

Changes over three decades in feeding success of young American Shad *Alosa sapidissima* are influenced by invading zebra mussels *Dreissena polymorpha*

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ABSTRACT: We analyzed the feeding ecology of young American Shad *Alosa sapidissima* over a 25 yr period in the Hudson River Estuary, USA, where population declines have been attributed in part to food web alterations associated with invasive zebra mussels *Dreissena polymorpha*. We hypothesized that feeding success was positively associated with the standing crop or abundance of lower trophic level organisms and negatively associated with indicators of competition for resources, including the grazing rate of zebra mussels. Based on reports of feeding by larval American Shad on zebra mussel veligers, we considered an alternative hypothesis that zebra mussels have had a positive effect on feeding success. To test hypotheses, we employed 2 metrics of feeding success: amount of material in the gut, and condition. Hypotheses were tested separately for 2 early life stages of American Shad: post yolk-sac larvae and postmetamorphic juveniles. In larvae, short-term feeding success was positively associated with chlorophyll *a* concentration and negatively associated with conspecific abundance. In juveniles, short-term feeding success was negatively associated with conspecific abundance. Condition of larvae was positively associated with chlorophyll *a* concentration and with copepod abundance; condition of larvae and juveniles was negatively associated with cladoceran abundance. Our results on feeding success generally support the inference of previous studies that zebra mussels reduced the availability of essential prey for early-stage American Shad, perhaps contributing to recruitment losses in the Hudson River population of the species.

KEY WORDS: Feeding ecology · Estuary · Larval fish · Juvenile fish · Invasion · Gut contents · Condition

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1. INTRODUCTION

Changes in the trophic ecology of estuaries can have broad consequences. Estuaries are nurseries for many coastal fishes (Able & Fahay 2010), some of which are harvested. Because good feeding conditions for early-stage fishes can yield high cohort survival and a strong year-class (evidence reviewed by Heath 1992, Leggett & Deblois 1994, Cowan et al. 2000, Nunn et al. 2012), environmental factors affecting feeding ecology of larvae and juveniles may influence the population dynamics of economically im-

portant coastal species. Identifying these factors can require long-term data. Data and well-curated specimens from long-term surveys (Lindenmayer et al. 2012, Strayer et al. 2014a, Manoel & Azevedo-Santos 2018) or compilations of multiple studies taken over a broad timespan (Overton et al. 2015) provide valuable insights into ecological response to environmental changes, such as species invasions and climate change, thus aiding management.

Extensive, long-term monitoring programs in the Hudson River Estuary (reviewed and evaluated by Heimbuch et al. 1992) permit analyses of how eco-

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logical changes over recent decades have affected early-stage fishes. One such program was the Hudson River Utilities Longitudinal River Survey, which began in 1973 and ended in 2017. It yielded data on the distribution and abundance of pelagic early life stages of fish species and associated physicochemical parameters throughout the estuary.

The present study was motivated by indications that the zebra mussel *Dreissena polymorpha* invasion of the Hudson River Estuary has affected the feeding ecology of early-stage American Shad *Alosa sapidissima*. Zebra mussels became abundant in freshwater areas of the estuary in the early 1990s (Strayer et al. 2011). Owing to high filtration rates by the suspension-feeding mussel, profound changes rapidly occurred in lower trophic levels: total phytoplankton biomass decreased 85 % (Caraco et al. 1997, 2006), zooplankton biomass decreased more than 70 % (Pace et al. 1998), and zoobenthos biomass decreased 40 % (Strayer & Smith 2001). These alterations in estuarine energy flow could have severe consequences for the feeding success and diet composition of early life stages of fishes. In fact, changes over time in abundance, growth, and distribution among multiple species of pelagic fish larvae in the Hudson River Estuary have occurred that are consistent with losses of resources (Strayer et al. 2004). Since 2005, the abundance of zooplankton and some benthic invertebrates has partially or fully recovered, despite persistent depletion of phytoplankton biomass (Pace et al. 2010, Strayer et al. 2014b). Invasive zebra mussel impacts on other aquatic ecosystems have been similarly well documented (Vanderploeg et al. 2002).

American Shad are anadromous clupeids that spawn in spring in estuaries, such as the Hudson River, but spend most of their lives in the Atlantic Ocean from Virginia to Maine, USA. American Shad abundance in the Hudson River Estuary has dramatically declined since the 1950s, and a 2007 stock assessment summarized the stock as historically low (Atlantic States Marine Fisheries Commission 2007). The principal known causes of this decline were in-river overharvest and ocean fisheries by-catch; however, several other factors have been detrimental to American Shad stock health, including habitat loss due to dredging and channelization of the river, water pollution, and introduction of zebra mussels (Strayer et al. 2004, Kahnle & Hattala 2010). In the decade after the zebra mussel invasion, early-stage American Shad abundance decreased and apparent individual growth rate declined, judging from changes in the seasonal shift in size distribution (Strayer et al. 2004). Zebra mussels may competitively reduce resources

for young fish by feeding on primary producers, i.e. food of zooplankton that are prey for young fish. However, recent work has suggested that zebra mussels may be prey, in their veliger life stage, as well as competitors for early-stage fishes (Nack et al. 2015b). While indicators strongly suggest that the zebra mussel has had a substantial detrimental impact on the feeding ecology of early-stage American Shad, this study is the first to test this link. A similar investigation of early-stage Striped Bass *Morone saxatilis* found that feeding success was affected by the abundance of prey, competition from zebra mussels, and physicochemical parameters; in upriver areas where zebra mussels are abundant, their grazing rate had a depressing effect on young Striped Bass feeding success (Smircich et al. 2017).

