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The feeding ecology of *Morone americana* larvae in the Chesapeake Bay estuarine turbidity maximum: the influence of physical conditions and prey concentrations

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Feeding ecology of white perch *Morone americana* larvae, a major component of the ichthyoplankton community in the estuarine turbidity maximum (ETM) region of upper Chesapeake Bay, was evaluated in years of contrasting physical conditions. In 1998, high river flow led to an ETM with high turbidity and pronounced salinity stratification. In 1999, under low river flow conditions, turbidities in the ETM region were lower and the salt front was located 15 km up-stream of its location in 1998. Copepodites and adults of *Eurytemora affinis* were the predominant prey in guts of all length classes of larvae (3·2–9·8 mm standard length, L_S) that were examined. Repeated-measures, multiple regression analyses were conducted to evaluate the influence of several factors on feeding success by determining if physical conditions (temperature, current velocity, salinity, turbidity and light) and prey concentrations explained variability in mean gut fullness (gut contents mass per body mass) of small (<5 mm L_S) and large (>5 mm L_S) white perch larvae. *Eurytemora affinis* concentrations were significant in the statistical models for both small and large larvae. High concentrations of *E. affinis*, which enhanced encounter rates of white perch larvae with prey, may have been the most important factor determining feeding success in the ETM region. Larval feeding incidence (percentage of guts with food) was higher in 1998, suggesting that annual variability in river flow influenced larval feeding success by controlling physical and biological conditions in the ETM region.

Key words: copepoda; *Eurytemora*; gut contents; recruitment; river flow.

INTRODUCTION

The estuarine turbidity maximum (ETM) is a physical feature in the upper reaches of many coastal plain estuaries (Schubel, 1968) that is characterized by elevated turbidity and high concentrations of suspended sediments, mesozooplankton and ichthyoplankton. The ETM region is an important nursery

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area for estuarine-dependent fishes in the St Lawrence River estuary (Dodson *et al.*, 1989; Dauvin & Dodson, 1990; Sirois & Dodson 2000*a*), the San Francisco Bay estuary (Jassby *et al.*, 1995; Bennett *et al.*, 2002), the upper Chesapeake Bay (North & Houde, 2001) and potentially in the Dollard-Ems estuary in the Netherlands (Jager, 1998). High prey concentrations in the ETM, compared to areas down- and up-stream, are believed to be advantageous to feeding and growth of early-life stages of fishes in the ETM region (Laprise & Dodson, 1989; North & Houde, 2003). In tidal fresh waters of Chesapeake Bay, zooplankton concentrations fluctuate from <50 to $>1000\,l^{-1}$ during spring months (Heinle & Flemer, 1975; Lippson *et al.*, 1980). Zooplankton prey of larval fishes are abundant in the upper Chesapeake Bay ETM, an important nursery area for anadromous white perch *Morone americana* (Gmelin) and striped bass *Morone saxatilis* (Walbaum) larvae (Roman *et al.*, 2001; North & Houde, 2003).

The abundant white perch is important in recreational and commercial fisheries and is a major constituent of the fish community in Chesapeake Bay (Jung & Houde, 2003). White perch larvae are one of the major species of ichthyoplankton in upper Chesapeake Bay during spring months (Dovel, 1971). In Chesapeake Bay, white perch spawn up-stream of the salt front during spring. Larvae are transported down-stream after hatching (Mansueti, 1964) and peak in abundance near the salt front (Dovel, 1971) and ETM (North & Houde, 2001). Previous gut contents analysis indicated that the copepod *Eurytemora affinis* (Poppe) was one of the most important prey items of white perch larvae within the Potomac River tributary (Setzler-Hamilton *et al.*, 1982) and in the ETM region of upper Chesapeake Bay (North, 2001). Other important prey of white perch larvae include rotifers, cladocerans, and calanoid and cyclopoid copepods (Setzler-Hamilton *et al.*, 1982; North, 2001). In the Hudson River estuary, larval white perch consumed primarily copepods and cladocerans during the spring pulse of zooplankton production (Limburg *et al.*, 1997).

