

Consumption, Selectivity, and Use of Zooplankton by Larval Striped Bass and White Perch in a Seasonally Pulsed Estuary

K. E. LIMBURG,¹ M. L. PACE, AND D. FISCHER

Institute of Ecosystem Studies, Millbrook, New York 12545, USA

K. K. AREND

Oberlin College, Oberlin, Ohio 44074, USA

Abstract.—Many estuaries exhibit seasonal pulses of phytoplankton and zooplankton production. Larval fishes that co-occur with these “blooms” should be at a growth and survival advantage compared with larvae that occur before or after the bloom, although this has been difficult to observe in many systems. We tested this potential advantage for larval (< 10 mm notochord length) striped bass *Morone saxatilis* and white perch *M. americana* in the Hudson River by examining consumption and feeding selectivities with respect to zooplankton blooms. The cladoceran *Bosmina longirostris* and large copepodite and adult copepods together composed 97.4% and 90.9% of larval striped bass and white perch diets, respectively. Peak consumption rates of *Bosmina* coincided with the bloom, whereas copepod consumption rates continued to increase throughout the sampling period. Selectivity for copepods was inversely related to selectivity for *Bosmina* and was high, except at those sites and times when *Bosmina* densities exceeded 14 animals/L. Per capita energy consumption was highest (0.75 and 0.39 J/individual for striped bass and white perch, respectively) after the bloom period, but specific consumption (energy consumed/mg wet weight fish) during and after the bloom were similar (2.39 versus 2.35 J/mg dry weight during the bloom versus after the bloom for striped bass and 2.58 versus 2.63 J/mg for white perch). Our energetics analyses indicate that different-sized fish experience different benefit–cost (consumption benefit : respiration cost) ratios, but strong trends exist with respect to the zooplankton bloom. Prebloom cohorts have the least available food and lowest metabolic costs (respiration). Postbloom cohorts have both high consumption and respiration rates due to increased temperatures. Cohorts coincident with the bloom have moderately high specific consumption rates and lower metabolic costs relative to late cohorts. We conclude that larval cohorts coincident with the bloom possess an energetic advantage relative to early cohorts but not relative to late cohorts.

Processes that affect the survival and recruitment of individuals to populations form a central theme in fisheries ecology. Egg and larval stages are widely recognized as being most vulnerable (Rothschild 1986; Houde 1987; Wootton 1990), both to abiotic and biotic forces, so that year-class success is often established before metamorphosis (Cushing 1982). For fish larvae, physical factors, such as temperature and advection by currents, are important to survival (Sinclair 1988); but predation (McGurk 1986; Bailey and Houde 1989) and food availability (Cushing 1990) can be critical as well.

In temperate and boreal estuaries, seasonal water temperature and flow conditions may lead to pulsed developments of phytoplankton and zooplankton populations (Boynton et al. 1982; Day et al. 1989). In estuaries with pulsed plankton dynamics, plankton biomass and productivity typically increase in the spring as freshwater flows

decline and water temperatures increase. Marked cycles of plankton abundance may occur with rapid increases (“blooms”) and equally rapid declines. For consumers of secondary production like fish larvae, there are windows of opportunity in these systems for highly successful foraging, distinct in time and often in space.

In this study, we consider a case of extreme pulsed productivity and the significance of this pulse to food consumption and prey use by larvae of white perch *Morone americana* and striped bass *M. saxatilis*. We focus on white perch and striped bass as significant resident and anadromous species, respectively, within the Hudson River estuary, as well as numerous other estuaries along the East Coast of North America. Because of its commercial and recreational value, the striped bass has been the subject of many studies. The white perch, although of lower economic value, is of interest both as a fishery resource and because its high abundance gives it a pivotal role in estuarine food webs.

¹ Present address: Department of Systems Ecology, University of Stockholm, S-106 91 Stockholm, Sweden.

The cladoceran *Bosmina longirostris* (hereafter

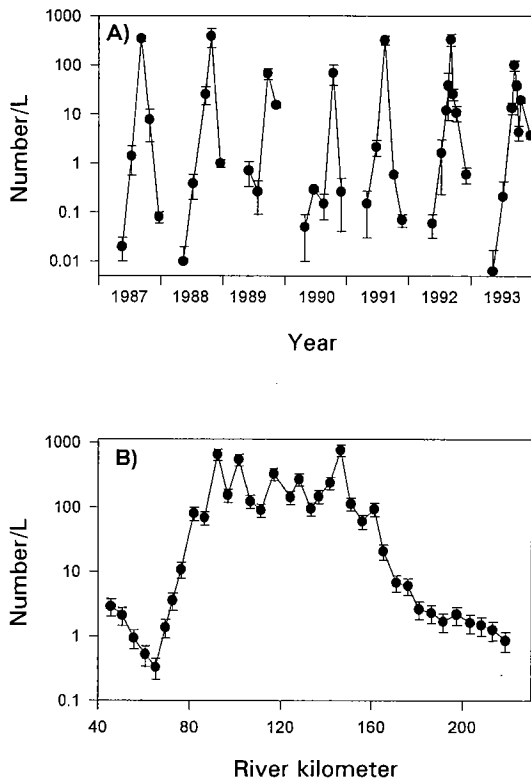


FIGURE 1.—Densities (number/L) of *Bosmina longirostris* in the Hudson River. (A) The patterns of increase and decline in May and June 1987–1993 and (B) the spatial distribution during a period of high abundance (“bloom”) are shown. Error bars are \pm SD and are based on three replicates (A) or are estimated from a model predicting variances from means (B) (Pace et al. 1991).

referred to as *Bosmina*) blooms each year in the tidal, freshwater portion of the Hudson River estuary (Pace et al. 1992). This population surges from less than 0.1 animal/L to 100 animals/L, and then declines rapidly to less than 1 animal/L (Figure 1A). These changes occur predictably over a few weeks from late May through mid-June. The *Bosmina* population bloom is also spatially discrete, occurring over an 80-km section of the 240-km long estuary (Figure 1B). In this 80-km section (freshwater at this time of year), *Bosmina* biomass is approximately 25 metric tons of carbon during the population maximum, and volumetric biomasses are in excess of 100 μ g C/L. These levels exceed prey biomasses of 40–80 μ g C/L required for growth by striped bass larvae, as measured in the laboratory with nauplii of *Artemia* sp. (Chesney 1989).

We hypothesized that the seasonal pulse of zooplankton in the Hudson River should provide a

clear advantage in terms of food availability to *Morone* larvae. Larvae that co-occur with the bloom should have higher feeding rates and, subsequently, higher growth rates and lower morbidity than larvae outside of this spatiotemporal window. Here, we test this idea with observations of larvae before, during, and after the zooplankton bloom in both freshwater and oligohaline sections of the estuary.

Prior studies have indicated a number of possible factors that influence and, in some cases, may determine larval survival in *Morone*. Striped bass larvae are affected directly by temperature (Dey 1981; Morgan and Rasin 1982; Boreman 1983; Uphoff 1989; Rutherford and Houde 1995; Secor and Houde 1995), salinity (Turner and Farley 1971; Morgan et al. 1981), and dissolved oxygen (Turner and Farley 1971), as well as contaminants and low-pH events (Hall et al. 1985; Hall 1987; Uphoff 1989). Temperature has also been implicated in survival of white perch eggs and larvae (Morgan and Rasin 1982; Margulies 1989). Generally, starvation-induced mortality is difficult to observe, but starvation does produce reduced growth rates and negative physiological impacts. If starvation occurs long enough, the effects are irreversible, and morbidity is increased during the larval stage (Martin et al. 1984; Wright and Martin 1985; Hung et al. 1993). Moreover, recent population models of striped bass indicate the critical importance of feeding and interactions between feeding and environmental temperature on growth and survival (Cowan et al. 1993; Rose and Cowan 1993). Fourfold differences in food availability can lead to 10-fold differences in larval survival to the juvenile stage (Cowan et al. 1993). In the Hudson River, the variations in food availability exceed an order of magnitude, if food limitation is important, food variability and effects on larval dynamics should be evident in this system.