We characterized early-stage American Shad feeding ecology in the Hudson River Estuary for 15 yr over a 25 yr period (1988–2012). We analyzed the feeding ecology of post yolk-sac larvae and of postmetamorphic young-of-year individuals (referred to hereafter as juveniles). Our goal was to determine what biotic environmental factors most influenced feeding success. We hypothesized that feeding success is positively related to the availability of prey resources, hence positively associated with the standing crop or abundance of lower trophic levels and negatively associated with indicators of competition for resources. To test the hypothesis, we measured short-term feeding success of individuals as amount of material in the gut, reflecting past feeding over hours before capture, and long-term feeding success as condition, reflecting feeding over multiple days before capture. Our predictions were that measures of feeding success (1) varied in time and covaried, as would be the case if volume of gut contents and condition both reflected variability in feeding success but on different time scales; (2) increased with standing crop of producers (i.e. bacteria and/or phytoplankton) because producer abundance may indicate secondary production rates; (3) increased with abundance of ≥ 1 taxa of prey (i.e. zooplankton and benthic grazers); and/or (4) decreased with abundance of competitors (i.e. zebra mussels and conspecifics). A corollary hypothesis that zebra mussels have had a detrimental effect would be most strongly supported if feeding success was positively associated with standing crop of phytoplankton, with prey taxa that have been depleted by zebra mussels, and/or if feeding success was negatively associated with zebra mussel abundance. Based on recent findings by Nack et al. (2015b), an alternative hypothesis is that zebra mussels have had a positive effect on early-stage American Shad feeding success.

2. MATERIALS AND METHODS

2.1. Source and workup of samples

Early-stage American Shad were collected in the Hudson River Utilities Longitudinal River Survey. The sampling design and handling of the samples have been consistent over time; details are available in the monitoring program's annual Yearclass Reports (e.g. ASA Analysis and Communication 2017). For sampling multiple habitats, a 1.0 m² Tucker trawl fitted with 500 µm mesh was towed in the water column or was mounted on an epibenthic sled. The survey used a stratified random design; sampling was typically weekly from early April through the end of June or early July, then every other week until September. To maximize ichthyoplankton capture success, all samples were taken at night (0.8 to 8.7 h after sunset: mean 4.8 h). We analyzed samples from 1988, 1991–1995, 1997, 1999, 2003, 2005–2006, and 2009–2012; the years were selected according to availability of samples and to represent the period before zebra mussels became abundant (before the late summer of 1992), the period when the mussel impacts were most pronounced (1993–2004), and the subsequent period of impact moderation. Samples were fixed upon collection in 10 % formaldehyde and remained in fixative until processing. Samples had already been sorted and enumerated so that the availability and number of American Shad in them were known.

Undamaged early-stage specimens were selected for analysis based on development stage, time of year, and sample location. To the extent possible, we maintained the same criteria for selecting samples containing early-stage American Shad throughout the time series, to minimize the influence of unconsidered environmental influences. Size distribution, seasonal distribution, and spatial distribution of specimens analyzed in each year for this study are provided in Supplement 1 (all Supplements available at www.int-res.com/articles/suppl/m628p141_supp.pdf). We selected samples that were collected in early summer (mean date = 4 July); 84 % of the samples were collected from mid-June through the first week of July, when the abundance of post yolk-sac larvae was typically just past peak but still high, and the abundance of juveniles was increasing. To balance sample size, we extended the range of sample dates in years when juveniles were scarce (1992, 1994, and 2003), as much as from late May to mid-September. Thirty specimens per year were analyzed for a total of 450 specimens. Specimens were separated into post yolk-sac larvae and juveniles. Post yolk-sac larvae were

<25 mm standard length, which is the size at which metamorphosis is complete (Maxfield 1953, Walburg & Nichols 1967). Fifteen fish per group were analyzed per year when possible (post yolk-sac larvae $n = 210$, standard length: 15 to 25 mm, mean = 20.9 mm, standard deviation = 3.3 mm; juveniles $n = 240$, standard length: 25.1 to 80 mm, mean = 38.4 mm, standard deviation = 10.4 mm). All samples were taken above river kilometer 96 (mean for all specimens = 150 km, standard deviation = 32 km), ensuring that they were taken in a portion of the river in which zebra mussels were abundant. Each selected specimen was dissected for gut contents and then dried. All specimens were digitally measured (notochord length of larvae, standard length of juveniles) to the nearest 0.01 mm and weighed for dry mass after drying for 48 h at 60°C. Gut contents were preserved, and their settled volume was measured (further details of methods in Smircich 2016).

2.2. Quantification of feeding success

We quantified individual feeding success in the short term and long term. The quantity of gut contents represented short-term feeding success. Among post yolk-sac larvae, 58 % of guts were apparently empty, and for this reason short-term feeding success was analyzed as a binary fullness variable, i.e. empty or nonempty; body length was included as a covariate. Among juveniles, only 4 % of guts were apparently empty, and short-term feeding success was analyzed as volume of gut contents; body length was included as a covariate. In both larvae and juveniles, body condition represented long-term feeding success. We quantified body condition as dry mass-at-length, i.e. the specimen's residual from the predicted value in regression of the log (dry mass) vs. log (length) dataset. The regressions for predicted dry mass-at-length were estimated separately for post yolk-sac larvae and juveniles. This representation of condition is comparable to the residual condition advocated by Jakob et al. (1996); it is similar to relative condition factor Kn (Wuenschel et al. 2019) but maintains length as a predictor rather than incorporating it into an index as a denominator.

2.3. Analysis of temporal variability in and covariation between measures of feeding success

To test Prediction 1 regarding variation and covariation in predictors of feeding success, we conducted

analyses of variance and correlation analyses (analysis chart and details provided in Supplement 2; all analyses were conducted in SAS for Windows 9.4). These analyses provided justification and context for subsequent analyses; tests of interannual variability justified further analysis of environmental predictors, and tests of concordance between short-term feeding success and condition revealed the extent to which there are common environmental drivers. Initial tests yielded evidence for temporal variability in feeding success (see Section 3), and we therefore evaluated which environmental predictors were most associated with success.