Variation in freshwater input from the Susquehanna River (Fig. 1) influences the physical characteristics of the upper Chesapeake Bay ETM region. The ETM and salt front were displaced down-stream during high flows in 1998. In contrast, during low flow conditions in 1999, the salt front shifted 15 km up-stream of its position in 1998, and the ETM was separated from the salt front (North & Houde, 2001). Abundant white perch larvae, and high young-of-the-year (YOY) recruitment, coincided with high flow conditions in 1998, whereas low flow conditions corresponded to low larval abundance and recruitment in 1999. In addition, in a 23 year time series, YOY white perch abundance (at ages 2–4 months post-hatch) in the upper Chesapeake Bay was significantly correlated with spring freshwater discharge from the Susquehanna River (North & Houde, 2001). High flows may enhance prey productivity (Turner & Chadwick, 1972; Boynton *et al.*, 1977), increase retention of larvae and their prey in the ETM region, and promote better spatial overlap of larvae with high prey concentrations and high turbidities, resulting in high growth and low predation mortality (North & Houde, 2001, 2003).

Many factors within the ETM may influence feeding success of larvae. In laboratory experiments, Margulies (1988) reported that short-term variations in food abundance and temperature resulted in significant changes in growth and survival of white perch larvae. Physical factors such as light, turbidity, turbulence and tidal currents can have a significant effect on larval feeding (Chesney,

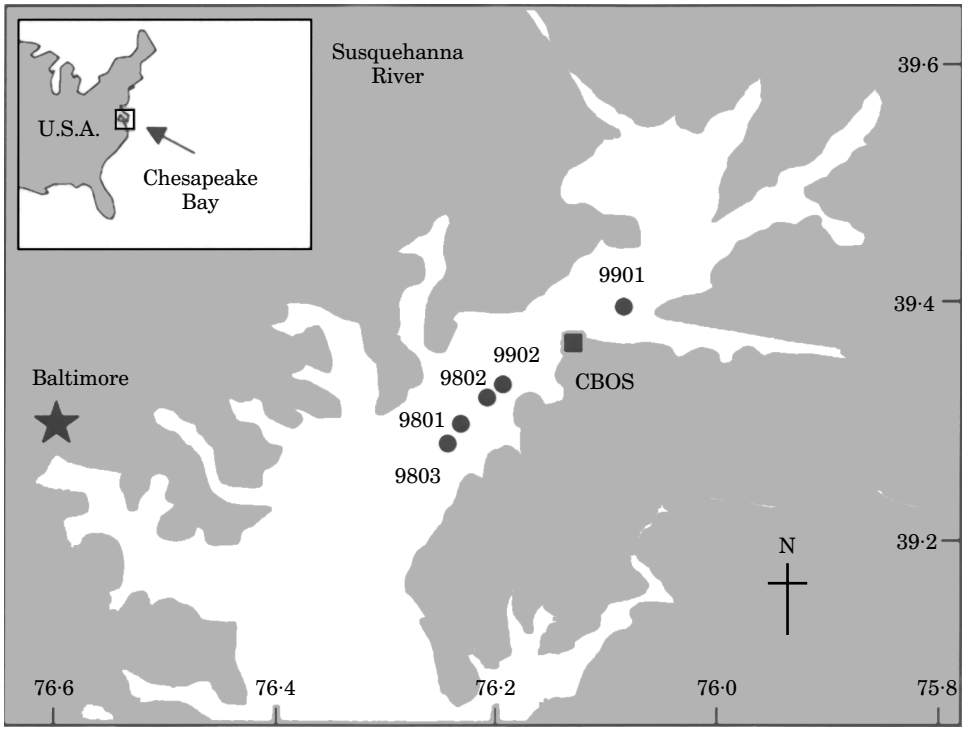

FIG. 1. Map of the upper Chesapeake Bay with sampling stations (●) for research cruises in 1998 (9801, 9802 and 9803) and 1999 (9901 and 9902). The location of the Chesapeake Bay Observing System (CBOS) buoy (■) is indicated.