Methods

Study site and field sampling.—The Hudson River, a partially stratified estuarine river system in New York State, is tidal up to the Troy Lock and Dam (Green Island Dam), 245 km from the mouth (Figure 2). The location of the salt front (defined by a salinity of 0.1‰) varies seasonally, but generally is located below river kilometer (KM) 100 (measured from the mouth of the river) during the spring and summer. White perch adults and juveniles are found throughout the estuary (Klauda et al. 1988). Striped bass adults migrate into the estuary in spring to spawn. Larvae of both species

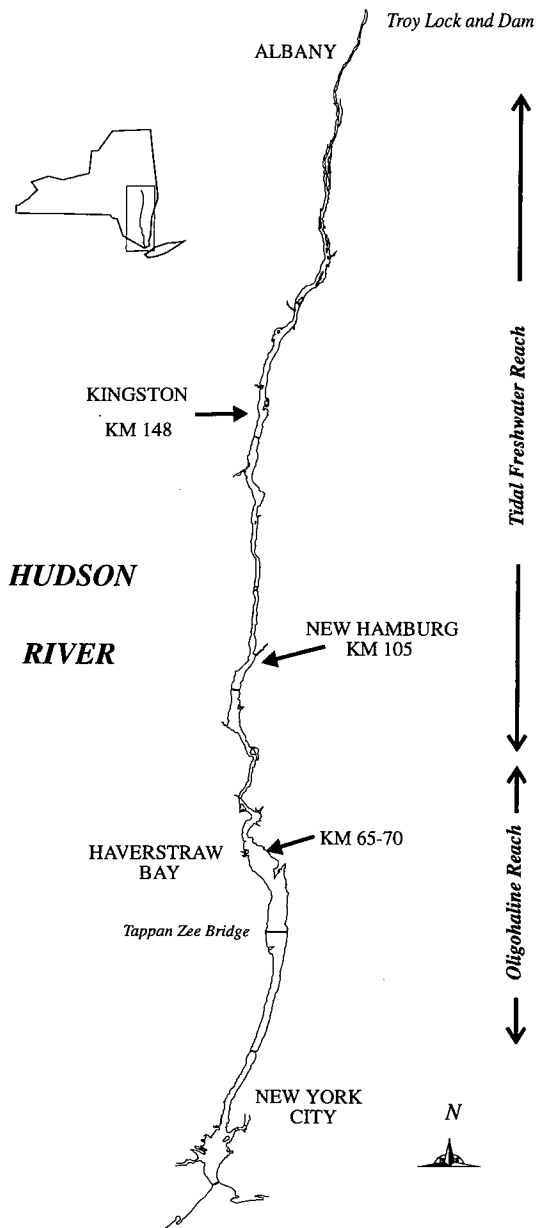


FIGURE 2.—Map of the Hudson River with study sites indicated by arrows; KM = river kilometer, measured from the mouth of the river.

are found in both freshwater and oligohaline sections and are retained there from egg through sac fry and larval stages (Boreman and Klauda 1988; Klauda et al. 1988). Juveniles spread throughout the estuary and move seaward during the late summer and fall (Dovel 1992).

We conducted our study of larval trophic dynamics to bracket, in space and time, the expected

bloom of *Bosmina longirostris*. In 1994, we selected two sampling sites (Kingston, KM 148, and New Hamburg, KM 105) within the tidal freshwater zone where *Bosmina* predominates. From long-term ichthyoplankton monitoring, it is known that white perch larvae are more abundant than striped bass larvae (5–10-fold) at the Kingston site and striped bass larvae are more abundant than white perch larvae (2–10-fold) at New Hamburg (Boreman and Klauda 1988; Klauda et al. 1988; K. E. Limburg, unpublished analysis). We selected a third site downriver in the oligohaline portion of the estuary (Haverstraw Bay, KM 65–70) where *Bosmina* is rare, but where estuarine copepod populations rise and fall with a dynamic and timing similar to, but of lower magnitude than, *Bosmina*. Larval striped bass outnumber larval white perch in this reach of the estuary.

Sampling of zooplankton and fish larvae was conducted weekly before the onset of the *Bosmina* bloom, every 3 d during the bloom, and weekly after the bloom from 13 May through 7 July. With the exception of the final date, all sampling took place in daylight. Temperature, secchi depth, and dissolved oxygen were measured 1 m below the surface concurrently with sample collection.

Ichthyoplankton were sampled by towing bongo nets (each net with 0.5 m opening, 500- μ m mesh) obliquely through the water column from about 2 m off the bottom to the surface for 5 min. Five replicate tows were made at each site on each date. Both nets were equipped with a General Oceanics flowmeter to calculate filtered volumes. The contents of both nets were concentrated and rinsed into a single container containing pure ethanol, resulting in final concentrations of about 75% ethanol or greater.

At each site, crustacean zooplankton were sampled by pumping 105 L of water from 0.5 m below the surface through a 73- μ m-mesh plankton net. Because the Hudson River is completely mixed, surface samples are adequate to characterize the water column for small particles, including small zooplankton (Findlay et al. 1991).

Laboratory.—In the laboratory, fish eggs and larvae were sorted from the collected material and transferred to fresh 100% ethanol in vials. At each site, three replicates were chosen at random from each sampling date, and twenty *Morone* larvae were randomly selected from each replicate ($N = 60$); more replicates were used when larval abundances were low. White perch and striped bass larvae are difficult to distinguish and require quantification of both internal and external characters

(Drewry 1978; Fritzsche and Johnson 1980; Olney et al. 1983). The larvae were rehydrated, measured to the nearest 0.1 mm notochord length (NL), and examined for external characters. Subsequently, they were soaked for 15 min in a 30% saturated sodium borate buffer solution and cleared by adding a small quantity of trypsin to the buffer. Following clearing (0.25–4 h), internal characters were quantified and teeth counted. For larvae less than 8 mm SL, identification to species was carried out according to characters described by Drewry (1978) and by relative tooth size, teeth of striped bass being conspicuously larger than those of white perch for any given body length (R. E. Schmidt, Simons Rock College, personal communication). When larvae were large enough to have developed clearly visible skeletal elements (usually 8 mm), the methods of Fritzsche and Johnson (1980) and Olney et al. (1983), as modified by Schmidt (1994) were used to distinguish species.

Contents of the gut lumen were enumerated under 25–60 \times magnification. Species were mostly identified to general taxon (e.g., rotifer, copepod), but specific zooplankton community dominants were noted (e.g., *Bosmina longirostris*). Copepods were classified as either naupliar or non-naupliar (i.e., both copepodites and adults); when egg masses of female copepods were consumed, eggs were enumerated as well.

A length–weight relationship was developed by measuring lengths and wet weights of 55 striped bass larvae and 99 white perch larvae. Larvae, which included formalin-preserved specimens collected for a different study on similar dates and sites, were rehydrated for 1 h prior to measurement. Larvae were measured as described above, then gently blotted and weighed on a Mettler AE240 balance. Smallest larvae (<4 mm NL) were weighed in groups of two or more.

Zooplankton were counted with a stereomicroscope at 25 \times magnification from either whole samples or by subsampling up to 400 individuals. Major taxa were quantified as for gut contents samples and expressed as numbers per liter.

Data analysis.—Larval lengths (L , mm) were converted to wet weight (W , mg) by using the relationship $W = 3.763 \times 10^{-4} \times L^{4.2879}$, which gave the best fit for both species ($R^2 = 0.98$). We assumed that dry weight was 20% of wet weight (Peters 1983).

Food item means and variances (numbers per gut for each taxon and for total zooplankton) were calculated for each fish species for each site and

date. Between-replicate variability was sufficiently small that replicates could be pooled for each species (on average, $P > 0.5$). Analysis of variance (ANOVA) tested for significant differences between means by species (white perch versus striped bass), site, and time of sampling with respect to the *Bosmina* bloom. Sampling times were aggregated into three periods for ANOVA: before (13 May to 2 June), during (3 June to 13 June), and after (14 June to 7 July) the bloom.

Energy value of food was calculated from average dry weights of zooplankters (Pace et al. 1992) and multiplied by energy values (J/mg dry weight; Cummins and Wuychek 1971; rotifers were assumed to have a caloric value of 20.9 J/mg). The resulting values are *Bosmina*, 16.2×10^{-3} J/individual; copepods, 29.1×10^{-3} J/individual; nauplii, 8.75×10^{-3} J/individual; and rotifers, 6.78×10^{-4} J/individual. Veligers of the zebra mussel *Dreissena polymorpha*, which were found in some white perch larvae, and copepod eggs were assigned energetic values that were half the value of a nauplius, based on relative size. For the ANOVA, both total counts of food items ingested and total energy intake were log-transformed as $\log_e(1 + \text{variable})$ to stabilize the variance.

