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**Cladoceran Dynamics  
and the Recruitment of Larval *Morone*  
in the Hudson River Estuary**

**FINAL REPORT TO THE HUDSON RIVER FOUNDATION**

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## I. Introduction and Overview

### Background and Motivation

Each year, in late spring, the zooplankton populations of the Hudson River rise dramatically for a few weeks. Highest densities occur in the freshwater stretch between river km 80 and 160 and this is due to the seasonal population explosion of the cladoceran, *Bosmina longirostris*. This "bloom" phenomenon is constrained in both time and space, and represents an important potential food resource for larval fish.

We tested the hypothesis that the bloom of *Bosmina* (primarily) and other zooplankton (secondarily) provides a growth and survival advantage to larval striped bass (*Morone saxatilis*) and white perch (*M. americana*), two key species in the estuarine fish fauna of the Hudson. Earlier analysis (Pace et al. 1993) of the utilities' long-term data sets of *Morone* spp. failed to show strong relationships between abiotic factors (temperature and river discharge) and year class strength, leading to the hypothesis that biotic factors, such as food availability, may play the key role in setting recruitment of larval moronids in the Hudson River.

We conducted a field study in May-July 1994, collecting both larvae and zooplankton before, during, and after the *Bosmina* bloom. We conducted to major sets of analyses which are presented here as separate papers. In the first paper (*Transactions of the American Fisheries Society*, in press), we analyzed gut contents of larvae and estimated the energetic benefits of consumption against the costs of respiration. In the second paper (to be submitted to *Fisheries Bulletin*), we used the technique of otolith microanalysis to estimate growth rates, hatch dates, and mortality rates of larvae of both species as well as juvenile (i.e.,

successfully recruited) striped bass.

### **Main Result**

In contrast to our initial hypothesis, *Bosmina* did not appear to be the key food item for either species of larval moronid. Copepods were highly selected for, and consumption of copepods increased throughout the study even as their densities declined. Consequently although feeding and growth was good during the *Bosmina* bloom, it was at least as good post-bloom. This was confirmed by the gut, energetics, and otolith analyses.

Nevertheless, comparison of hatch dates of recruited striped bass juveniles with those of larvae from the same 1994 year class revealed strong differential mortality, with highest mortality on the later, fastest-growing cohorts. Although temperatures and food availability provided a good environment for growth, we conclude that predation was the likely cause of mortality on these later cohorts. Thus, greatest survival of the 1994 year class of striped bass came from those cohorts associated with the *Bosmina* bloom. Larval cohorts that co-occurred with high densities of *Bosmina* (as well as copepods), whose densities peaked simultaneously but downriver of the *Bosmina* bloom) encountered a habitat that had adequate resources for good growth, and presumably fewer predators, than later cohorts. Thus, under the conditions of 1994, the *Bosmina* bloom period was optimal for survival of moronid larvae.

### **Summary of Activities**

The project generated at least two papers for peer-reviewed publication (included in this

report). Additionally, oral presentations were made at the 1995 Estuarine Research Federation meeting (Corpus Christi, TX), at the 1996 annual meeting of the New York Chapter of AFS (Syracuse), at the 1997 winter meeting of the American Society of Limnology and Oceanography, and at several seminars given at universities and regional meetings. Limburg also prepared a data set of comparative characteristics for distinguishing between larval striped bass and white perch. This information will be incorporated into a larger study headed by John Waldman at HRF.

Two undergraduate students were involved in aspects of this prospect. One, a volunteer from Germany (Angelica Denk), examined the role of a predatory cladoceran, *Leptodora kindtii* as a third potential consumer of *Bosmina*. The other (Kristi Arend) was an integral participant in both gut and otolith studies, and her efforts are reflected in co-authorship on the papers. Kristi completed her otolith studies on a Polgar fellowship.

Consumption, Selectivity, and Utilization  
of Zooplankton by Larval *Morone* spp.  
in a Seasonally Pulsed Estuary

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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 striped bass (SB) and white perch (WP) 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; it was high except at those sites and times when Bosmina densities exceeded 14 L<sup>-1</sup>. Per capita energy consumption was highest (0.75 (SB) and 0.39 (WP) joules individual<sup>-1</sup>) after the bloom period, but specific consumption (energy consumed per mg wet weight fish) during and after the bloom were similar (2.39 vs. 2.35 (SB) and 2.58 vs. 2.63 (WP) joules mg dry weight<sup>-1</sup> during vs. after the bloom). Our energetics analyses indicate that different-sized fish experience different "benefit:cost" (food ingested:respiration) ratios, but strong trends exist with respect to the zooplankton bloom. Pre-bloom cohorts have the least available food and lowest metabolic costs (respiration). Post-bloom 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 but not 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 (cf. 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 (Bailey and Houde 1989; McGurk 1986) and food availability (Cushing 1990) can be critical as well.