1989; Sirois & Dodson, 2000*b*) and may influence fish larvae in ETM regions where these factors vary. The aim of the present study were to evaluate the link between larval feeding success and physical and biological characteristics of the ETM region in the upper Chesapeake Bay. Objectives were to: 1) describe the diet and feeding incidence of white perch larvae within the upper Chesapeake Bay ETM, 2) determine the influence of small-scale physical and biological factors on larval feeding and 3) examine the relationship between larval feeding success and annual variability in physical conditions in the ETM region.

MATERIALS AND METHODS

FIELD SAMPLING

Ichthyoplankton sampling and hydrographic surveys were conducted during three research cruises in May 1998 (9801, 9802 and 9803) and two in May 1999 (9901 and 9902) on the 16 m RV *Orion* in the upper Chesapeake Bay (Fig. 1 and Table I). The location of the ETM during each cruise was determined from a CTD survey along the axis of the bay in which a Seabird CTD equipped with a SeaTech 5 cm-pathlength transmissometer was deployed to profile temperature, salinity and turbidity. Details of the sampling area and physical conditions are described in North & Houde (2001, 2003).

Ichthyoplankton was collected repeatedly at a fixed station within the ETM during each cruise. Depth-stratified tows with a 1 m^2 opening-closing Tucker trawl were made at

TABLE I. Chesapeake Bay, ETM-region sampling. Number of station occupations and number of depth-stratified samples collected during each cruise. The mean and range (in parentheses) of water temperature, salinity and turbidity within the estuarine turbidity maximum are listed for each cruise

Cruise	Date	Number of stations (number of samples)	Temperature (° C)	Salinity	Turbidity (NTU)
9801	3 May 1998	7 (21)	15·9 (14·2–16·4)	0·7 (0·1–4·4)	19·8 (11·5–55·0)
9802	13 May 1998	8 (24)	15·5 (14·7–16·0)	1·0 (0·1–3·4)	19·8 (14·1–43·1)
9803	20 May 1998	8 (23)	19·1 (16·3–20·6)	1·7 (0·1–5·0)	23·5 (10·6–53·6)
9901	5 May 1999	14 (40)	14·4 (13·1–16·1)	4·6 (2·1–7·4)	7·9 (2·2–33·1)
9902	18 May 1999	14 (42)	18·4 (17·1–19·1)	3·7 (2·1–7·2)	13·6 (8·2–40·1)

3 m depth intervals. Each tow followed a CTD cast made at 1·5 h intervals at the station for 10 or 12 h during 1998 cruises and for 24 h during 1999 cruises. The Tucker trawl was equipped with 280 μm mesh nets, flow meters and a temperature-depth recorder. Most tows were made in 0–3·5, 3·5–7 and 7–11 m depth intervals, yielding three samples for each collection. The average depth of the upper Bay channel is *c.* 12·5 m. The number of repeated station collections for depth-stratified tows was seven or eight during the 1998 cruises and 14 during the 1999 cruises (Table I). Ichthyoplankton samples were preserved in ethanol, and transferred to fresh ethanol within 24 h.

LIGHT MEASUREMENTS AND CALCULATIONS

During both years, a LI-COR LI-100 DataLogger with a LI-190SA Quantum Sensor light meter was used to measure light intensity (μmol photon $m^{-2} s^{-1}$) at the water surface. Irradiance just below the water surface (I_o) was estimated after adjusting light intensity measurements for reflectance based on solar declination and zenith angle, assuming 4 m s^{-1} wind speeds following the methods in Kirk (1994). A nonlinear regression model (E.W. North, unpubl. data) was used to estimate irradiance at a specific depth (I_z):

