numbers of fish per 1000 m^3) by 0.5-mm size class were computed and corrected for differences in day and night catch efficiencies, and for extrusion of smallest individuals, by using regressions in Houde et al.[2]

Age distributions of fish collected on different sampling dates were estimated from the otolith-aged fish. Rather than estimate variance from an age–length regression and use it to assign probabilities of age-at-length (Secor and Houde, 1995), we estimated the mean and variance in ages for each 0.5-mm size group and used those parameters to assign age-at-length probabilities (*z*-scores).

The corrected catch densities, separated into 0.5-mm size classes, were multiplied by the appropriate size-based age distributions to obtain numbers of fish of different ages. Following Secor and Houde (1995), hatching dates were calculated and fish were grouped into 6-d cohorts. In some of the cohorts, the age-estimation technique resulted in very small initial numbers of fish. If these numbers were tenfold smaller than the maximum calculated densities of a cohort, they were deleted from the data set. Then mortality rates (Z) of the cohorts were estimated by fitting an exponential decay model to abundances of fish within specific cohorts over time.

We used an index (Rutherford and Houde, 1995; Secor and Houde, 1995) of mean instantaneous growth (estimated for an individual fish as $G = \ln(W_t/W_0)/t$, where t = age at capture, W_t = weight at capture, and W_0 = weight at hatch) over instantaneous mortality rate (G/Z) to compare the benefits accrued in growth versus the costs expressed as mortality for larvae occurring before, during, and after the zooplankton bloom. Weights were estimated from lengths by the equation

$$W = 3.763 \times 10^{-4} \times L^{(4.2879)} \quad [n=67,\ r^2=0.92,\ P<10^{-6}];$$

where W = mg wet weight; and
L = length in mm (Limburg et al., 1997).

Finally, we estimated the dates of first-feeding for striped bass larvae and juveniles with respect to the zooplankton bloom. We assumed that fish begin to feed at day 5 after hatching. We used an age-length regression from the 63 juvenile striped bass to estimate ages of the remaining juveniles. We assumed that little or no out-migration would be occurring in July and August (Dovel, 1992), so that fish collected during these months would show the effect of differential recruitment without the confounding process of out-migration.

Table 1

Mean (± SD) somatic growth rates (GR, mm/d) of larval white perch and striped bass, by site and date, 1994. (n=526 white perch and 248 striped bass; n.d.=no data; — = zero fish in samples.)

	White perch			Striped bass		
Date	Mean GR	SD	*n*	Mean GR	SD	*n*
Haverstraw Bay (rkm 65–70)						
18 May	0.181	0.067	15	0.072	0.069	9
24 May	—	—	0	—	—	0
3 June	0.186	0.054	17	0.185	0.111	29
7 June	0.409	0.215	9	0.286	0.128	25
10 June	0.211	0.086	8	0.178	0.111	8
13 June	0.382	—	1	0.250	0.046	17
22 June	0.427	0.199	3	0.293	0.088	36
29 June	0.313	—	1	0.284	0.007	3
6 July	n.d.			n.d.		
New Hamburg (rkm 105)						
18 May	—		0	—		0
24 May	0.155	0.037	37	0.069	0.022	3
3 June	0.192	0.060	47	0.162	0.127	11
7 June	0.218	0.070	42	0.216	0.084	14
10 June	0.236	0.085	35	0.247	0.030	4
13 June	0.210	0.081	29	0.224	0.039	8
22 June	0.265	0.083	11	0.207	0.056	9
29 June	0.306	0.049	11	0.252	0.084	20
6 July	0.331	0.052	9	0.264	0.062	40
Kingston (rkm 148)						
18 May	—		0	—		0
24 May	0.205	0.061	9	0.044	0.027	3
3 June	0.167	0.053	52	0.032	0.054	6
7 June	0.200	0.053	47	0.146	0.189	2
10 June	0.201	0.089	59	0.017	—	1
13 June	0.196	0.086	35	—	—	0
22 June	0.245	0.113	12	—	—	0
29 June	0.300	0.099	37	—	—	0
6 July	n.d.			n.d.		