To assess the energetic benefit of the zooplankton bloom relative to metabolic costs, we estimated total daily consumption rate (J/d) from gut evacuation rate and compared it with calculated respiration rate (J/d) for each larva. (Note that these rates can be compared either on a per capita or weight basis.) We assumed that day length was 12 h and that feeding occurred only during daylight hours. We assumed further that gut evacuation rate was inversely proportional to body size (Meng 1993) and directly proportional to temperature (He and Wurtsbaugh 1993; Arrhenius and Hansson 1994). Data from Meng (1993) were used to fit an exponential decay model of gut evacuation rate to body size: $\log_e(\text{gut evacuation rate, h}) = 2.619 - 0.882 \log_e(\text{standard length, mm})$ ($N = 4$, $R^2 = 0.88$). The resulting gut evacuation rate was divided by a Q_{10} relationship, with the Q_{10} parameter set to 1.9 (Rose and Cowan 1993: equation 22) and T_r , the temperature at which the rate multiplier equals 1, set to 17°C (the temperature used in Meng's experiment). Respiration rate was calculated with equation (20) in Rose and Cowan (1993), assuming 12 h of active and 12 h resting (routine) metabolism. It was then converted from mg dry weight/d (Rose and Cowan 1993) to J/d by applying the conversion factor 20.9 J/mg dry

weight (Houde and Schekter 1983). Because of the difficulties that arise from extrapolation and error inflation in making these calculations (often with several links of dependency), we chose to express consumption benefit (C) and respiration cost (R) as a ratio (C/R) rather than as an absolute difference. We then compared the C/R ratios of larvae before, during, and after the zooplankton bloom.

Feeding selectivity of *Morone* larvae was evaluated first with the Manly-Chesson index of feeding selectivity (Chesson 1983). This index is calculated as

$$\alpha_i = \frac{r_i}{n_i} / \sum_{j=1}^m (r_j/n_j),$$

$i = 1 \dots m$; r_i is the number or proportion of the i th food type found in the gut and n_i is the corresponding number or proportion of prey type i in the environment. The index ranges from 0 to 1; zero indicates negative selection relative to environmental densities; 1 indicates that the consumer's diet consists only of the i th food item; and $1/m$ indicates neutrality. These relationships were explored further with nonlinear regression analysis. Holling type II functional response curves (Holling 1965) were fit separately to the numbers of both *Bosmina* and copepods found in white perch and striped bass respectively, as a function of riverine densities.

Results

We examined 880 white perch larvae and 483 striped bass larvae. Larval *Morone* densities increased steadily through May. Mean larval length increased with time, although few individuals larger than 9.0 mm NL were captured due to gear constraints. At the first sample date (18 May) white perch larvae averaged 4.4 ± 0.6 (SD) mm and striped bass larvae averaged 4.8 ± 0.7 mm; on the final date (6 July), white perch were 7.1 ± 1.2 mm and striped bass were 8.1 ± 1.4 mm. Seasonal changes of sizes were not large, and size ranges generally overlapped through time. Striped bass larvae dominated at the oligohaline site (Haverstraw Bay, KM 65–70; mean, 71.3%; range, 36.7–94.1%), and white perch larvae dominated at Kingston (KM 148; mean, 96.6%; range, 90.6–100%). At New Hamburg (KM 105), striped bass became increasingly more abundant than white perch during the sampling period (mean, 35.6%; range, 7.1–91.7%).

Zooplankton densities were low in May (Figure 3). By early June, *Bosmina* densities increased at the upriver and midriver sites, peaking at 516 an-

imals/L at New Hamburg on 10 June (a nearly 4,000-fold increase) and at 111.5 animals/L at Kingston on 13 June. Whereas *Bosmina* densities were low in Haverstraw Bay (maximum, 9 animals/L on 10 June), copepod and naupliar dynamics were similar to *Bosmina* at the two upriver sites, increasing over 50-fold to a peak density on 10 June of 86 animals/L (copepods) and 45-fold to peak at 777 animals/L on 13 June (nauplii) (Figure 3). Zooplankton other than *Bosmina* and copepods were not abundant.

Gut contents of both species of *Morone* consisted predominantly of copepods and *Bosmina* (Table 1). Smaller fish larvae tended to consume smaller organisms (rotifers, nauplii, and zebra mussel veligers); nevertheless, more copepods and *Bosmina* were consumed by even the smallest size-class (<5.0 mm NL).

With the exception of the smallest size-class of white perch at Kingston, all size-classes of both species consumed more copepods than any other single food item. Spatial and temporal differences in copepod versus *Bosmina* consumption patterns were evident (Figure 4). Elevated consumption of *Bosmina* coincided with the large increase in *Bosmina* densities, whereas copepod consumption increased steadily throughout the observation period, despite the decline in copepod numbers. The frequency of occurrence of fish with empty guts declined over time but reached a low, with lowest variance, on 13 June when densities of *Bosmina* (tidal freshwater zone) and copepods (oligohaline zone) were at or near peak.

Copepods were highly selected for at all times, except during the *Bosmina* bloom (Figure 5). Selection for copepods dropped sharply and increased for *Bosmina* when *Bosmina* densities first exceeded 10 animals/L. Striped bass larvae continued to select for *Bosmina* during the height of the bloom, whereas white perch larvae showed selection for copepods, despite an absolute increase in *Bosmina* consumption. Selectivity for other taxa (nauplii, rotifers, and veligers) was close to zero at all times and sites.

Both species of fish appeared to attain maximum feeding rates at high zooplankton densities (Figure 6). Functional responses were similar in magnitude for both fish species, yet differed between prey types. The Holling type II functional response, which described feeding on *Bosmina*, explained 81% and 87% of the variance for white perch and striped bass, respectively. Incorporating fish size into the functional response relation did not substantially improve the fit. Copepod consumption

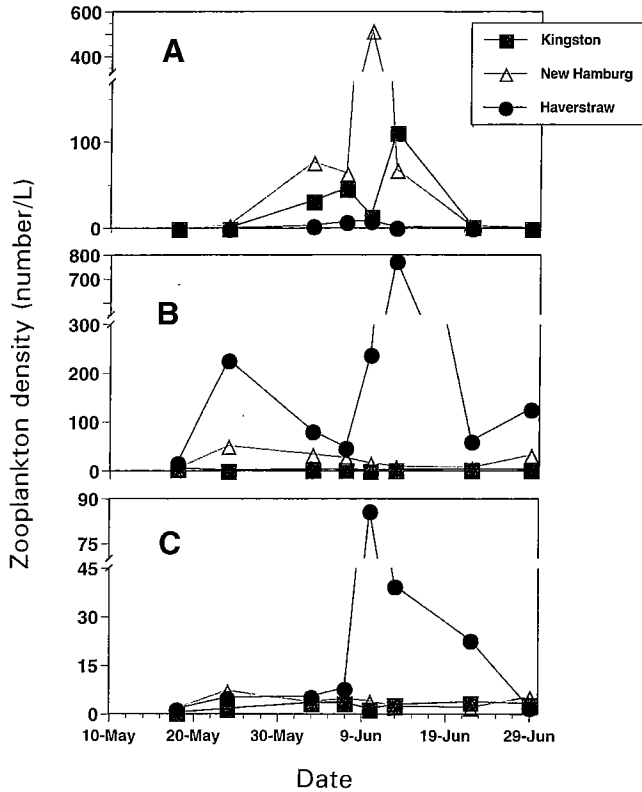


FIGURE 3.—Zooplankton densities at three locations on the Hudson River during May–June 1994. Densities are given for (A) *Bosmina longirostris*, (B) copepod nauplii, and (C) copepodites and adults.

also increased with density, except at highest copepod densities, when consumption was depressed. Excluding this high density point, a type II functional response curve can also be fit to the data over the range of 0–40 copepods/L (Figure 6). Note that feeding rates of larvae on copepods increased far more rapidly at low (0–10 animals/L) densities than for similar densities of *Bosmina*. The apparent depression of feeding on copepods observed at high densities (86 animals/L) is based on one sampling at Haverstraw Bay. The depression is not due to the concurrent high abundance of *Bosmina* (516 animals/L) or to any large changes in larval fish or zooplankton size.