$$\ln I_z = -1{\cdot}08164Z + \ln I_o - 0{\cdot}06738T \qquad (\text{adjusted } r^2 = 0{\cdot}85, n = 3375) \qquad (1)$$

where Z is depth, T is near-surface turbidity (NTU) and I_o is near-surface irradiance. This regression model is based on data from CTD casts in the upper Chesapeake Bay ETM region made on 7–14 May 2001 from the RV *Cape Henlopen*. The CTD was equipped with a profiling QSP-200L Log Quantum Scalar Irradiance Sensor (Biospherical Instruments) and a SeaTech 5 cm-pathlength transmissometer calibrated to NTU units with a Formazin NTU standard. Light available in net tow depth intervals in 1998 and 1999 was calculated by inputting 1998–1999 near-surface turbidities, the mid-point depth of net tows, and I_o (from the LI-COR LI-100 DataLogger) into the regression equation.

LABORATORY PROCEDURES

White perch larvae were identified and removed from samples under a dissecting microscope. Standard length (L_S) was measured to the nearest 0·1 mm. Gut contents of white perch larvae ($n = 1072$) in two length classes (<5 mm and >5 mm L_S) were removed and identified. Five to 10 <5 mm and three to 10 >5 mm larvae were randomly selected from each tow for gut contents analysis. Each prey item was identified and measured (length and width) using an ocular micrometer. Estimated prey masses were calculated from previously reported length-mass relationships of Sirois & Dodson (2000*b*). Gut fullness [F_G, in μg dry (μg dry^{-1})] for each white perch larva was calculated as:

$F_G = M_p M_1^{-1}$, where M_p is prey mass and M_1 is larval mass in μg estimated from a length-mass relationship for white perch larvae (Houde & Lubbers 1986), assuming dry mass is 20% of wet mass (Limburg *et al.*, 1997).

After removal of ichthyoplankton, Tucker-trawl samples were processed to estimate concentrations (number m^{-3}) of mesozooplankton (copepods, cladocera and rotifers) that were potential prey of white perch larvae (Setzler-Hamilton *et al.*, 1982). Gut content analysis indicated that *E. affinis* copepodites and adults were the dominant prey of white perch larvae in the ETM region. *Eurytemora affinis* copepod concentrations were used in subsequent statistical analyses to relate larval gut fullness to prey availability.

STATISTICAL ANALYSIS

Feeding incidence (F_i) was calculated as the percentage of white perch larvae with prey in their guts. Possible differences among cruises and between years in F_i were evaluated in a contingency table analysis for two larval L_S classes (<5 and >5 mm).

Repeated-measures, multiple regression analyses were conducted to reveal effects of environmental factors on variability in larval feeding success. Water temperature, current velocity, salinity, turbidity, light, tow depth and $\log_{10}$-transformed prey concentrations were used to describe the variability in mean gut fullness of <5 and >5 mm larvae (SAS 8.0 PROC MIXED with Kenward–Rogers d.f. method). A repeated-measures design was selected to model covariance between samples at adjacent depths and at adjacent times, thereby correcting for any lack of independence. An 'unstructured' covariance matrix was selected to allow the covariance between depths to vary between stations. A 'first-order autoregressive' covariance structure was used to model covariance in time. Models passed tests for normality (Shapiro–Wilks test), homogeneity of variance (Pearson correlation tests of absolute value of residuals *v.* predicted values) and multicolinearity (tolerance >0·37, condition index <3·72, SAS 8.0 PROC REG, PROC PRINCOMP).