2.4. Data sources for candidate predictors of feeding success

Data for tests of Predictions 2 through 4 were collected on time scales ranging from weekly to annually (Table 1). Data on producers (Bacteria, phytoplankton biomass as chlorophyll *a*), prey (Amphipoda, Cladocera, Copepoda, zebra mussel veligers), and a measure of competition from zebra mussels were collected in monitoring programs of the Cary Institute of Ecosystem Studies (methods used to collect these data are described by Pace et al. 1992, Findlay et al. 1998, Strayer & Smith 2001, Caraco et

al. 2006, Strayer et al. 2011). Amphipoda, Cladocera, and Copepoda were chosen as predictors of feeding success because they predominated in the diet of our specimens (Smircich 2016). Data on these variables were collected at river kilometer 152, close to the mean location for specimens we analyzed. Excepting Amphipoda and zebra mussel competition, which were annual estimates, data for these variables were collected every other week; we selected values that were taken during the same week (or the previous week), as the American Shad specimens we analyzed. The variable representing competition from zebra mussels was the estimated population filtration rate, which combines measures of mussel abundance and size. Data on Amphipoda were missing for 5 yr (1988, 2003, 2009–2011), and values for mussel veligers were missing from 1992 to 2001. We assumed values of 0 for mussels as veliger prey and as competitors for pre-invasion years 1988 and 1991. Data on the abundance of American Shad post yolk-sac larvae, a measure of year-class success (Kahnle & Hattala 2010) and potential intraspecific competition, were provided in reports of the Hudson River Utilities monitoring programs (e.g. ASA Analysis and Communication 2017). We tested for among-year temporal trends in each environmental variable and intercorrelations among the variables using Kendall rank correlation tests and Pearson product-moment

Table 1. Simple correlations of variables used in mixed modeling, including producer-level variables: Bacteria abundance (Bac), chlorophyll *a* concentration (Chl); prey-level variables: Amphipoda abundance (Amp), Cladocera abundance (Cla), Copepoda abundance (Cop), zebra mussel veliger abundance (Vel); competitor-level variables: American Shad *Alosa sapidissima* larva abundance (Sha), zebra mussel filtration rate (Mus); and year (Yr) to test for changes over time. Sample size is listed below column headers as number of values for larval dataset/number of values for juvenile dataset. Entries in the table for intercorrelations among variables are Pearson product-moment correlation coefficients, and for changes over time are Kendall Tau correlation coefficients. Values above diagonal are for larval dataset; values below diagonal are for juvenile dataset. Entries in *italics* indicate those with nominal $p < 0.05$, and entries in **bold** indicate those with p -values less than the Bonferroni critical value, determined as 0.05/36

	Bac ^a 22/32	Chl ^a 22/32	Amp ^a 10/10	Cla ^a 22/32	Cop ^a 22/32	Vel ^a 12/17	Mus ^a 15/15	Sha ^b 15/15	Yr 15/15
Bac		0.41	<i>0.67</i>	−0.15	0.06	−0.18	−0.12	0.21	−0.26
Chl	0.33		<i>0.79</i>	−0.16	−0.33	−0.32	<i>−0.73</i>	<i>0.64</i>	−0.33
Amp	<i>0.85</i>	<i>0.69</i>		−0.28	−0.34	−0.77	<i>−0.68</i>	<i>0.71</i>	−0.42
Cla	−0.26	−0.14	−0.54		0.23	−0.06	0.29	−0.46	<i>0.39</i>
Cop	−0.07	−0.28	−0.32	0.20		<i>0.75</i>	0.15	<i>−0.59</i>	0.37
Vel	−0.05	−0.17	−0.85	−0.10	<i>0.55</i>		−0.02	−0.43	<i>0.62</i>
Sha	−0.20	<i>−0.67</i>	<i>−0.68</i>	0.40	0.20	−0.04		<i>−0.52</i>	0.23
Mus	0.36	<i>0.53</i>	<i>0.71</i>	−0.42	<i>−0.64</i>	−0.41	<i>−0.52</i>		−0.79
Yr	<i>−0.43</i>	−0.35	−0.42	0.33	0.43	<i>0.62</i>	0.23	−0.79	

^aCary Institute of Ecosystem Studies data; values used are each year's means of measurements at the Kingston long-term monitoring station taken in the same period as ichthyoplankton sampling, excepting values for Amphipoda and mussels which were taken in a single sample each year

^bLongitudinal River Survey data; values used are indices of year class abundance

correlation tests, respectively. The environmental predictor datasets differed for larval and juvenile samples because of differences in sample date and location; therefore, we conducted temporal trend and intercorrelation analyses on each dataset.

2.5. Analysis of biotic predictors of feeding success

For each of the 4 feeding success datasets (short-term feeding success and condition of both larvae and juveniles), we selected models with the best combination of environmental predictors (listed in Table 1). We used information-theoretic approaches, and structured model selection around *a priori* Predictions 2 through 5 rather than using an all-subsets or data-dredging approach. Individual specimens were represented as repeated or clustered observations within their ichthyoplankton sample (the net tow in which they were collected), and year was included as a random effect. In analyses of short-term feeding success, every model included specimen length and the time of the sample relative to sunset. In analyses of condition, every model included specimen length. We quantified the relative variable importance of each variable that was included in selected models (Burnham & Anderson 2002). The extent to which the best model explained variability in feeding success was estimated as the coefficient of determination (R^2) and also as effect size; for the latter, we evaluated the best model with observed values of predictors yielding low and high estimates of the response variable. Descriptions of the models used for each of the 4 analyses and how models were selected are provided in Supplement 3. Missing years of data for Amphipoda and zebra mussel veligers meant that models including either variable as a predictor would omit data on any variable for these years. Therefore, we evaluated whether including these 2 prey predictors would affect our conclusions, by separately selecting models using only years when data on Amphipoda and veligers were available.