Results

Growth rates

Mean somatic growth rates (GRs) of both species of *Morone* tended to be lowest prior to the bloom (before 3 June); rates were higher after the bloom (22 June and later), especially for white perch (Table 1;

[2] Houde, E. D., E. J. Chesney, R. M. Nyman, and E. S. Rutherford. 1988. Mortality, growth and growth rate variability of striped bass larvae in Chesapeake subestuaries. Interim Report to Maryland Department of Natural Resources. Chesapeake Biological Laboratory, Solomons, MD. Ref. No. [UMCEES]CBL 88-96, 126 p. [Available: Chesapeake Biological Laboratory, Box 38, Solomons, MD 20688.]

Fig. 1). There were significant site, species, and site × species effects on mean somatic GRs ($P<10^{-4}$), with highest GRs at the southernmost site (Haverstraw Bay). Mean somatic growth rate for striped bass was 0.053, 0.232, and 0.238 mm/d at Kingston, New Hamburg, and Haverstraw Bay, respectively (greater than an eightfold difference between highest and lowest; it should be noted that the total number of fish sampled at Kingston was very small). Growth rates for white perch did not vary as greatly but did vary in the same longitudinal direction (0.209, 0.215, and 0.245 mm/d at Kingston, New Hamburg, and Haverstraw Bay). Time series of somatic GRs, averaged over all sites for each species (Fig. 1), revealed species-specific patterns of growth with respect to the zooplankton bloom period. Striped bass GRs accelerated more strongly during the bloom period than did GRs of white perch.

Somatic growth rates were related to water temperature as

$$GR = -0.050 + 0.013 \times MWT \quad [r^2=0.15,\ n=774,\ P<10^{-6}],$$

where MWT = mean water temperature during the life of the individual larva (calculated as the temperature midway through the larva's life).

The effect of temperature was removed by calculating residuals of this regression and by using the residuals as a new data set (temperature-adjusted GRs) to assess growth relative to zooplankton dynamics. Temperature-adjusted somatic GRs for white perch showed little trend with respect to the zooplankton bloom, whereas striped bass GRs peaked during the bloom (Fig. 2). This peak was not significantly greater than the adjusted GRs after the bloom, but both differed significantly from the prebloom-adjusted GRs.

Our comparisons of somatic growth rates are based on fish larvae of different sizes and ages. Comparisons of growth rates for a standardized age (we chose age=7 days) can eliminate this potential source of bias. Mean 7-d GRs (Fig. 3) showed a pattern similar to that for overall mean GR, indicating that growth rates did not peak during the zooplankton bloom. Although both species' 7-d GRs varied significantly with respect to the bloom (with highest GRs after the bloom), white perch 7-d GRs did not differ significantly from striped bass 7-d GRs.

Recruitment potential at New Hamburg

Ten 6-d age cohorts, grouped arbitrarily starting 1 May (cohort A) and extending through the period beginning 24 June (cohort J), were identified in the catches at New Hamburg (rkm 105). Insufficient numbers prohibited estimation of Z for the last striped bass cohort (J, 24–29 June) and the last two white perch cohorts (I and J). Estimates of white perch starting densities (natural log of N_0) were highest in early cohorts (A and B; Table 2). Striped bass initial density estimates were highest in later cohorts (E, G, and H; Table 2). Earliest and latest cohorts were poorly estimated owing to low sample numbers.

Estimated mortality rates were highest in cohort A for both species (Table 2). Cohort A (period starting 1 May) appeared only in two samples; presumably recruitment from this group was very low. For white perch, mortality rates declined more or less monotonically with time (and therefore also with increasing temperature). Striped bass mortality rates were also lowest in the latest cohorts, but there did not appear to be a systematic decline (Table 2).