The multiple regression analyses were conducted on the mean value for F_G of larvae from each depth-stratified net tow. Salinity, water temperature and turbidity values were the averaged CTD measurements within Tucker-trawl tow-depth intervals. Salinity was coded as a dichotomous variable to represent fresh or saline waters (0 when <1 and 1 when ≥1). In 1998, current velocities for analysis at the fixed station were derived from the near-surface current meter on the nearby Chesapeake Bay Observing System (CBOS) buoy (Fig. 1). These current records were adjusted to better match the magnitude and phase of currents at the fixed stations using predicted tides (Tides and Currents Pro 2·5 software) and the equation $V_{fs} = V_{CBOS} + (P_{fs} - P_{CBOS})$, where V_{fs} = adjusted current velocity at the fixed station, V_{CBOS} = velocity measured by the CBOS surface current meter, P_{fs} = predicted current velocity at the fixed station and P_{CBOS} = predicted current velocity at the CBOS buoy (North, 2001). In 1999, near-surface current velocities were measured directly with a 1·2 MHz Acoustic Doppler Current Profiler (ADCP) towed alongside the RV *Orion*. The light available for visual feeding by fish larvae was calculated as irradiance at the mid-point depth of each net tow using equation 1.

In addition to physical factors, tow depth and $\log_{10}$-transformed prey concentrations (*E. affinis* copepodites and adult copepods) were included in the regression model as fixed effects. Data from cruise 9902 were excluded from the multiple regression analysis because too few white perch larvae were collected. Cruise (9801, 9802, 9803 and 9901) and year (1998 and 1999) were included as random effects but, because they were not significant in the models, were not included in the tabulated results.

RESULTS

PHYSICAL CONDITIONS

Physical conditions in the ETM, described in detail by North & Houde (2001, 2003), differed between May 1998 and May 1999. In 1999, a year with low

freshwater discharge in spring, the ETM and sampling stations were located further up-stream than in 1998, a high-discharge spring. In general, temperatures and turbidities were higher, and salinities were lower, in 1998 compared to 1999 (Table I).

GUT CONTENTS OF THE LARVAE

The gut contents analysis revealed a diet of low diversity, based principally on the copepod, *E. affinis* (Table II). The percentage of *E. affinis* by mass exceeded 80% of total gut contents in two cruises in 1998 (9801 and 9803). Rotifers, the cladoceran *Bosmina longirostris* (Müller), copepod eggs, copepod nauplii, the copepod *Acartia tonsa* Dana and unidentified cyclopoid copepods accounted for lower percentages. Much of the partially digested gut contents consisted of unidentified calanoid copepods.

Feeding incidence, calculated for each cruise and year by larval L_S class, ranged from 16·7 to 96·3% (Table III). There were significant differences among cruises with respect to larval feeding incidence for both <5 mm (χ^2, d.f. $= 4$, $P < 0{\cdot}0001$) and >5 mm (χ^2, d.f. $= 4$, $P < 0{\cdot}0001$) L_S classes. Feeding incidence was highest in cruise 9803 for both larval L_S classes (94·3% for <5 mm and 96·3% for >5 mm). Year also had a significant effect on feeding incidence in both <5 mm (χ^2, d.f. $= 1$, $P < 0{\cdot}0001$) and >5 mm (χ^2, d.f. $= 1$, $P < 0{\cdot}0001$) L_S classes, indicating that feeding incidence was higher in 1998 than in 1999.

Gut contents of the white perch larvae were mainly *E. affinis* regardless of larval L_S (Fig 2; data from 2 years were combined). Percentage (by mass) of copepod nauplii was $<10\%$ for all larval L_S classes from 3 to >8 mm. First-feeding white perch larvae fed on copepodites and adult copepods. Mean prey size increased from *c.* 0·3 mm at 3·5 mm L_S to 0·5 mm at 6·0 mm L_S (Table IV). The CV of prey size for each larval L_S class ranged from 33·8 to 49·3%.

ENVIRONMENTAL FACTORS AND LARVAL FEEDING

The repeated-measures, multiple regression analysis indicated that small-scale physical conditions at the sampling stations, such as temperature, turbidity, current velocity, light and salinity did not explain a significant amount of variability in larval F_G (Table V). Log_{10}-transformed prey (*E. affinis*) concentrations did explain a significant amount of variability in F_G of larvae in the <5 mm and >5 mm L_S classes. Parameter estimates were 0·0108 and 0·0082 for prey concentration in the model for larvae <5 mm and >5 mm, indicating a positive relationship between F_G and prey concentrations. Plots of mean F_G *v.* log_{10}-transformed prey concentrations showed the positive, but variable, relationship between these factors in the 1998 cruises (Fig. 3).