3. RESULTS

3.1. Temporal variability in and covariation between measures of feeding success

Prediction 1 was supported; short-term feeding success and condition varied among years and were partially concordant. Short-term feeding suc-

cess varied among years in American Shad *Alosa sapidissima* larvae (Fig. 1A; logistic regression $p < 0.05$) and juveniles (Fig. 1B; linear mixed effects model, $F_{14,144} = 2.5$; $p = 0.003$). Other predictors of short-term feeding success were time after sunset (negative effect: $p = 0.0009$ and $p < 0.0001$ in larvae and juveniles, respectively) and length (positive effect: $p < 0.0001$ for both larvae and juveniles). Condition varied among years in larvae (Fig. 2A; linear mixed effects model, $F_{14,141} = 17$; $p < 0.0001$) and juveniles (Fig. 2B; linear mixed effects model, $F_{14,144} = 5$; $p = 0.002$). Short-term feeding success and condition were concordant in larvae (logistic regression, $p = 0.0001$) but not juveniles (multiple linear regression, $p = 0.2$). Neither of the feeding success indicators showed a clear temporal pattern in larvae or juveniles.

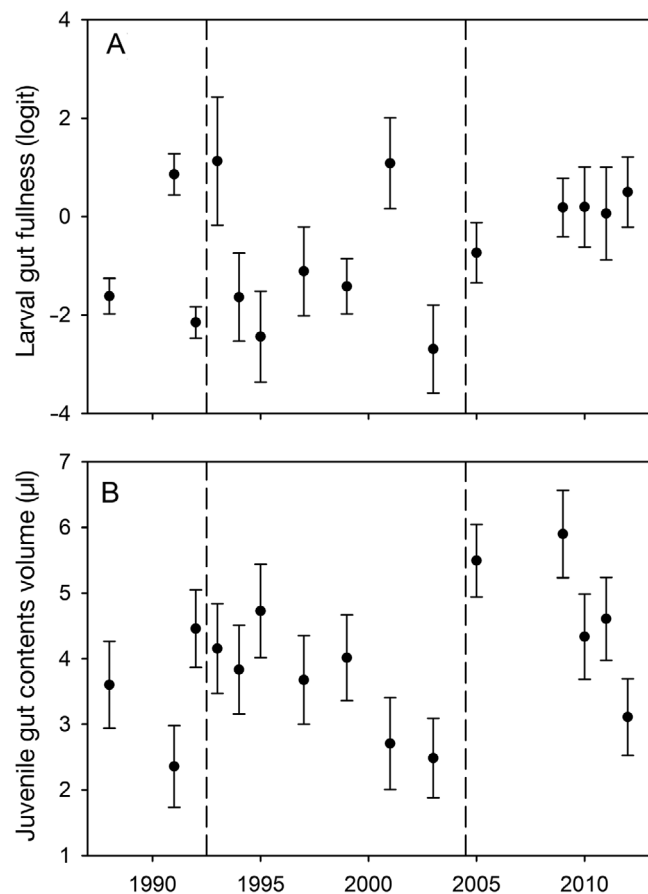


Fig. 1. Annual mean values of short-term feeding success of larval and juvenile American Shad *Alosa sapidissima* over a 25 yr period in ichthyoplankton samples from the Hudson River Estuary. Vertical dashed lines mark the onset and end of the period of highest zebra mussel *Dreissena polymorpha* impact on the ecosystem, referred to by Strayer et al. (2014b) as the early invasion period. (A) Mean (± 1 SE) length-adjusted logit of the proportion of nonempty guts in larvae. (B) Mean (± 1 SE) volume of gut contents in juveniles