Instantaneous growth rates (G) in striped bass did not vary

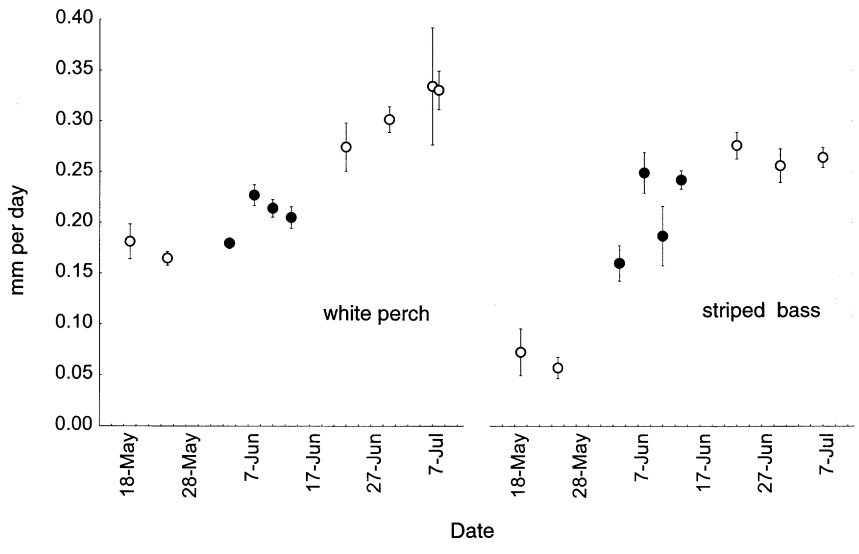

Figure 1

Mean (±SE) somatic growth rates of larval white perch and striped bass, averaged across all sampling sites, 18 May–6 July 1994. The darkened points on each graph indicate the period of the *Bosmina* bloom.

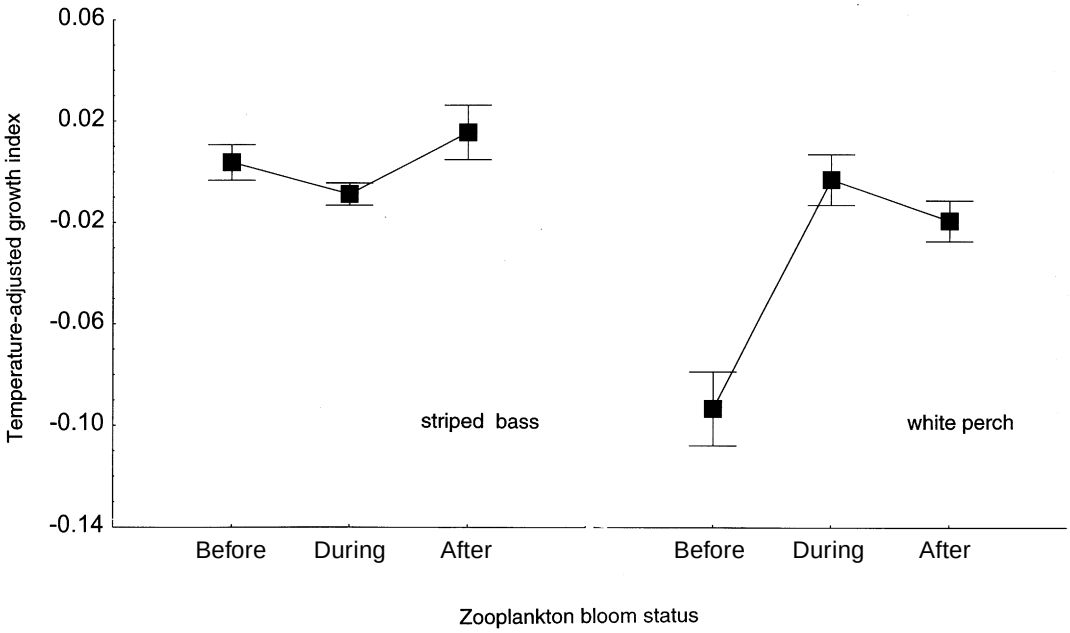

Figure 2

Mean (±SE) somatic growth rates (residuals) of larval white perch and striped bass with the effect of temperature removed, grouped with respect to the *Bosmina* bloom.