DISCUSSION

PRIMARY PREY

The actual contribution of *E. afffinis* to the diets of white perch larvae was probably higher than calculated in the gut contents analysis because most unidentified calanoid copepods in the guts were probably *E. affinis*. North

TABLE II. Gut contents composition of white perch larvae by cruise from samples collected within the estuarine turbidity maximum in 1998 and 1999. The number of larvae examined, larval standard length, number of prey items and per cent prey by number (*N*%), mass (*M*%) and frequency of occurrence (*F*%) are also included

Cruise	9801			9802			9803			9901			9902		
Number of larvae examined	206			240			223			382			21		
L_S range (mm)	3·3–8·5			3·2–9·8			3·3–9·8			3·4–6·9			3·5–7·8		
Mean ± S.E. L_S	5·52 ± 0·10			5·33 ± 0·11			5·01 ± 0·10			4·59 ± 0·03			4·52 ± 0·22		
Total number of food item	218			652			462			303			9		
Food item	*N*%	*M*%	*F*%	*N*%	*M*%	*F*%	*N*%	*M*%	*F*%	*N*%	*M*%	*F*%	*N*%	*M*%	*F*%
Rotifer				0·2	0·1	0·4									
Bosmina longirostris	0·5	0·3	0·5	5·5	11·8	12·1	3·7	3·4	6·7	0·3	0·3	0·3			
Copepoda egg	5·5	0·6	4·4	61·2	11·4	9·2	0·2	0·0	0·4	19·8	4·4	15·7			
Copepod nauplius	5·0	0·3	2·9	0·2		0·4	21·9	2·0	11·7	14·5	2·2	8·9	44·4	81·5	4·5
Acartia tonsa				0·2	0·8	0·4									
Eurytemora affinis	53·2	82·3	35·4	6·1	24·4	10·0	54·1	85·9	60·5	13·5	31·9	10·7	11·1	13·1	4·8
Unidentified calanoid	22·0	12·3	18·9	15·6	33·8	28·3	12·3	5·9	21·5	37·3	51·4	29·1			
Unidentified cyclopoid	0·5	0·3	0·5	0·5	0·6	1·3	0·4	0·2	0·9	0·7	0·1	0·3			
Unidentified copepod	3·7	2·7	1·9	8·0	12·2	18·3	0·4	0·2	0·9	9·2	8·1	7·3			
Unidentified material	9·6	1·1	10·2	2·6	4·8	7·1	6·9	2·4	14·3	4·6	1·6	3·7	44·4	5·3	19·1

TABLE III. Comparison of feeding incidence (percentage of guts with food) for white perch larvae among cruises and between years for two larval standard length classes

	<5 mm L_S		>5 mms L_S	
	Number of fish	FI	Number of fish	FI
Cruise				
9801	95	70·5	111	70·3
9802	136	56·6	104	84·6
9803	141	94·3	82	96·3
9901	291	59·5	91	57·1
9902	15	40·0	6	16·7
Year				
1998	372	74·5	297	82·5
1999	306	58·5	97	54·6

(2001) reported that 85% of all calanoid copepodites in the ETM during 1998 and 1999 were *E. affinis*. Roman *et al.* (2001) reported that zooplankton, including *E. affinis*, are retained within the upper Chesapeake Bay ETM through passive accumulation in this convergence zone. High concentrations of *E. affinis* retained in the ETM would enhance encounter rate between white perch larvae and prey, promoting larval feeding success.