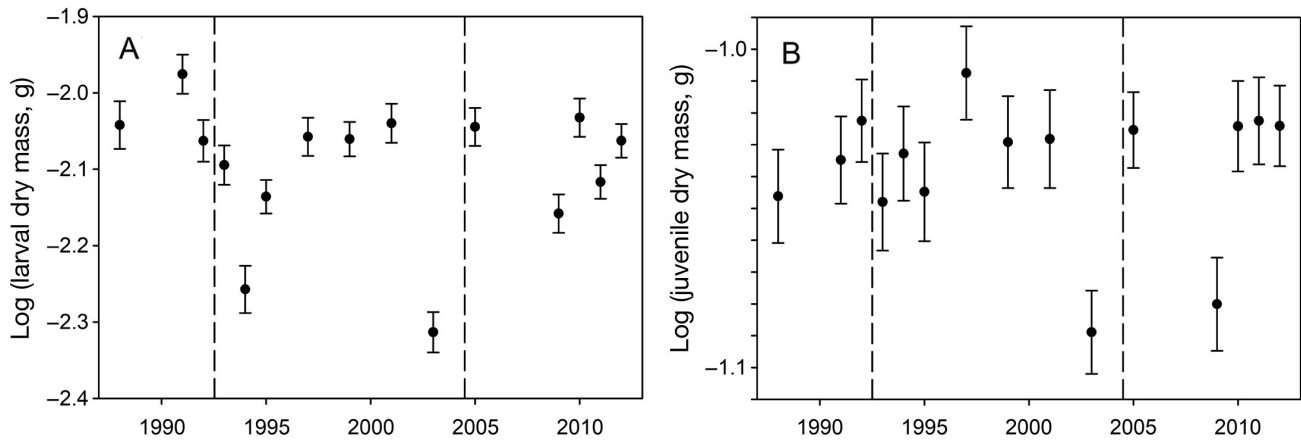
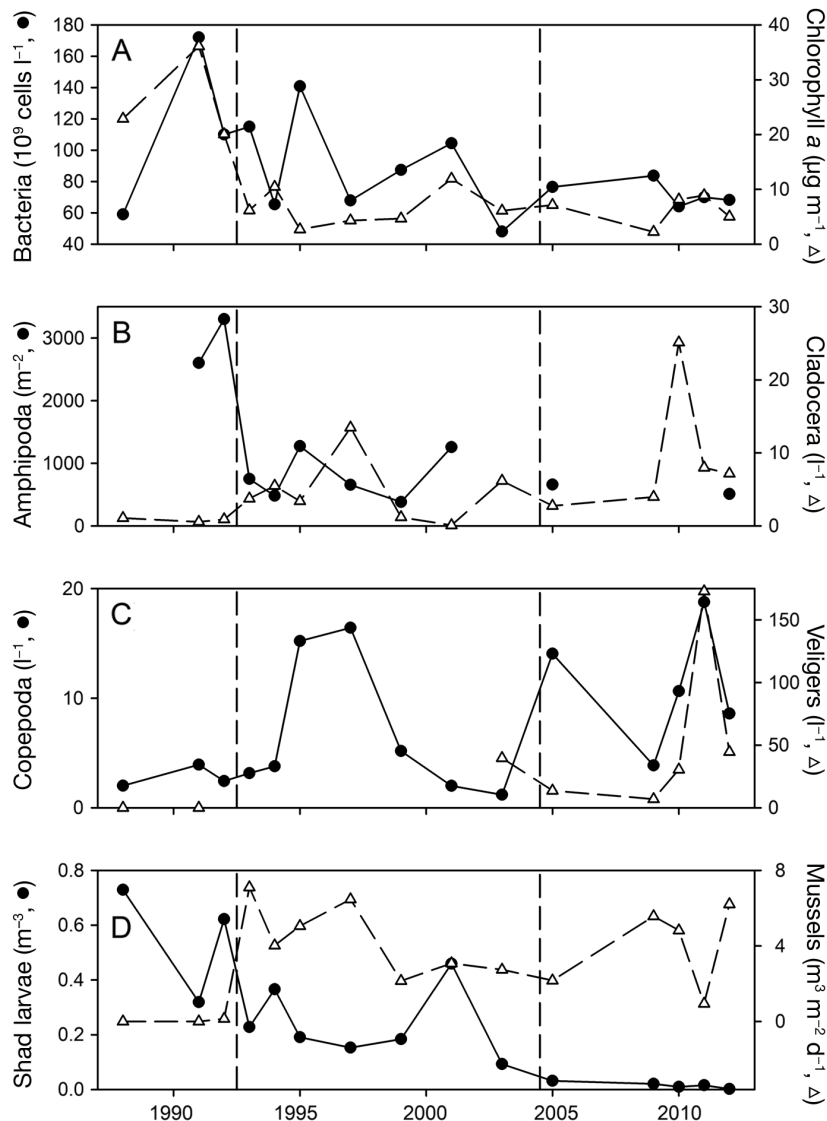


Fig. 2. Annual mean values of long-term feeding success (± 1 SE) as condition (dry mass at mean length) of (A) larval and (B) juvenile American Shad over a 25 yr period in ichthyoplankton samples from the Hudson River Estuary. Vertical dashed lines represent the onset and end of the period of highest zebra mussel impact on the ecosystem



3.2. Temporal variability in candidate predictors of feeding success

Environmental predictors varied over wide ranges over the time series, some by 2 orders of magnitude (Fig. 3). Some predictors exhibited temporal trends (Table 1). The abundance of Bacteria nominally declined over time ($p < 0.05$ but greater than Bonferroni criterion for significance), and the abundance of Cladocera and zebra mussels veligers nominally increased over time. Shad larva abundance declined over

Fig. 3. Annual mean values of biotic and abiotic environmental variables that were tested as predictors of feeding success of American Shad over a 25 yr period from the Hudson River Estuary. Values plotted are annual means for specimens of larval American Shad analyzed in the study. Source for each variable is listed in Table 1. Vertical dashed lines represent the onset and end of the period of highest zebra mussel impact on the ecosystem. (A) Variables representing producer trophic level: Bacteria abundance and chlorophyll *a* concentration. (B) Variables representing 2 taxa in the prey trophic level: abundance of Amphipoda and Cladocera. (C) Prey variables: abundance of Copepoda and zebra mussel veligers. Zebra mussel veliger abundance was assumed to be 0 in years before the zebra mussel invasion. (D) Variables representing competitor trophic level: American Shad larval abundance and zebra mussel filtration rate. Zebra mussel filtration rate was assumed to be 0 in years before the zebra mussel invasion

time. Estimates of primary production were intercorrelated with abundance of organisms at higher trophic levels, as we postulated (Table 1): abundance of Bacteria was positively correlated with Amphipoda, and chlorophyll *a* concentration was positively correlated with Amphipoda and larval shad abundance but negatively correlated with zebra mussel filtration rate. Larval shad abundance and zebra mussel filtration rate were also negatively correlated.

3.3. Predictors of short-term feeding success

Analyses of short-term feeding success of larvae and juveniles yielded partial or full support for 2 of 3 predictions and partially supported the hypothesis that zebra mussels have had a detrimental effect. As per Prediction 2, and consistent with the negative effect of zebra mussels via depletion of phytoplankton, chlorophyll *a* concentration was positively associated with the probability that larvae had a non-empty gut (Table 2A). Prediction 4 was also partially supported: conspecific abundance was negatively associated with the probability that larvae had a non-empty gut and with length-adjusted volume of gut contents in juveniles (Table 2). When conspecific abundance was omitted from the most-supported model of larval short-term feeding success, filtration rate of zebra mussels appeared as a positive predictor, albeit with lower support (Table 2A). The

selected models explained ~50 % of the variability in short-term feeding success of larvae and juveniles. The probability of larvae having a nonempty gut changed from a low of 0.08 to a high of 0.82 when the best-selected model was parameterized over the observed range of environmental variability. Among juveniles, predicted volume of gut contents changed ~27 % (low = 3.2 μ l; high = 4.2 μ l, at a mean length of 37 mm) over the observed range of environmental variability. These findings were not substantially altered when we restricted analysis to years when there were data on Amphipoda and zebra mussel veligers. Amphipoda was included as a negative predictor of larval short-term feeding success in 1 of 6 selected models but was not influential (relative variable importance, RVI = 0.20; results not tabulated); Amphipoda was not included as a predictor of juvenile short-term feeding success, and veligers were not included as predictors in selected models associated with either larval or juvenile short-term feeding success.