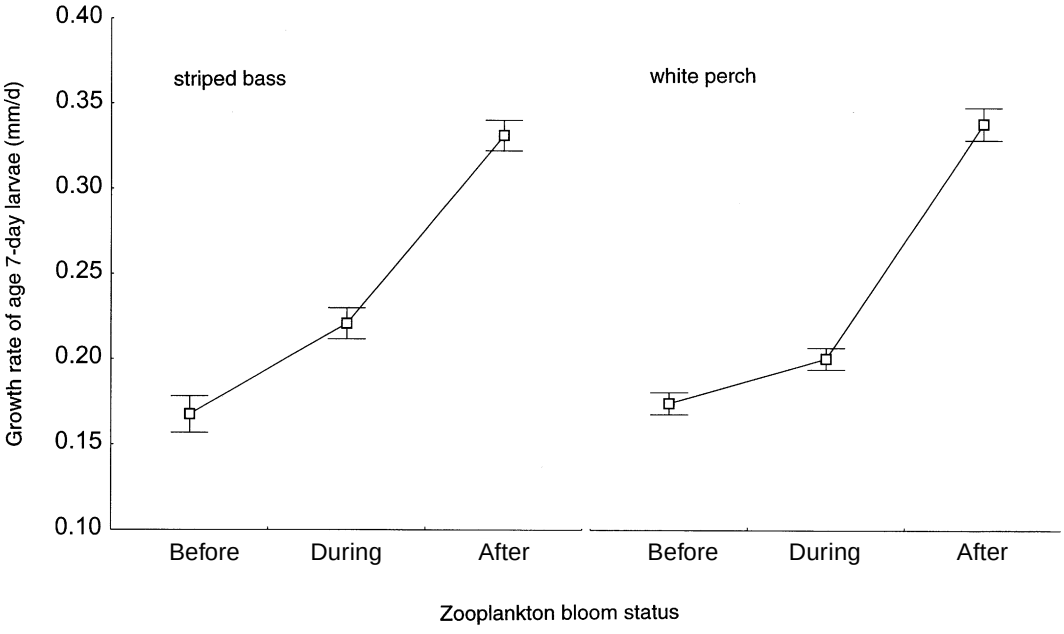

Figure 3

Mean (±SE) growth rates of 7-day old larval white perch and striped bass, grouped with respect to the *Bosmina* bloom.

in a consistent manner, either with temperature or zooplankton density (Table 3). Striped bass *G* peaked in cohort E (those hatched 25–30 May), as did *G*/*Z*. Neither *G*, *Z*, nor *G*/*Z* for striped bass were significantly affected by either temperature or zooplankton densities estimated during the week of hatching.

Table 2

Estimates of natural logs of initial densities (N_0, numbers per 1000 m^3) and mortality rates (Z) for 6-d cohorts of striped bass and white perch in the Hudson River (New Hamburg site). Letters designate cohorts referred to in text.

Date	Cohort	ln(N_0)	SE	Z	SE	r^2	P	n
Striped bass								
1–6 May	A	4.132		1.51				2
7–12 May	B	7.598	6.153	0.262	0.315	0.41	0.55	3
13–18 May	C	6.919	2.070	0.263	0.132	0.66	0.19	4
18–24 May	D	5.941	2.207	0.296	0.110	0.64	0.05	6
25–30 May	E	7.690	0.751	0.260	0.034	0.94	0.001	6
31 May–5 June	F	6.502	0.549	0.176	0.027	0.91	0.002	6
6–11 June	G	8.808	0.103	0.221	0.005	0.99	0.01	3
12–17 June	H	7.645	0.767	0.163	0.048	0.92	0.18	3
18–23 June	I	6.977		0.145				2
White perch								
1–6 May	A	16.653		0.785				2
7–12 May	B	12.484	2.905	0.509	0.138	0.87	0.07	4
13–18 May	C	9.221	1.299	0.328	0.064	0.87	0.007	6
18–24 May	D	8.058	1.284	0.241	0.064	0.78	0.02	6
25–30 May	E	9.682	1.022	0.304	0.051	0.90	0.004	6
31 May–5 June	F	7.861	0.807	0.187	0.049	0.83	0.03	5
6–11 June	G	5.811	1.295	0.044	0.087	0.21	0.70	3
12–17 June	H	7.885		0.137				2
18–23 June	I	insufficient data						

Table 3

Estimated instantaneous growth (G) rates (± standard error), and index of recruitment potential (G/Z) for 6-d cohorts of larval striped bass (SB) and white perch (WP), New Hamburg (rkm 105), 1994. Calculated water temperatures (see "Methods") and zooplankton densities (copepods and *Bosmina*, no./L), corresponding to each cohort, are included. Zooplankton densities are offset by 5–7 d from actual sample dates (e.g. the zooplankton sample associated with cohort G was collected on 10 June) to approximate the lag in initial feeding by larvae. n.d. = no data. G/Z in parentheses were calculated with the previous cohorts' Z estimates but were not used in analyses.