Bosmina consumption, copepod consumption, total number of food items ingested, and total caloric intake exhibited significant differences (ANOVA, $P < 0.01$) as a function of time (bloom status) and site by time interactions. These differences, however, were related to different patterns in the temporal and spatial exploitation of *Bosmina* and copepods by larvae and also to more subtle differences (marginally significant, $P < 0.1$) be-

tween fish species. *Bosmina* consumption was low before and after the *Bosmina* bloom, and at all times in Haverstraw Bay; consumption increased during the bloom in the tidal freshwater. Copepod consumption, in contrast, increased monotonically with time. White perch tended to consume more *Bosmina* than did striped bass at any time and site, although the differences were not significant. Striped bass tended to consume more copepods than did white perch ($P < 0.1$). Total food items consumed also increased monotonically with time, as did total caloric intake. Striped bass consumed significantly more calories than white perch ($P < 0.05$), particularly after the bloom; this difference was due to consumption of more copepods and the eggs of female copepods by striped bass (Figure 7A).

Although the energy value of ingested food increased over the study period, so did the average size of larvae. Consequently, the specific energy value of consumed food (i.e., energy consumed per mg dry weight of larvae) increased to a maximum during the zooplankton bloom (0.48 and

TABLE 1.—Per capita consumption of zooplankton by larval striped bass and white perch. Values are mean numbers per individual; SDs are given in parentheses. River kilometers (KM) are measured from the mouth of the Hudson River.

Species	Size-class (mm)	N	<i>Bosmina longirostris</i>	Copepods	Nauplii	Rotifers
Kingston (KM 148)						
Striped bass	<5	10	0	0.2 (0.42)	0.1 (0)	0
White perch ^a	<5	285	0.88 (1.22)	0.38 (0.61)	0.05 (0.25)	0.02 (0.14)
	5–6.4	104	0.78 (1.28)	0.82 (0.97)	0.01 (0.10)	0.02 (0.20)
	6.5–7.9	41	0.90 (1.67)	1.39 (1.28)	0	0
	≥8	23	0	1.96 (1.40)	0	0
New Hamburg (KM 105)						
Striped bass	<5	18	0.17 (0.71)	0.83 (1.04)	0	0
	5–6.4	46	0.56 (1.27)	1.15 (1.44)	0	0
	6.5–7.9	62	0.50 (1.11)	1.47 (1.65)	0	0.02 (0.13)
	≥8	39	0.08 (0.48)	2.18 (1.67)	0	0
White perch	<5	202	0.64 (1.03)	0.77 (0.94)	0.02 (0.17)	0.02 (0.16)
	5–6.4	91	1.11 (1.50)	0.63 (0.83)	0	0
	6.5–7.9	43	1.30 (2.70)	1.60 (1.71)	0.02 (0.15)	0
	≥8	4	0	3.75 (2.63)	0	0
Haverstraw Bay (KM 55–60)						
Striped bass	<5	32	0.03 (0.18)	0.59 (2.03)	0.19 (0.54)	0
	5–6.4	147	0.01 (0.12)	2.91 (3.11)	0.05 (0.36)	0
	6.5–7.9	96	0.01 (0.10)	2.88 (2.53)	0.03 (0.18)	0.02 (0.20)
	≥8	30	0	6.17 (6.24)	0	0.03 (0.18)
White perch	<5	51	0.06 (0.31)	0.67 (1.26)	0.22 (0.61)	0.22 (0.55)
	5–6.4	13	0.08 (0.28)	0.62 (1.12)	0.15 (0.56)	0
	6.5–7.9	19	0	2.37 (1.50)	0	0
	≥8	4	0	3.75 (2.22)	0	0

^a Veligers of the zebra mussel *Dreissena polymorpha* were consumed by white perch larvae at Kingston on 13 June. Per capita consumption rates were 0.19 ± 0.74 veligers (<5 mm larvae), 0.03 ± 0.17 veligers (5–6.4 mm larvae), and 0.02 ± 0.16 veligers (6.5–7.9 mm larvae).

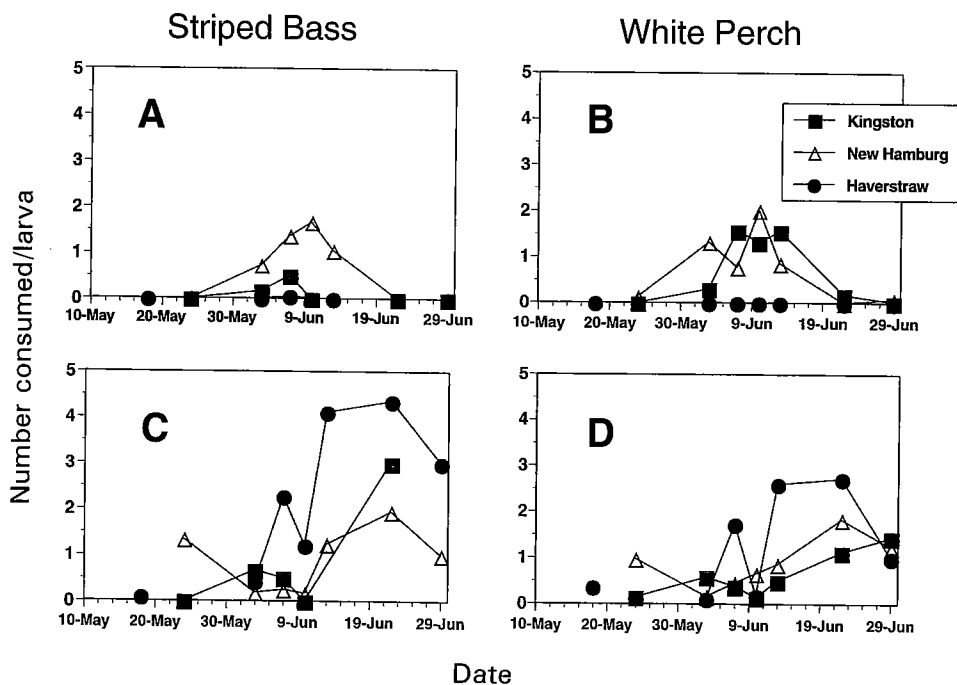


FIGURE 4.—Per capita consumption of (A, B) *Bosmina longirostris* and (C, D) copepods by striped bass (A, C) and white perch (B, D) larvae, at three sites on the Hudson River, May–June 1995.

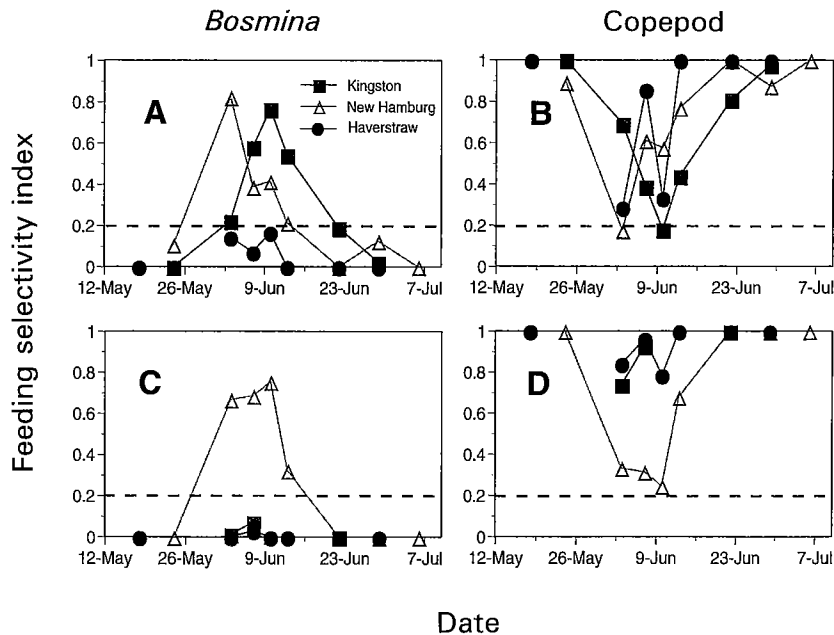


FIGURE 5.—Larval (A, B) white perch and (C, D) striped bass feeding selectivities for *Bosmina longirostris* (A, C) and copepods (B, D). The dashed line indicates neutral selectivity (based on five prey types).