In this study, even the smallest white perch larvae fed mainly on copepodites and adult copepods (Fig. 2). In the Hudson River estuary, gut contents of white

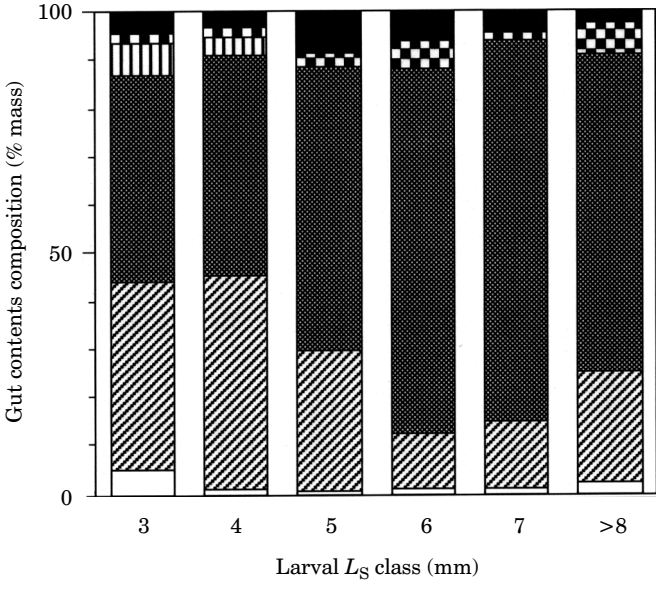

FIG. 2. Gut contents (per cent by mass) of white perch larvae by length class: *Bosmina longirostris* (■), copepod egg (▪), copepod nauplius (▥), *Eurytemora affinis* copepod (▩), unidentified calanoid copepod (▨) and other (□). Data from 1998 and 1999 were combined.

TABLE IV. Mean, S.D. and coefficient of variation of prey size within the guts of white perch larvae by larval standard length class

Larval L_S (mm)	n	Mean prey length (mm)	S.D.	CV
3·0–3·9	145	0·314	0·144	45·86
4·0–4·9	501	0·349	0·172	49·28
5·0–5·9	205	0·462	0·169	36·58
6·0–6·9	135	0·510	0·186	36·47
7·0–9·8	236	0·541	0·183	33·83

n, number of larvae.

perch larvae consisted predominantly of copepods and *B. longirostris* (Cladocera), with higher selection for copepods (Limburg *et al.*, 1997). White perch larvae in the Hudson River estuary had negative preference for smaller zooplankton such as nauplii and rotifers, leading Limburg *et al.* (1997) to conclude that white perch larvae were not gape limited with respect to copepod prey. The present results support this conclusion.

FACTORS AFFECTING LARVAL FEEDING

Prey concentration was the most important small-scale factor affecting white perch feeding success. It was the only factor analysed which consistently had a significant effect on larval feeding success in multiple regression models. Feeding success of first-feeding white perch larvae must be highly dependent on

TABLE V. Results of repeated measures, multiple regression analysis to investigate the influence of small-scale factors on larval feeding success. Models were fitted to mean gut fullness of <5 mm and >5 mm standard length white perch larvae. Explanatory variables were turbidity, salinity, temperature, $\log_{10}$-transformed prey concentrations (number m^{-3}) of *Eurytemora affinis* copepodites and adults, current velocities ($m\,s^{-1}$), light levels and the depth of Tucker-trawl tows. Salinity was coded as a dichotomous variable (1 when salinity was >1 and 0 otherwise)

	<5 mm L_S				>5 mm L_S			
Effect	NDF	DDF	F	P	NDF	DDF	F	P
Depth	2	25·3	0·47	0·6291	2	17·2	0·75	0·4890
Velocity	1	25·5	0·06	0·8138	1	12·7	0·14	0·7126
Log_{10} *Eurytemora*	1	43·7	13·77	0·0006	1	23·1	11·43	0·0026
Turbidity	1	20·6	0·15	0·7036	1	24·9	0·13	0·7245
Temperature	1	1·12	1·91	0·3805	1	13·7	0·02	0·8932
Salinity	1	13·7	0·55	0·4720	1	27·5	0·01	0·9422
Light	1	21·5	0·5	0·4884	1	14·1	0·06	0·8086

NDF, numerator d.f.; DDF, denominator d.f.