Cohorts	Dates	Temperature (°C)	Zooplankton density	G_{SB}	SE	G/Z_{SB}	G_{WP}	SE	G/Z_{WP}
A	30 Apr 1994								
B	5 May 1994	12.2	n.d.				0.125	0.006	0.245
C	12 May 1994	13.6	1.88	0.205	0.056	0.779	0.125	0.006	0.380
D	18 May 1994	15.0	10.9	0.205	0.056	0.693	0.141	0.043	0.583
E	24 May 1994	16.4	35	0.564	—	2.169	0.132	0.010	0.436
F	30 May 1994	18.0	80.5	0.070	0.009	0.398	0.159	0.007	0.850
G	05 Jun 1994	19.4	520	0.092	0.012	0.416	0.378	—	8.521
H	11 Jun 1994	20.8	70	0.113	0.021	0.693	0.196	—	1.427
I	17 Jun 1994	22.2	4.1	0.097	0.035	0.671	0.150	0.036	(1.095)
J	23 Jun 1994	23.5	5.6	0.171	0.228	(1.179)			

In contrast, white perch G was significantly correlated with zooplankton density ($G_{WP}=0.136+4.64\times10^{-4} \times$ (*zooplankton density*), $r^2=0.96$, $P<10^{-4}$). The high significance was due to the highest growth at a time of maximum zooplankton density (520 individuals/L), but the regression relationship remained the same even with removal of the influential point. Lowest mean G/Z occurred before the bloom (0.35 ±0.18 SD, $n=4$), intermediate G/Z during the bloom (1.27 ±1.06, $n=2$) and highest afterward (2.53 ±2.04, $n=2$), but these were not significantly different. Although there is a tendency toward increasing G/Z with time (and temperature), it was not statistically significant either.

Table 4

Mean growth (mm/d, calculated from otoliths) at age 7 d after hatching of larval and juvenile striped bass, 1994.

	Bloom status	Mean	SD	*n*
Larvae	Before	0.167	0.072	45
	During	0.221	0.062	47
	After	0.331	0.079	77
Juveniles	Before	0.199	0.080	18
	During	0.215	0.063	33
	After	0.223	0.056	12

Retrospective early life histories of juvenile versus larval striped bass

Larval and juvenile striped bass from the 1994 year class had similar patterns of early growth, as measured by mean growth (mm/d) through age 7 days after hatching. In both groups, growth rates increased monotonically from May through early July corresponding with before, during, and after the zooplankton bloom ($P<0.01$; Table 4). Juvenile mean growth rates before and during the zooplankton bloom were higher (though not significantly so) than larval growth rates in the corresponding periods. However, mean 7-d growth rates of postbloom juveniles were significantly ($F(1,87)=21.03$, $P<10^{-4}$) lower than growth rates of postbloom larvae.

The frequency (distribution of hatching dates) of juvenile striped bass born in the 6-d cohorts beginning 1 May did not correlate well with the index of recruitment (G/Z) developed from the larval data (*Frequency*=0.118+0.021 (G/Z), $r^2=0.03$).

Because of our ability to "hind-cast" the distribution of hatching dates of juveniles and larvae, we estimated the relative proportions of both larvae and juvenile striped bass that would have begun to feed during the zooplankton bloom (assuming that feeding begins at day 5 after hatching). For this analysis, we analyzed the fish response to *Bosmina* and copepods. For *Bosmina* we assumed that fish with hatching dates between 29 May and 8 June would be able to feed on *Bosmina*; we further assumed that fish hatched between 5 June and 17 June would also be able to take advantage of the bloom of copepods (note that in this analysis we assume that *Bosmina*-feeders occurred above Haverstraw Bay and that copepod feeders occurred throughout the river).

Larval distributions indicated that 37% of the population began to feed after the bloom of *Bosmina* (Fig. 4A), and 26% initiated feeding during the bloom. Of larvae that occurred in the geographic range of *Bosmina* (at New Hamburg and Kingston), over half began to feed after the bloom and less than 20% began feeding during the bloom. In contrast, 44% of juvenile striped bass began to feed during the bloom of *Bosmina* (Fig. 4A); and of the fish identified as first feeding prior to the onset of the bloom, 23% were hatched after 25 May, so that these fish would have been relatively close to first feeding at the time that *Bosmina* numbers increased exponentially. Those survivors to the juvenile stage that began to feed after the *Bosmina* bloom composed the smallest fraction (26%). The first-feeding distributions of larvae and juveniles differed significantly with respect to the *Bosmina* bloom (2×3 contingency analysis, $\chi^2=13.4$, df=2, $P<0.01$), whereas distributions of larvae and juvenile fish with respect to the bloom of copepods did not differ from one another ($\chi^2=3.7$; Fig. 4B). Thus the time period associated with the *Bosmina* bloom, and not the copepod bloom, appears to have been related to successful striped bass recruitment.