0.69 J mg dry weight for striped bass and white perch, respectively) and declined thereafter (Figure 7B). However, this decline was not significant for either fish species (Tukey's honestly significant difference, HSD, test for unequal sample sizes). In Haverstraw Bay, both species obtained most of their energy from copepods, but *Bosmina* became an important energy contributor during its bloom period at New Hamburg (42.9% of energy intake for striped bass, 52.0% for white perch) and Kingston (17.3% for striped bass, 60.3% for white perch).

Estimated energy consumption rates peaked for striped bass in the 5.0–5.4 mm size group (Figure 8A); calculated respiration rates declined as a function of body size but increased as a function of temperature (Figure 8B). The resulting ratio (Figure 8C) indicates that larvae had very low C/R before the bloom. Bloom size-classes had the highest C/R. For some size-classes, (e.g., 5.0–5.4 mm), bloom C/R exceeded postbloom by 1.5–2-fold. Such differences suggest that the bloom provides an important consumption advantage for small size-classes of striped bass.

White perch larvae also had lowest C/R for all size-classes present before the zooplankton bloom (Figure 8F), but no clear consumption advantage was evident for bloom versus postbloom cohorts. Highest C/R occurred for a postbloom size-class

(4.5–4.9 mm) due to high consumption rate in this group (Figure 8D). Mean C/R over all size-classes was not significantly different for the bloom versus postbloom periods but was significantly lower before the bloom (Tukey HSD with unequal sample sizes, $P < 0.05$ for striped bass, $P < 0.001$ for white perch; Figure 9).

Discussion

Feeding and Its Ecological Implications

Our findings provide only partial support for our initial hypothesis that zooplankton blooms represent an energy advantage for co-occurring fish larvae. Consumption of zooplankton by larvae increased more from the period prior to the bloom than from the bloom to postbloom periods (Figure 7). Although the mean specific (weight basis) energy value of food consumed peaked during the bloom period (Figure 7B), this peak was not significantly different from the postbloom value. Energy gain versus metabolic costs also showed the same trend (Figures 8, 9). Note that this result depends on the particular assumption of temperature dependence of gut evacuation because the actual relationship is unknown for larval moronids. In our calculation, we assumed that the Q_{10} relationship of gut evacuation is the same as that of respiration. If the slope of the gut evacuation

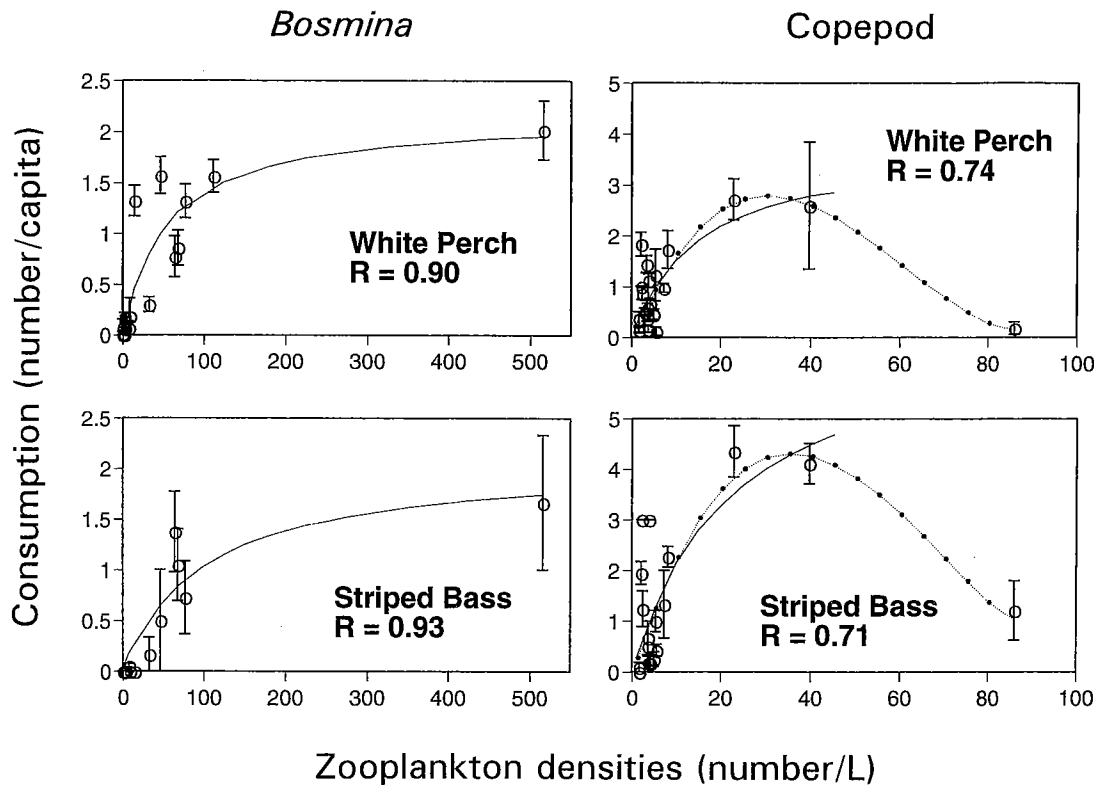


FIGURE 6.—Nonlinear regressions of larval white perch and striped bass per capita consumption of *Bosmina longirostris* (left panels) and copepod (right panels) as a function of river densities, modeled as Holling type II functional response curves: $Y = aX/(1 + bX)$. For *Bosmina*–striped bass, coefficients are $a = 0.01996$, and $b = 0.0095$; for *Bosmina*–white perch, $a = 0.0392$, and $b = 0.0181$. For copepod–striped bass, $a = 0.3064$, and $b = 0.0430$; for copepod–white perch, $a = 0.2564$, and $b = 0.0668$. Note that functional response fits in right panels do not include highest copepod density. Dotted line in right panels shows third-order polynomial fit of all data. Error bars are \pm SE.

Q_{10} is actually lower, then postbloom consumption rates would be subsequently lower as would the resulting C/R ratios. Furthermore, parameters for both species of fish were taken from striped bass models because no comparable models exist for white perch. The degree to which white perch early development differs from that of striped bass might produce different results were those parameters known.

Different assumptions about assimilation efficiency can also alter the C/R ratio; a lower assimilation efficiency will lower the ratio. However, if one assumes that assimilation efficiency is only affected by the quantity and quality of food in the gut and not temperature (Pandian 1987), then the relative magnitudes in C/Rs across time (i.e., comparing the C/R of a given size-class before, during, and after the zooplankton bloom) will not change.

The chance of finding food was greatest and

most predictable during the bloom, as shown by the low number of fish found with empty guts. Nevertheless, consumption patterns also show the strong influence of both spatial variation and larval “decision” behavior. Both factors should be considered when developing models and other estimates of larval foraging and consequent growth and survival.

Larval moronids fed primarily on the largest prey available. Data on mouth gape sizes (Limburg, unpublished data) show that the smallest larvae (3.5 mm NL) have gapes large enough to accommodate adult copepods, so we conclude that the fish are not gape limited with respect to copepods. *Bosmina* and copepods formed the overwhelming bulk of the diet of larvae smaller than 9 mm NL, and copepods were fed on selectively at most times. Smaller zooplankton were strongly avoided, relative to their availability.

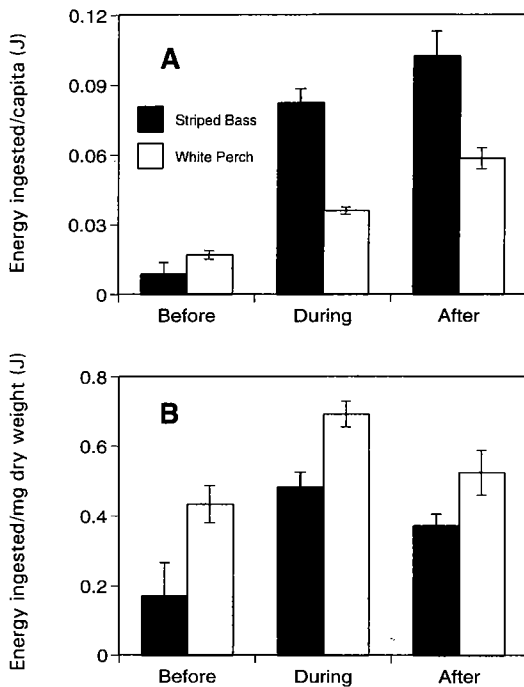


FIGURE 7.—River-wide averages (\pm SE) of total energy ingested (J) per individual striped bass or white perch larva based on (A) energy ingested per capita and (B) energy ingested per milligram dry weight before, during, and after the zooplankton bloom.