3.4. Predictors of long-term feeding success

Analyses of larval American Shad condition supported one prediction and yielded mixed support for a second prediction. As per Predictions 2 and 3, and consistent with the negative effect of zebra mussels via depletion of primary and secondary production,

Table 2. Environmental factors predicting short-term feeding success in larval and juvenile American Shad. Each subtable presents the best explanatory models. The relative variable importance (RVI) is given for each environmental predictor that was included in the selected models. Entries are information criteria (QAIC or AIC), change in criteria between models (Δ QAIC or Δ AIC), model weight (QAICWt or AICWt), and the slopes (with standard error in parentheses) for each predictor included in the model. Models are presented only if Δ QAIC or Δ AIC is low (≤ 4) and if all simpler nested models had larger Δ QAIC or Δ AIC. Variables that were not included in the model represented on that row are indicated with a dash. (A) Larvae. Maximum-rescaled generalized coefficients of determination (R^2_N), estimated as in Nagelkerke (1991), ranged from 0.46 to 0.47 in logistic regression models with these predictors. (B) Juveniles. Coefficient of determination values (R^2) in regression models with these predictors was 0.51 to 0.52

(A) Larvae							
QAIC	Δ QAIC	QAICWt	Length	Time after sunset	Chlorophyll <i>a</i> (RVI = 0.72)	Mussels (RVI = 0.32)	Shad (RVI = 0.43)
205.2	0.0	0.21	270 (5.1)	-0.0058 (0.0016)	0.063 (0.022)	–	-2.5 (1.3)
205.8	0.7	0.15	280 (4.3)	-0.0057 (0.0018)	0.069 (0.027)	-0.24 (0.13)	–
207.9	2.7	0.05	270 (4.2)	-0.0050 (0.0016)	0.025 (0.016)	–	–
208.3	3.2	0.04	270 (4.2)	-0.0047 (0.0016)	–	–	–
(B) Juveniles							
AIC	Δ AIC	AICWt	Length	Time after sunset	Shad (RVI = 0.80)		
1006.6	0.00	0.57	18 (1.5)	-0.0079 (0.0015)	-1.2 (1.2)		
1009.9	3.3	0.11	18 (1.5)	-0.0079 (0.0015)	–		

Table 3. Environmental factors predicting long-term feeding success in larval and juvenile American Shad. Each subtable presents the best explanatory model(s). The relative variable importance (RVI) is given for each environmental predictor that was included in the selected models. See Table 2 for more details. (A) Larvae. Coefficient of determination values (R^2) in regression models with these predictors ranged from 0.86 to 0.88. (B) Juveniles. Coefficient of determination values (R^2) in regression models with these predictors was 0.99

(A) Larvae							
AIC	Δ AIC	AICWt	Length	Chlorophyll <i>a</i> (RVI = 0.80)	Cladocera (RVI = 0.48)	Copepoda (RVI = 0.97)	Shad (RVI = 0.26)
–460.2	0.0	0.20	4.6 (0.1)	0.0061 (0.0022)	–	0.0073 (0.0026)	–
–456.6	3.6	0.03	4.6 (0.1)	–	–0.0010 (0.0006)	0.0095 (0.0030)	0.20 (0.11)
(B) Juveniles							
AIC	Δ AIC	AICWt	Length	Cladocera (RVI = 1.00)			
–864.9	0	0.15	3.6 (0.030)	–0.0022 (0.00037)			

condition of larvae was positively associated with chlorophyll *a* and with copepods (Table 3A). The selected models explained nearly 90 % of the variability in condition of larvae. Predicted dry mass (back-transformed from $\log[\text{dry mass}]$) of larvae varied >100 % (low = 6.3 μg ; high = 13.5 μg , at a mean length of 20.5 mm) over the observed range of environmental variability. Another selected model included Cladocera, which was negatively associated with condition, and omitted chlorophyll *a*. One sample of larvae, taken in 2010, was collected when Cladocera abundance was unusually high (Cladocera = 105 m^{-3} ; all other values 0.1 to 26 m^{-3}). We omitted this sample to determine whether its high leverage in the model had altered the conclusions. In the revised dataset, a negative association between condition and Cladocera remained, as did positive associations between condition and chlorophyll *a* and between condition and Copepoda.

Among juveniles, condition was unexpectedly negatively associated with Cladocera (Table 3B), in contradiction to Prediction 3. The selected model explained 99 % of the variability in condition of juveniles. Predicted dry mass of juveniles changed 5 % (low = 89 μg ; high = 94 μg , at a mean length of 37 mm) over the observed range of environmental variability. Restricting the years analyzed to include Amphipoda or zebra mussel veligers as predictors did not alter these findings. One sample of juveniles, taken in 2012, was collected when Cladocera abundance was unusually high (Cladocera = 88 m^{-3} ; all other values 0.8 to 26 m^{-3}). We omitted this sample to determine whether its high leverage in the model had altered the conclusions. In the revised dataset, Cladocera remained as the only predictor, with a negative slope, aside from length.