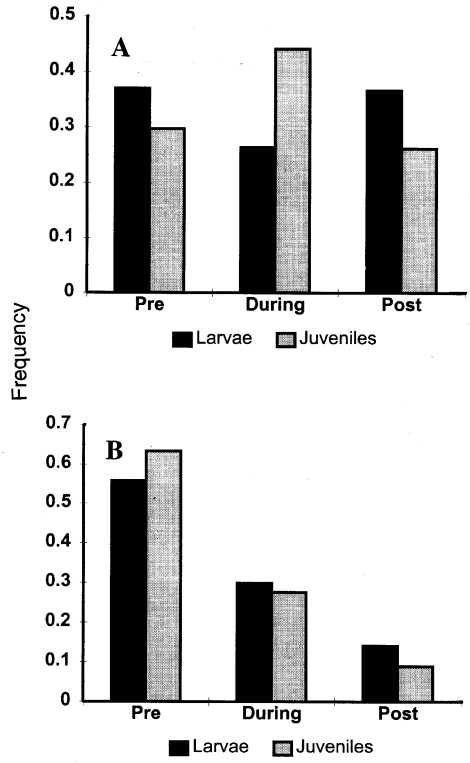

Figure 4

Fraction of larval (black bars) and juvenile (gray bars) 1994 striped bass populations that were estimated to be feeding before, during, and after blooms of (**A**) *Bosmina freyi* and (**B**) copepods in the Hudson River.

Discussion

Evidence from this study provides some support for the relation between larval growth rates and tem-

perature found by Rutherford and Houde (1995) for the Potomac River and Upper Chesapeake Bay and by Secor and Houde (1995) for striped bass larvae in the Patuxent River. However, the relationship we found was weak (r^2 only 0.15). Some measures of growth were also enhanced with increased food availability. Because of the similarity of our approach with that of these previous Chesapeake researchers, we can compare the fates of striped bass larvae in the Chesapeake and Hudson systems.

Temperatures during the larval period were more variable in the Chesapeake tributaries in the studies referred to above than in the Hudson in 1994. In the Patuxent in 1991, water temperatures in April (when nearly 90% of eggs were produced) fluctuated erratically between approximately 13° and 20°C. In May, temperatures rose through the month from 20° to 29°C (Secor and Houde, 1995). In the Potomac (1987–89) and Upper Bay (1988–89) (Rutherford and Houde, 1995), water temperatures also fluctuated, dropping in 1989 during one event from above 16°C to around 12°C, the lower lethal limit for striped bass larvae (Morgan et al., 1981). April and May water temperatures in the Nanticoke, another Chesapeake tributary, also fluctuated in 1992 and 1993 (Kellogg et al.[3]). In contrast, 1994 water temperatures in the Hudson River increased linearly from mid-April through mid-July with little fluctuation.

In spite of the overall warmer temperatures, calculated instantaneous growth rates of larval striped bass grouped into 6-d cohorts were lower in the Patuxent River (mean instantaneous G=0.126/d, range 0.11–0.14) than in the Hudson (mean G=0.190/d, range 0.070–0.564). Nanticoke River growth rates were intermediate (0.166 in 1992, 0.159 in 1993; Kellogg et al.[3]). Hudson striped bass larvae grew at rates similar to those for Potomac River (0.208 and 0.181/d for 1987 and 1989) and Upper Chesapeake Bay larvae (0.183/d). In terms of growth in length, both moronid species in the Hudson grew faster than Patuxent River striped bass larvae (Hudson white perch=0.212 mm/d ±0.101 SD, Hudson striped bass=0.218 mm/d ±0.121 SD, Patuxent striped bass=0.17 mm/d for 0–25 d). Note that Dey (1981) estimated Hudson River striped bass larval growth rates (in 1973–76) as ranging from 0.1 to 0.2 mm/d, based on analysis of weekly changes in mean lengths of larvae. Growth rates in the present study are higher than Dey's estimate and fall within the range of the Potomac (mean growth rates 0.18–0.26 mm/d, 1987–89; Rutherford and Houde, 1995). Differences in growth rates are likely due to a combination of factors in any given year and site; unfortunately, multiyear studies of larval growth rates, which would provide ranges of variation, are few.