Beaven and Mihursky (1979) and Haroon (1979) both reported strong, positive selection by all sizes of striped bass larvae for adults of the estuarine copepod *Eurytemora affinis* in the Chesapeake Bay. Rotifers were the second most abundant food item for striped bass larvae, although selectivity was negative. *Bosmina*, which is also abundant (at times >1,000 animals/L) in the Chesapeake Bay, was also positively selected, although details are not given as to the time sequence of electivities.

Selectivity for Copepods

There are several possible reasons why larvae would prefer adult copepods over *Bosmina* or over copepod nauplii. First, we might propose a priori that the amount of gross available energy represented by copepod densities exceeds that of other prey items. If fish feed nonselectively, then the food species with highest energy density (i.e., energy per volume of water searched) should be consumed in proportion to that density. Our proposition is undermined because during the *Bosmina* bloom in the tidal freshwater zone, energy densities of *Bosmina* exceeded that of copepods by an

average of 17.8-fold (range, 4.8–70.1-fold). Fish do select more heavily for *Bosmina* during the bloom, but not directly in proportion to the energy density in the river; rather, copepods continue to compose a large fraction (approximately 60% for striped bass, 40% for white perch) of the energy ingested for those times and sites. Thus a simple energy density argument does not explain the selection of copepods by larval moronids.

Optimal foraging theory offers a second way to evaluate the preference for copepods (Pyke 1984; Townsend and Winfield 1985). In optimal foraging, consideration is made of the energetic costs (search, pursuit, and handling) and benefits of the captured prey. Again, in the case of *Bosmina* versus copepods, we might expect *Bosmina* to be the preferred prey; not only does it represent far more energy per unit of water volume, but as a small cladoceran, it is less mobile (Lehman 1977; Kerfoot 1978; Costello and Colin 1994) and thus more readily captured (Drenner and McComas 1980; Link 1996) than are adult copepods. Nevertheless, adult copepods are most selected.

A third possibility is that adult copepods may offer nutritional benefits that go beyond a simple energetic returns approach. For example, certain biochemical compounds, including many fatty acids and amino acids, are synthesized by primary producers and transferred through the food chain (e.g., Fraser et al. 1989; Linko et al. 1992; Ederington et al. 1995). Certain combinations of these compounds (particularly the highly unsaturated and polyunsaturated fatty acids) promote increased growth and egg production in zooplankton (Ahlgren et al. 1990; Ederington et al. 1995; Jonasdottir 1995; Kleppel and Burkart 1995; Müller-Navarra 1995) and increased growth and survival of fish larvae (Lemm and Lemarie 1991; Craig et al. 1994). Adult copepods may offer a richer supply of amino and fatty acids than other available zooplankters, or at least in proportions that favor growth of *Morone* larvae. For instance, Tsai (1991) found a gradient of growth and survival of striped bass larvae when fed different stages of the copepod *Eurytemora affinis*; the nauplii were the worst food source and adults the best.

Finally, because small fish larvae do not have well-developed optical systems, adult copepods may simply be more apparent to small fish larvae due to their larger size (Blaxter 1988; Hairston et al. 1982; Li et al. 1985), pigmentation (Loew et al. 1993), or movement (Kerfoot et al. 1980).

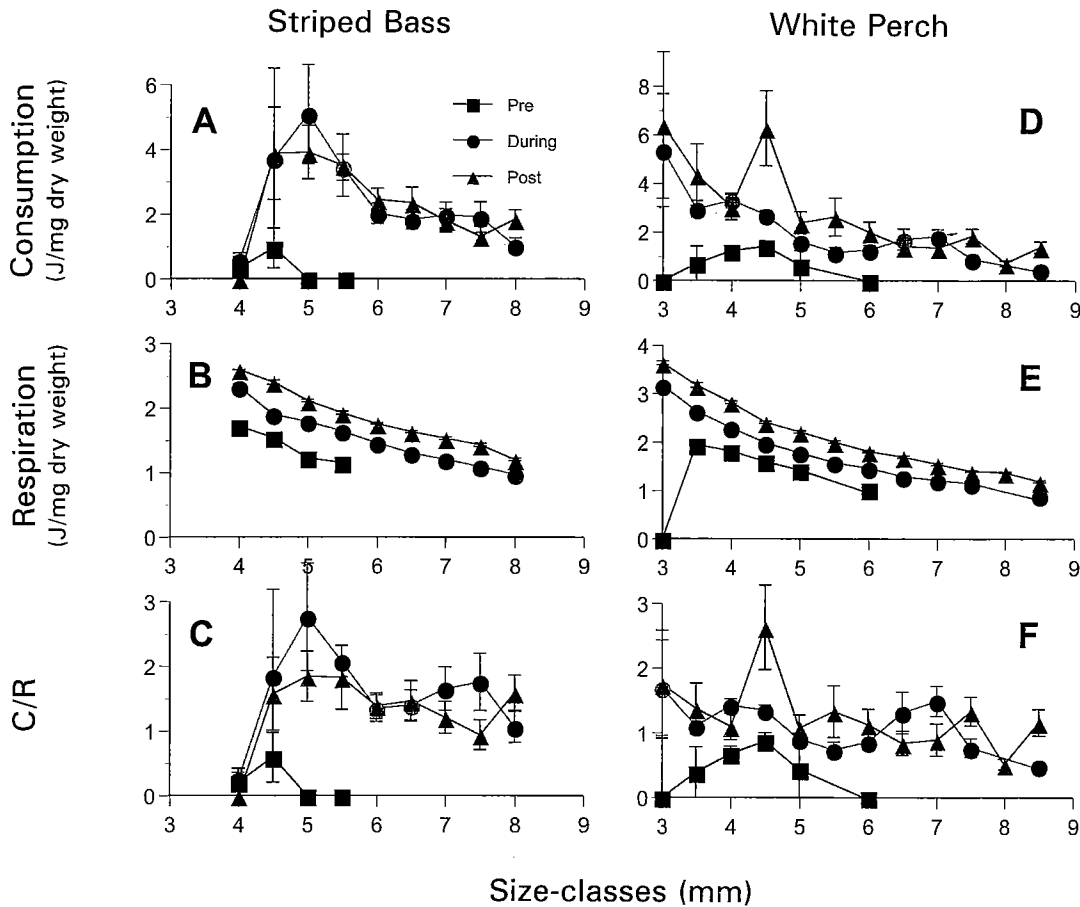


FIGURE 8.—Partial energy budgets for larval striped bass (left panels) and white perch (right panels) as a function of body length, calculated for times corresponding to before (pre), during, and after (post) the zooplankton bloom: (A, D) consumption (C) rates; (B, E) respiration (R) rates; and (C, F) the ratio of consumption over respiration (C/R). Error bars are \pm SE.

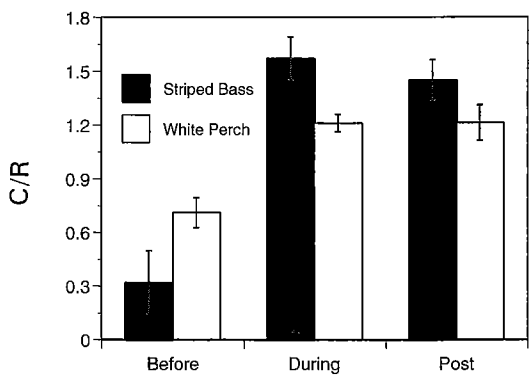


FIGURE 9.—Mean (\pm SE) relative energetic benefit (C/R, the ratio of consumption rate over respiration rate) for striped bass and white perch larvae as a function of the status of the zooplankton bloom.