4. DISCUSSION

Results were mostly consistent with the hypothesis that feeding success of early-stage American Shad was positively related to food availability. Producers (as represented by chlorophyll *a*; 3 of 4 analyses) and prey (abundance of Copepoda; 1 of 4 analyses) were positive predictors of feeding success. The abundance of conspecifics was, as expected, a negative predictor of feeding success in 2 of 4 analyses. However, one prey variable (abundance of Cladocera, 2 of 4 analyses) unexpectedly appeared as a negative predictor of feeding success, and a variable of competition, the filtration rate of zebra mussels, unexpectedly appeared in one analysis as a positive predictor of feeding success, albeit with less support than the countervailing effect of conspecific abundance.

4.1. Impact of zebra mussels on feeding success and year class strength

These findings strengthen the evidence for a negative effect of zebra mussel on early life stages of American Shad. The abundance of American Shad larvae, hence year-class success, has declined over recent decades (Strayer et al. 2004, 2014b, Atlantic States Marine Fisheries Commission 2007, Kahnle & Hattala 2010). Further, Strayer et al. (2004) found that American Shad and other species whose early life stages live in open water had declined in abundance, had decreased apparent growth rates, and had shifted their distribution to less-impacted areas of higher salinity as zebra mussels became established. In contrast, species that inhabited the littoral zone

had increased in abundance, had higher apparent growth rates, and had shifted their distribution up-river. Given evidence presented in other studies (Caraco et al. 1997, Pace et al. 1998) that zebra mussel grazing had sharply reduced phytoplankton abundance, with concomitant reductions in some components of the zooplankton, Strayer et al. (2004, see also Strayer et al. 2014b) suggested that zebra mussels diverted energy flow away from pools available to ichthyoplankton. That suggestion gave impetus to the current study and a similar analysis of Striped Bass (Smircich et al. 2017), wherein we have sought to confirm that one or more biotic environmental factors that have been altered by zebra mussels have in fact affected feeding success of early-stage open-water fishes.

We suggest that the decline in larval fish abundance early in the zebra mussel invasion was partly attributable to decreased production of essential prey as mussel grazing increased. This may have impeded the recovery of the Hudson River American Shad population. A century-long history of hypotheses and empirical tests concerning the relationship between early-stage feeding ecology and population dynamics in marine fishes (most recently reviewed by Leggett & DeBlois 1994, Cowan et al. 2000) supports the idea that availability of food for larval and/or early juvenile fishes can have a decisive impact on year-class success and that such food limitation can have a regulating, density-dependent effect. In a sense it is surprising that we found these effects in Hudson River American Shad, given that this population's abundance is historically low; even in the early years of our time series, early-stage American Shad were probably sparse relative to previous decades, given documented trends in American Shad and other diadromous fishes of the North Atlantic (Limburg & Waldman 2009). Feeding opportunities for young American Shad have evidently diminished because of ecosystem-wide changes arising from the zebra mussel invasion and other stressors. Thus, studies of early-stage feeding ecology that are placed in an ecosystem context will enhance our ability to predict, and manage or prepare for, population responses in a species subject to harvest like American Shad (Brodeur et al. 2017).

The zebra mussel invasion was preceded by other stressors on Hudson River American Shad stocks, which to this day contribute to poor recruitment. Shad populations coast-wide have been declining since the late 19th century, owing to damming, other degradations of spawning habitat, and overfishing (Limburg et al. 2003, Atlantic States Marine Fisheries

Commission 2007). A directed ocean-intercept fishery ended in 2005, but American Shad are still harvested in mixed-stock ocean fisheries. Although commercial fishing continues in major rivers of the region (Atlantic States Marine Fisheries Commission 2018), it was closed in the Hudson River in 2010. Striped Bass predation may play an additional top-down role. Decline of American Shad and other alosines over several decades has coincided with a recovery of Striped Bass stocks after severe overfishing (Savoy & Crecco 2004), and a link between burgeoning Striped Bass and declining river herring has been indicated by bioenergetics modeling (Hartman 2003) and more direct analyses of Striped Bass diet and population modeling (Davis et al. 2012, Davis 2016). In the Hudson River, Striped Bass feeding on adult American Shad appears to be minimal (Atlantic States Marine Fisheries Commission 2007), but the predation rate of Striped Bass on juvenile American Shad has not been assessed.

We envision the interaction between zebra mussel and early-stage American Shad as essentially competitive, although the interaction is indirect because zebra mussels graze on the base of the food web rather than on the fish's prey. Why then was the rate of mussel grazing not a negative predictor of feeding success? One possible explanation is that the interaction is mediated through phytoplankton, and the relationship between mussel grazing and phytoplankton biomass is highly nonlinear, with low phytoplankton biomass even at relatively low grazing rates (Strayer et al. 2019).

We found no evidence that zebra mussel veligers are important prey for American Shad larvae or juveniles. Nack et al. (2015b) found that zebra mussel veligers accounted for >26% of the biomass of early-stage American Shad diet and suggested that the species may be an additional important food source in the early summer months in the Hudson River Estuary. Similarly, zebra mussel and quagga mussel *Dreissena bugensis* veligers were identified in about half of the young-of-year and adult alewives *Alosa pseudoharengus* collected in Lake Ontario less than a decade after the mussel invasions there, albeit as small components of the diet (Mills et al. 1995). We found no zebra mussel veligers in the diet of larval or juvenile American Shad in our samples (Smircich 2016), but the absence of veligers in our samples may be the result of sample preservation. Our samples were preserved in formalin which could dissolve veliger shells, making them difficult to detect. The size range of our specimens is unlikely to be a contributing factor, judging from previous studies (Mills et al. 1995, Nack et al.

2015b) reporting dreissenid veliger consumption by alosines of comparable life stage and size as our specimens. In any case, if veligers were an important component of the diet, their abundance should positively predict short-term feeding success and/or condition; we found no such effects.

4.2. Effects of other predictors on feeding success

The potential for interspecific competitive effects was limited in this study to that arising from zebra mussel grazing. In particular, we did not incorporate abundance indices of other alosines, Alewife *A. pseudoharengus* and Blueback Herring *A. aestivalis*, into our regression models. A previous study of diet overlap in the Connecticut River (Crecco & Blake 1983) indicated that interspecific competition was less important than intraspecific competition in early-stage alosines, but this possibility warrants further investigation.