An index of population growth, G/Z, has been used as an index of striped bass recruitment success (Rutherford and Houde, 1995, Secor and Houde, 1995, Rutherford et al., 1997, Kellogg et al.[3]) in Chesapeake tributaries because the index corresponded, at least on a seasonal basis, with production of 8-mm larvae, which is, in turn, correlated with year-class strength in the Chesapeake system. The G/Z did not correlate well with our index of recruitment, i.e. juvenile striped bass recruits. We did not examine juvenile recruitment of white perch, nor are we aware of any otolith-based studies of white perch recruitment in other ecosystems.

The G/Z method as applied at New Hamburg must be viewed cautiously, as calculations of mortality (Z) for individual cohorts are based on a few samples and are not well constrained (hence the large standard errors for some cohorts, Table 2). Further, although in aggregate a large number of individuals were examined in this study, growth rates for individual cohorts were estimated from a limited sample size. Finally, there is likely a substantial variability in time and space for both G and Z that currently exceeds measurement capacity even in the most diligent field study. Given these issues of accuracy and precision, our analyses should indicate general trends, but they cannot yet be viewed as conclusive.

In both the Chesapeake Bay and Hudson River, it appears that lowest mortality rates in striped bass larvae fall within a constrained temperature range. Secor and Houde (1995) found a convex parabolic relationship of Patuxent striped bass mortality rates with temperature; minimum mortality rates were associated with cohorts that experienced water temperatures of 16–18°C in the first 25 days of life. Rutherford and Houde (1995) did not find so neat a relationship but rather noted that low mortality rates occurred in early May cohorts of Potomac striped bass larvae, which coincided with water temperatures around 16°C. Mortality rates of Hudson River striped bass in 1994 were also lowest in cohorts associated with water temperatures of 16.4° to 18.0°C during the week of hatching (31 May to 5 June, Table 2); however, first feeding by these cohorts also coincided with the zooplankton blooms. White perch mortality rates appeared to decline with increasing temperature.

[3] Kellogg, L. L., E. D. Houde, and D. H. Secor. 1996. Egg production and environmental factors influencing larval population dynamics in the Nanticoke River, 1992–1993. Chapter 1 *in* E. D. Houde and D. H. Secor (eds.), Episodic water quality events and striped bass recruitment: larval mark-recapture experiments in the Nanticoke River. Final Rep. to Maryland Dep. Natural Resources, Chesapeake Bay Research and Monitoring Division. University of Maryland, Ref. No. [UMCEES]CBL 96-083. [Available: Chesapeake Biological Laboratory, Box 38, Solomons, MD 20688.]

In the Chesapeake system, temperature can play a key role in setting year-class strength for striped bass (Rutherford and Houde, 1995; Secor and Houde, 1995), although it is not always the determining factor (e.g. Kellogg et al.[3]). Complete failures of individual cohorts were associated with rapid temperature drops down to 12°C (Rutherford and Houde, 1995). Dey (1981) hypothesized that early cohorts of Hudson River striped bass were eliminated by a sudden drop in water temperatures in late May 1976, and simulation analysis by Boreman (1983) supported this inference.

Nevertheless, there was no relationship between temperature and year-class strength for Hudson River moronids over the period 1974–90 (Pace et al., 1993). Examining a 40-yr record of Hudson River temperatures, we found that the likelihood of lethal low temperature events (defined as ≤12°C) declines rapidly during the latter half of April (Fig. 5). Early spawned cohorts of both moronid species have a risk for low-temperature mortality events, but most cohorts are spawned after early May and are highly unlikely to experience this direct source of mortality (Fig. 5).

We have demonstrated that, like Chesapeake striped bass growth rates, larval moronid growth rates are linked (albeit weakly) to temperature in the Hudson River. Nevertheless, differential mortality occurred on the faster-growing, late cohorts of striped bass. We postulate that this mortality was due to predation. Secor and Houde (1995) also speculated that increased mortality rates observed in late Patuxent cohorts was due to predation. Hudson River moronid larvae that co-occurred with the zooplankton blooms were able to benefit energetically from increased food availability in relation to prebloom conditions (Limburg et al., 1997). Consumption rates continued to be high after the bloom, however, so that energetically the larvae continued to do well. Warmer temperatures after the bloom would have enabled larvae to swim faster and encounter more prey, but they would also potentially have encountered more predators. Thus, we infer that late cohorts suffered differentially greater predation.