Conclusion and Perspective

Large interannual variations in abundance of *Morone* larvae are not correlated with indices of juvenile abundance (Pace et al. 1993). If the measures of juvenile abundance are representative, then mortality of both striped bass and white perch larvae must be density dependent. Zooplankton, although variable seasonally, are predictable interannually (Figure 1; Pace et al. 1992). Finite zooplankton production may limit larvae on an annual basis and thereby promote density dependence. This study indicates that larvae from bloom and postbloom periods would contribute most to total recruitment, whereas early larvae may not survive at all because of food limitation. Others have noted the tandem importance of both food availability and temperature for estuarine fish larvae (Crecco

et al. 1983; Secor and Houde 1995; Limburg 1996). Interactions of food, predators, and physical factors such as temperature within the estuary may limit successful larval recruitment to specific times and places. Interannual variation in timing and duration of spawning could add further complexity. This latter model would suggest recruitment could be driven by a shifting mosaic of conditions that is, in aggregate, density dependent. Testing this model is clearly more difficult and requires better resolution of growth and mortality over time and within different sections of the estuary.

In summary, adequate food is an oft-studied aspect of larval fish dynamics because of the presumed relationship between food supply and survival. Numerous studies, however, have found little support for a strong linkage between larval food supply and recruitment success (Leggett and DeBlois 1994). One key to assessing the importance of food to larval fish is to consider the issue in environments like the Hudson River where the dynamics of larval prey are extreme and highly predictable (Figure 1). The spatial and temporal variability in zooplankton provides a clear case where food is differentially available to larvae. Our findings suggest that the consumption of food relative to energetic needs is not entirely consistent with a "bloom advantage" hypothesis.

Acknowledgments

We thank H. Andreyko, A. Denk, R. Schmidt, J. Waldman, and J. Young for their assistance, and L. Rudstam, D. Strayer, R. Schmidt, J. Waldman, and two reviewers for their helpful comments on the manuscript. This work is a contribution to the program of the Institute of Ecosystem Studies and is a result of research funded by the Hudson River Foundation and by National Oceanic and Atmospheric Administration (NOAA) award R/FBM/15 to the Research Foundation of State University of New York for the New York Sea Grant Institute. The U.S. government is authorized to produce and distribute reprints for governmental purposes notwithstanding any copyright notation that may appear herein. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies.

References

- Ahlgren, G., L. Lundstedt, M. Breck, and C. Forsberg. 1990. Lipid composition and food quality of some freshwater phytoplankton for cladoceran zooplankters. *Journal of Plankton Research* 12:809–818.
- Arrhenius, F., and S. Hansson. 1994. In situ food consumption of young-of-the-year Baltic Sea herring *Clupea harengus*: a test of predictions from a bioenergetics model. *Marine Ecology Progress Series* 110:145–149.
- Bailey, K. M., and E. D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology* 25:1–83.
- Beaven, M., and J. A. Mihursky. 1979. Analysis of striped bass larval stomachs. 1976. Potomac estuary collections. Report of University of Maryland, Chesapeake Biological Laboratory (UMCEES 79–45 CBL) to Maryland Department of Natural Resources, Power Plant Siting Program, Annapolis.
- Blaxter, J. H. S. 1988. Sensory performance, behavior, and ecology of fish. Pages 203–232 in J. Atema, R. R. Fay, A. N. Popper, and W. N. Tavolga, editors. *Sensory biology of aquatic animals*. Springer-Verlag, New York.
- Boreman, J. 1983. Simulation of striped bass egg and larva development based on temperature. *Transactions of the American Fisheries Society* 112:286–292.
- Boreman, J., and R. J. Klauda. 1988. Distributions of early life stages of striped bass in the Hudson River estuary, 1974–1979. Pages 53–58 in L. W. Barnt-house, R. J. Klauda, D. S. Vaughn, and R. L. Kendall, editors. *Science, law, and Hudson River power plants: a case study in environmental impact assessment*. American Fisheries Society, Monograph 4, Bethesda, Maryland.
- Boynton, W. R., W. M. Kemp, and C. W. Keefe. 1982. A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production. Pages 69–90 in V. S. Kennedy, editor. *Estuarine comparisons*. Academic Press, New York.
- Chesney, E. J., Jr. 1989. Estimating the food requirements of striped bass larvae *Morone saxatilis*: effects of light, turbidity and turbulence. *Marine Ecology Progress Series* 53:191–200.
- Chesson, J. 1983. The estimation and analysis of preference and its relationship in foraging models. *Ecology* 64:1297–1304.
- Costello, J. H., and S. P. Colin. 1994. Morphology, fluid motion and predation by the scyphomedusa *Aurelia aurita*. *Marine Biology* 121:327–334.
- Cowan, J. H. Jr., K. A. Rose, E. S. Rutherford, and E. D. Houde. 1993. Individual-based model of young-of-the-year striped bass population dynamics. II. Factors affecting recruitment in the Potomac River, Maryland. *Transactions of the American Fisheries Society* 122:439–458.
- Craig, S. R., C. R. Arnold, and G. J. Holt. 1994. The effects of enriching live foods with highly unsaturated fatty acids on the growth and fatty acid composition of larval red drum *Sciaenops ocellatus*. *Journal of the World Aquaculture Society* 25:424–431.
- Crecco, V., T. Savoy, and L. Gunn. 1983. Daily mortality rates of larval and juvenile American shad (*Alosa sapidissima*) in the Connecticut River with

- changes in year-class strength. *Canadian Journal of Fisheries and Aquatic Sciences* 40:1719-1728.
- Cummins, K. W., and J. C. Wuychek. 1971. Caloric equivalents for investigations in ecological energetics. *Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen* 18:1-158.
- Cushing, D. H. 1982. *Climate and fisheries*. Academic Press, London.
- Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology* 26:249-293.
- Day, J. W., Jr., C. A. S. Hall, W. M. Kemp, and Y. Yanez-Arancibia. 1989. *Estuarine ecology*. Wiley, New York.
- Dey, W. P. 1981. Mortality and growth of young-of-the-year striped bass in the Hudson River estuary. *Transactions of the American Fisheries Society* 110:151-157.
- Dovel, W. L. 1992. Movements of immature striped bass in the Hudson estuary. Pages 276-300 in C. L. Smith, editor. *Estuarine research in the 1980s*. SUNY Press, Albany, New York.
- Drenner, R. W., and S. R. McComas. 1980. The roles of zooplankton escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish. Pages 587-593 in W. C. Kerfoot, editor. *Evolution and ecology of zooplankton communities*. University Press of New England, Hanover, New Hampshire.
- Drewry, G. E. 1978. External features useful for separating the young of striped bass (*Morone saxatilis*) from those of white perch (*Morone americana*). University of Maryland, Chesapeake Biological Laboratory, Center for Estuarine and Environmental Studies, UMCEES 78-81 CBL, Solomons.
- Ederington, M. C., G. B. McManus, and H. R. Harvey. 1995. Trophic transfer of fatty acids, sterols, and a triterpenoid alcohol between bacteria, a ciliate, and the copepod *Acartia tonsa*. *Limnology and Oceanography* 40:860-867.
- Findlay, S., M. Pace, and D. Lints. 1991. Variability and transport of suspended sediment, particulate and dissolved organic carbon in the tidal freshwater Hudson River. *Biogeochemistry* 12:149-169.
- Fraser, A. J., J. R. Sargent, J. C. Gamble, and D. D. Seaton. 1989. Formation and transfer of fatty acids in an enclosed marine food chain comprising phytoplankton, zooplankton and herring (*Clupea harengus* L.) larvae. *Marine Chemistry* 27:1-18.
- Fritzche, R. A., and G. D. Johnson. 1980. Early osteological development of white perch and striped bass with emphasis on identification of their larvae. *Transactions of the American Fisheries Society* 109:387-406.
- Hairston, N. G., Jr., K. T. Li, and S. S. Easter, Jr. 1982. Fish vision and the detection of planktonic prey. *Science* 218:1240-1242.
- Hall, L. W. 1987. Acidification effects on larval striped bass, *Morone saxatilis*, in Chesapeake Bay tributaries: a review. *Water, Air, and Soil Pollution* 35:87-96.
- Hall, L. W., L. O. Pinkney, L. O. Horseman, and S. E. Finger. 1985. Mortality of striped bass larvae in relation to the contaminants and water quality conditions in a Chesapeake Bay tributary. *Transactions of the American Fisheries Society* 114:861-868.
- Haron, A. K. Y. 1979. Food selection of larval white perch (*Morone americana*) in the Patuxent estuary. University of Maryland, Chesapeake Biological Laboratory, UMCEES 79-116 CBL, Solomons.
- He, E., and W. A. Wurtsbaugh. 1993. An empirical model of gastric evacuation rates for fish and an analysis of digestion in piscivorous brown trout. *Transactions of the American Fisheries Society* 122:717-730.
- Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada* 45:3-60.
- Houde, E. D. 1987. Fish early life dynamics and recruitment variability. Pages 17-29 in R. D. Hoyt, editor. *10th annual larval fish conference*. American Fisheries Society, Symposium 2, Bethesda, Maryland.
- Houde, E. D., and R. C. Schekter. 1983. Oxygen uptake and comparative energetics among eggs and larvae of three subtropical fishes. *Marine Biology* 72:283-293.
- Hung, S. S. O., F. S. Conte, and E. F. Hallen. 1993. Effects of feeding rates on growth, body composition and nutrient metabolism in striped bass (*Morone saxatilis*) fingerlings. *Aquaculture* 112:349-361.
- Jonasdottir, S. H. 1995. Effects of food quality on the reproductive success of *Acartia tonsa* and *Acartia hudsonica*: laboratory observations. *Marine Biology* 121:67-81.
- Kerfoot, W. C. 1978. Combat between predatory copepods and their prey: *Cyclops*, *Epischura*, and *Bosmina*. *Limnology and Oceanography* 23:1089-1102.
- Kerfoot, W. C., D. L. Kellogg, Jr., and J. R. Strickler. 1980. Visual observations of live zooplankters: evasion, escape, and chemical defences. Pages 10-27 in W. C. Kerfoot, editor. *Evolution and ecology of zooplankton communities*. University Press of New England, Hanover, New Hampshire.
- Klauda, R. J., J. B. McLaren, R. E. Schmidt, and W. P. Dey. 1988. Life history of white perch in the Hudson River estuary. Pages 69-88 in L. W. Barnhouse, R. J. Klauda, D. S. Vaughn, and R. L. Kendall, editors. *Science, law, and Hudson River power plants: a case study in environmental impact assessment*. American Fisheries Society, Monograph 4, Bethesda, Maryland.
- Kleppel, G. S., and C. A. Burkart. 1995. Egg production and the nutritional environment of *Acartia tonsa*: the role of food quality in copepod nutrition. *ICES Journal of Marine Science* 52:297-304.
- Lehman, J. T. 1977. On calculating drag characteristics