In temperate and boreal estuaries, seasonal 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 North American east

coast. Because of its commercial and recreational value, striped bass has been the object of many studies. White perch, although of lower economic value, is of interest both as a fishery resource and because of its pivotal role in estuarine food webs due to its high abundance.

The cladoceran, Bosmina longirostris, 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 to 100 animals liter<sup>-1</sup> and then declines rapidly to less than 1 animal liter<sup>-1</sup> (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 interval during the population maximum (freshwater at this time of year), Bosmina biomass is approximately 25 metric tons of carbon with volumetric biomasses in excess of 100  $\mu\text{g C liter}^{-1}$ . These levels exceed prey biomasses of 40-80  $\mu\text{g C liter}^{-1}$  required for growth by striped bass larvae as measured in the laboratory using Artemia nauplii (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 spatio-temporal 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 indicate a series 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 1981; Boreman 1983; Uphoff 1989; Rutherford and Houde 1995; Secor and Houde 1995), salinity (Morgan et al. 1981; Turner and Farley 1971), dissolved oxygen (Turner and Farley 1971), and 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, which, if starvation occurs long enough, are irreversible and increase morbidity 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 (Rose and Cowan 1993; Cowan et al. 1993). Fourfold differences in food availability can lead to tenfold differences in larval survival to the juvenile stage (Cowan et al. 1993). In the Hudson River the variations in food exceed an order of magnitude and thus food variability and effects on larval dynamics should be evident in this system if food limitation is important.

## **Methods**

Study site and field sampling -- The Hudson River, a partially stratified estuarine river system in New York State, is tidal up to the Green Island dam, 245 km from the

mouth (Figure 2). The location of the salt front (defined as 0.1 ppt salinity) varies seasonally, but generally is located below river kilometer (KM) 100 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 are found in both freshwater and oligohaline sections and are retained there throughout the egg, yolk-sac, and post yolk-sac stages (Boreman and Klauda 1988, Klauda et al. 1988). Juveniles spread throughout the estuary and move seaward during 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 at the Kingston site (5- to 10-fold) and striped bass more abundant than white perch (2- to 10-fold) at New Hamburg (Boreman and Klauda 1988; Klauda et al. 1988; 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. Striped bass larvae outnumber white perch in this reach of the estuary.

Sampling of zooplankton and fish larvae was conducted weekly before the onset of the Bosmina bloom, then every three days during the bloom, and finally 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  $\mu$ m mesh) obliquely through the water column, from ca. 2 m off the bottom to the surface, for five minutes. Five replicate tows were made at each site on each date. Both nets were equipped with a General Oceanics flow meter 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-mm-mesh plankton net. Because the Hudson 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 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; Fritzche 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 teeth size, those of striped bass being conspicuously larger than white perch teeth 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 separate species.

Contents of the gut lumen were enumerated under 25-60 X 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 and 99 white perch larvae. Larvae, which included formalin-preserved specimens collected by a different study but on similar dates and sites, were re-hydrated 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 2 or more.

Zooplankton were counted with a stereomicroscope at 25 X 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 is 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 vs. 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 -- 2 June), during (3 June -- 13 June), and after (14 June -- 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 (joules  $\text{mg}^{-1}$  dry weight, Cummins and Wuychek 1971; rotifers were assumed to have a caloric value of  $20.9 \text{ J mg}^{-1}$ ). The resulting values are Bosmina,  $16.2 \times 10^{-3} \text{ J individual}^{-1}$ ; copepods,  $29.1 \times 10^{-3} \text{ J individual}^{-1}$ ; nauplii,  $8.75 \times 10^{-3} \text{ J individual}^{-1}$ ; rotifers,  $6.78 \times 10^{-4} \text{ J individual}^{-1}$ . Zebra mussel veligers, 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  $\ln(1 + \text{variable})$  to stabilize the variance.