We suggest that larger estuarine nurseries, such as the Hudson River, provide more damping of physical fluctuations in characteristics such as water temperature than do smaller estuaries with "flashier" drainage regimes. If this is the case, we might expect Chesapeake Bay moronid stocks to be more at risk for episodic, density-independent mortality events of the type described in Rutherford and Houde (1995). Klauda et al. (1980) noted that striped bass year-class strength, indexed by juvenile abundance, varied about 34-fold in the Hudson River, about 47-fold in Chesapeake Bay, and 160-fold in the Roanoke River (where upstream water temperatures are controlled by water regulation). The different lengths of the data sets, as well as the fact that Chesapeake Bay juvenile index reflects a mix of fish derived from tributaries and the Bay proper, make this comparison somewhat problematic to interpret. What is likely is that increased physical variability in smaller estuaries translate into greater recruitment variability.

Further, evidence from smaller streams suggests that recruitment improves in years with greater spring runoff (McGovern and Olney, 1996; Kellogg

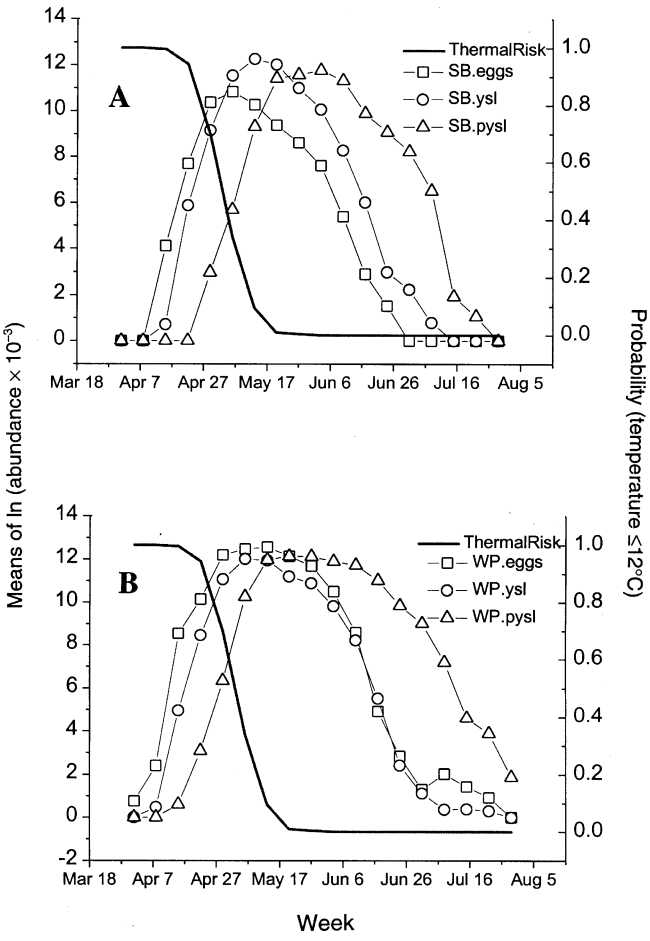

Figure 5

Probability of water temperature occurring at or below 12°C in Hudson River (based on 40-year database: Poughkeepsie Water Works, Poughkeepsie, NY) compared with means of log-transformed, river-wide abundances (1000s) of early life stages of (**A**) striped bass and (**B**) white perch. Squares = eggs, circles = yolksac larvae, and triangles = postyolksac larvae.

et al.[3]). Increased runoff in small streams could translate into more available habitat for larvae, including greater food availability (Bulak et al. 1997; Kellogg et al.[3]). Larger watercourses like the Hudson should, on average, provide a more constant amount of suitable habitat between years.

Further, we suggest that biotic controls on recruitment, if not as easily assessed as temperature and discharge, may play relatively greater roles in larger estuaries than in smaller ones, or at least in those systems with relatively predictable physical forcing. Our results implicate biotic factors for one year class of striped bass in the Hudson and are based on a comprehensive approach that included careful observation of larvae and retrospective analysis of juvenile early life histories. Had we not carried out the retrospective analysis, we likely would have predicted that later cohorts would have had the greatest recruitment potential.

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