The negative association between Cladocera abundance and the condition of larvae and juveniles is unexpected. Cladoceran abundance was more variable in our time series than other predominant prey (CV = 140%, vs. 76% for Copepoda and 83% for Amphipoda), probably owing to the occurrence of *Bosmina freyi* blooms, in which abundance rises to high densities (increasing from <0.1 to 100 l^{-1} , then falling to 1 l^{-1} ; Pace et al. 1992). Judging from their frequent appearance in the diet, *Bosmina* and other Cladocera are important prey for young shad (Maxfield 1953, Levesque & Reed 1972, Crecco & Blake 1983, Johnson & Dropkin 1996, Nack et al. 2015b) and other early-stage estuarine fishes (Able & Fahay 2010). At times, alosines exhibit a feeding preference (selectivity) for *Bosmina* (Pothoven & Vanderploeg 2004), perhaps in part because capture success is relatively high (Link 1996). The *Bosmina* bloom generally coincides with the appearance of early-stage American Shad and other species in the estuary, suggesting that larvae are more successful during a *Bosmina* bloom than before or after a bloom (Strayer et al. 2014a). Limburg et al. (1997) studied the impact of *Bosmina* blooms on prey preference in moronid (Striped Bass *Morone saxatilis* and White Perch *M. americana*) larvae. During a bloom, moronid larvae fed most heavily on and selected for *Bosmina* in preference to other prey. Prior to and after the bloom, larvae selected for Copepoda. The consumption and preference patterns could not be readily explained based on estimates of energy available in these prey species; moronid larvae were feeding on Copepoda

to a greater extent than they should according to energetic calculations. Larval American Shad have larger gapes and feed more heavily on Copepoda than larval Striped Bass (cf. Smircich et al. 2017), and our results suggest that they may deviate in the opposite direction from moronid larvae, feeding on *Bosmina* to an extent greater than they should.

The feeding rate of American Shad larvae is higher than expected from general literature on larval fish feeding, but comparable to results of previous studies of this species. In a geographically and taxonomically comprehensive review of marine and coastal larval fish feeding ecology, Llopiz (2013) found that feeding incidence is lower in estuarine larvae (median of 40%) than other marine habitats ($>80\%$) and is lower in clupeiform fishes (40%) than in other orders (e.g. Perciformes, $>80\%$). Our values for feeding incidence of American Shad, and those of several other studies, are higher than suggested by these values. We estimate from our regression model that 90% of 20 mm American Shad larvae had nonempty stomachs at sunset. Levesque & Reed (1972) reported feeding incidence of 64% for American Shad larvae of 14 to 28 mm, and Nack et al. (2015b) reported values of 60 and 89% for American Shad larvae ≤ 15 and >15 mm, respectively.

4.3. Concluding remarks

Assessments of the impact of environmental variability on feeding ecology should employ multiple indicators of individual condition, as we have done here. Short-term feeding success was correlated with condition in American Shad larvae but not in American Shad juveniles. These measures were positively correlated in early-stage Striped Bass (Smircich et al. 2017). Positive correlations suggest that different measures may have responded similarly to the same environmental drivers, whereas the lack of correlation in juvenile American Shad suggests that different measures may have responded differently to environmental variation. The relative merits of different condition indices are regularly appraised in fishes and other taxa (e.g. Ferron & Leggett 1994, Jakob et al. 1996, Wuenschel et al. 2019). As reflected in our choice of gut fullness and condition, the time course of response to changes in environmental conditions is an important criterion to consider in selecting indices. Life history may also be an important criterion. Coexisting early stages of species with different life histories may respond differently to temporal variability in environmental conditions, as

one recent study contrasting juvenile condition indices of migratory and resident estuarine fishes has demonstrated (Schloesser & Fabrizio 2016). The most informative condition index may differ with development; for example, growth rate in length was an indicator of habitat quality for American Shad larvae ≤ 15 mm, whereas relative body depth was an indicator of habitat quality for larvae > 15 mm (Nack et al. 2015a). In that regard, individual growth would have been a good complement to our condition-based measure of long-term feeding success, given the possibility that marginal increases in food consumption could be preferentially allocated to growth in length with no change in mass-at-length. In fact, it does appear that American Shad grew faster in years with little or no mussel impact, judging from interannual changes in apparent growth, meaning the rate at which mean size increased each season (Strayer et al. 2004, 2014b). Measures of individual growth based on the daily growth record in otoliths would yield a more direct test of this possibility. Unfortunately, preservation conditions of our specimens erased this individual record of growth. We recommend that ichthyoplankton monitoring programs handle a subset of samples in a way that preserves otolith integrity (e.g. immediate preservation in 95% ethanol) for analysis of growth and environmental history.

Well-designed monitoring studies, providing long-term data on ecosystem attributes, can shed light on process, yield parameters for ecosystem models, and facilitate hypothesis tests that use changes in the ecosystem as a natural experiment. A component of these monitoring programs that perhaps has not received the attention it deserves is the availability of samples. Some biological samples that are collected as part of monitoring studies must be preserved and retained for quantification, as is the case for ichthyoplankton. In such cases, long-term security of the samples should be considered in the planning of the survey. Ideally, the portion of the collection that is designated for long-term preservation will be conveyed to a facility that is capable of curating the samples and their data indefinitely, such as a museum. Identification of such a facility should occur at the outset, and the monitoring contract should include funds to maintain the samples and to accession a subset in a curated facility. Difficult issues attend the process we propose, entailing transfer of private property related to sensitive environmental issues to public facilities over which the original property owners would have no oversight. Because these issues are so difficult, we suggest that they should be resolved in advance.

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