To assess the energetic benefit of the zooplankton bloom relative to metabolic costs, we estimated total daily consumption rate ( $\text{J day}^{-1}$ ) from gut evacuation rate and compared it to calculated respiration rate ( $\text{J day}^{-1}$ ) 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 is 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:  $\ln(\text{gut evacuation rate, h}) = 2.619 - 0.882 \ln(\text{standard length, mm})$  ( $N = 4$ ,  $R^2 = 0.88$ ). 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, to  $17^\circ \text{C}$  (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 and converted from units of  $\text{mg dry weight d}^{-1}$  (Rose and Cowan 1993) to joules by applying the conversion factor  $20.9 \text{ J (mg dry weight)}^{-1}$  (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 and respiration cost 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 larval Morone was evaluated first with the Manly-Chesson index of feeding selectivity (Chesson 1983). This index is calculated as

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

,  $i = 1 \dots m$ , where  $r_i$  is the number or proportion of the  $i^{\text{th}}$  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, with zero indicating negative selection relative to environmental densities, 1, that the consumer's diet consists only of the  $i^{\text{th}}$  food item, and  $1/m$ , 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 and 483 striped bass larvae. Larval Morone densities increased steadily through May. Mean larval length increased with time, although due to gear constraints few individuals larger than 9.0 mm NL were captured. At the first sample date (18 May) white perch averaged  $4.4 \pm 0.6$  (s.d.) mm and striped bass  $4.8 \pm 0.7$  mm; on the final date (6 July) white perch were  $7.1 \pm 1.2$  mm and striped bass were  $8.1 \pm 1.4$  mm. Seasonal changes of sizes were not large, and

size ranges generally overlapped through time. Striped bass dominated at the oligohaline site (Haverstraw Bay, KM 65-70: mean 71.3%, range 36.7-94.1%), and white perch 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 L<sup>-1</sup> at New Hamburg on 10 June (a nearly 4,000-fold increase) and at 111.5 L<sup>-1</sup> at Kingston on 13 June. Whereas Bosmina densities were low in Haverstraw Bay (maximum 9 L<sup>-1</sup> 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 L<sup>-1</sup> (copepods) and 45-fold to peak at 777 L<sup>-1</sup> 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), but 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 vs. 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  $10 \text{ L}^{-1}$ . Striped bass 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 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 per liter (Figure 6). Note that feeding rates of larvae on copepods increased far more rapidly at low ( $0-10 \text{ L}^{-1}$ ) densities than for similar densities of Bosmina. The apparent depression of feeding on copepods observed at high densities ( $86 \text{ L}^{-1}$ ) is based on one sampling at Haverstraw

Bay. The depression is not due to the concurrent high abundance of Bosmina (516 L<sup>-1</sup>), 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,  $P < 0.1$ ) between 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 fresh water. Copepod consumption, in contrast, increased monotonically with time. White perch tended to consume more Bosmina than did striped bass larvae at any time and site, although the tendency was non-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 0.69 J (mg dry weight)<sup>-1</sup> for striped bass and white perch respectively) and declined thereafter (Figure 7B). However, this decline

was not significant for either fish species (Tukey's 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), while 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 post-bloom 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 vs. post-bloom cohorts. Highest C/R occurred for a post-bloom 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 vs. post-bloom periods, but pre-bloom was significantly lower (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, i.e. that zooplankton blooms represent an energy advantage for co-occurring fish larvae. Larval consumption of zooplankton increased more from the period prior to the bloom than from the bloom to post-bloom 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 post-bloom value. Energy gain vs. 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, since 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  $Q_{10}$  is actually lower, then post-bloom 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 (cf. 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 evidenced 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.

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  $> 1000 \text{ L}^{-1}$ ) in the Chesapeake, 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 non-selectively, 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 to 70.1). 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 vs. 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 and polyunsaturated fatty acids (HUFA, PUFA)) promote increased growth and egg production in zooplankton (Ahlgren et al. 1990; Ederington 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 larval Morone. For instance Tsai (1991) found a gradient of growth and survival of striped bass larvae when fed different stages of the copepod Eurytemora affinis with nauplii serving as the worst food source and adults the best.

Finally, since 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; Wahl et. al 1993), pigmentation (Loew et al. 1993), or movement (Kerfoot et al. 1980).

### Conclusion and Perspective

Large interannual variations in larval abundance of Morone 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 and 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 post-bloom periods would contribute most to total recruitment, whereas early larvae may not survive at all due to food limitation. Others have noted the tandem importance of both food availability and temperature for estuarine fish larvae (Crecco et al. 1983; Secor 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 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.

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