- for decelerating zooplankton. *Limnology and Oceanography* 22:170-173.
- Leggett, W. C., and E. DeBlois. 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? *Netherlands Journal of Sea Research* 32:119-134.
- Lemm, C. A., and D. P. Lemarie. 1991. Survival and growth of larval striped bass *Morone saxatilis* fed *Artemia* enriched with highly unsaturated fatty acids (HUFA). *Aquaculture* 99:117-126.
- Li, K. T., J. K. Wetterer, and N. G. Hairston, Jr. 1985. Fish size, visual resolution, and prey selectivity. *Ecology* 66:1729-1735.
- Limburg, K. E. 1996. Growth and migration of 0-year American shad (*Alosa sapidissima*) in the Hudson River estuary: otolith microstructural analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 53:220-238.
- Link, J. 1996. Capture probabilities of Lake Superior zooplankton by an obligate planktivorous fish—the lake herring. *Transactions of the American Fisheries Society* 125:139-142.
- Linko, R. R., M. Rajasilta, and R. Hiltunen. 1992. Comparison of lipid and fatty acid composition in vendace (*Coregonus albula* L.) and available plankton feed. *Comparative Biochemistry and Physiology* 103A:205-212.
- Loew, E. R., W. N. McFarland, E. L. Mills, and D. Hunter. 1993. A chromatic action spectrum for planktonic predation by juvenile yellow perch, *Perca flavescens*. *Canadian Journal of Zoology* 71:384-386.
- Margulies, D. 1989. Effects of food concentration and temperature on development, growth, and survival of white perch, *Morone americana*, eggs and larvae. *U.S. National Marine Fisheries Service Fishery Bulletin* 87:63-72.
- Martin, F. D., D. A. Wright, and J. C. Means. 1984. Fatty acids and starvation in larval striped bass (*Morone saxatilis*). *Comparative Biochemistry and Physiology* 77B:785-790.
- McGurk, M. D. 1986. Natural mortality of marine pelagic eggs and larvae: role of spatial patchiness. *Marine Ecology Progress Series* 34:227-242.
- Meng, L. 1993. Estimating food requirements of striped bass larvae: an energetics approach. *Transactions of the American Fisheries Society* 122:244-251.
- Morgan, R. P., II, and V. J. Rasin, Jr. 1982. Influence of temperature and salinity on development of white perch eggs. *Transactions of the American Fisheries Society* 111:396-398.
- Morgan, R. P., II, V. J. Rasin, Jr., and R. L. Copp. 1981. Temperature and salinity effects on development of striped bass eggs and larvae. *Transactions of the American Fisheries Society* 110:95-99.
- Müller-Navarra, D. C. 1995. Biochemical versus mineral limitation in *Daphnia*. *Limnology and Oceanography* 40:1209-1214.
- Olney, J. E., G. C. Grant, F. E. Schultze, C. L. Cooper, and J. Hageman. 1983. Pterygiophore-interdigitation patterns in larvae of four *Morone* species. *Transactions of the American Fisheries Society* 112:525-531.
- Pace, M. L., S. B. Baines, and H. Cyr. 1993. Relationships among early life stages of *Morone americana* and *Morone saxatilis* from long-term monitoring of the Hudson River estuary. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1976-1985.
- Pace, M. L., S. E. G. Findlay, and D. Lints. 1991. Variance in zooplankton samples: evaluation of a predictive model. *Canadian Journal of Fisheries and Aquatic Sciences* 48:146-151.
- Pace, M. L., S. E. G. Findlay, and D. Lints. 1992. Zooplankton in advective environments: the Hudson River community and a comparative analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1060-1069.
- Pandian, T. J. 1987. Fish. Pages 357-465 in T. J. Pandian and F. J. Vernberg, editors. *Animal energetics. Volume 2: Bivalvia through Reptilia*. Academic Press, San Diego, California.
- Peters, R. H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge, UK.
- Pyke, G. H. 1984. Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics* 15:523-538.
- Rose, K. A., and J. H. Cowan, Jr. 1993. Individual-based model of young-of-the-year striped bass population dynamics. I. Model description and baseline simulations. *Transactions of the American Fisheries Society* 122:415-438.
- Rothschild, B. J. 1986. *Dynamics of marine fish populations*. Harvard University Press, Cambridge, Massachusetts.
- Rutherford, E. S., and E. D. Houde. 1995. The influence of temperature on cohort-specific growth, survival, and recruitment of striped bass, *Morone saxatilis*, larvae in Chesapeake Bay. *U.S. National Marine Fisheries Service Fishery Bulletin* 93:315-332.
- Schmidt, R. E. 1994. Identification of Hudson River *Morone* larvae. Final report to the Hudson River Foundation, New York.
- Secor, D. H., and E. D. Houde. 1995. Temperature effects on the timing of striped bass egg production, larval viability, and recruitment potential in the Patuxent River (Chesapeake Bay). *Estuaries* 18:527-544.
- Sinclair, M. 1988. *Marine populations: an essay on population regulation and speciation*. Washington Sea Grant Program, University of Washington Press, Seattle.
- Townsend, C. W., and I. J. Winfield. 1985. The application of optimal foraging theory to feeding behaviour in fish. Pages 67-98 in P. T. Calow, editor. *Fish energetics: new perspectives*. Johns Hopkins University Press, Baltimore, Maryland.
- Tsai, C.-F. 1991. Prey density requirements of the striped bass, *Morone saxatilis* (Walbaum) larvae. *Estuaries* 14:207-217.
- Turner, J. L., and T. C. Farley. 1971. Effects of temperature, salinity, and dissolved oxygen on the survival of striped bass eggs and larvae. *California Fish and Game* 57:268-273.
- Uphoff, J. H., Jr. 1989. Environmental effects on survival of eggs, larvae, and juveniles of striped bass

in the Choptank River, Maryland. Transactions of the American Fisheries Society 118:251-263.
Wootton, R. J. 1990. Ecology of teleost fishes. Chapman and Hall, New York.
Wright, D. A., and F. D. Martin. 1985. The effect of

starvation on RNA : DNA ratios and growth of larval striped bass, *Morone saxatilis*. Journal of Fish Biology 27:479-485.

Received April 25, 1996
Accepted December 23, 1996