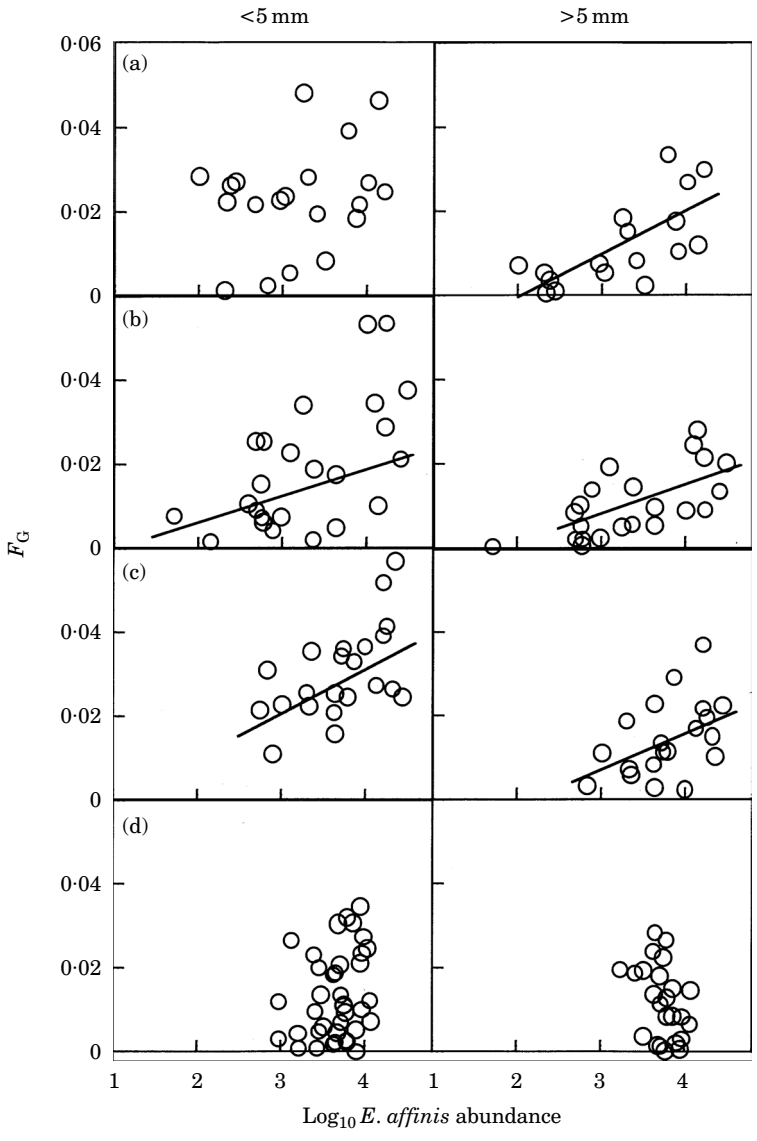

FIG. 3. Mean gut fullness of white perch larvae in relation to $\log_{10}$-transformed *E. affinis* abundance (number m^{-3}) for two larval length classes for cruises (a) 9801, (b) 9802, (c) 9803 and (d) 9901. The curves were fitted by: (a) >5 mm, $y = -0{\cdot}0199 + 0{\cdot}0100x$ ($n = 16$, $r^2 = 0{\cdot}49$, $P = 0{\cdot}0018$), (b) <5 mm, $y = -0{\cdot}0168 + 0{\cdot}0107x$ ($n = 24$, $r^2 = 0{\cdot}33$, $P = 0{\cdot}0035$), >5 mm, $y = -0{\cdot}0143 + 0{\cdot}00743x$ ($n = 21$, $r^2 = 0{\cdot}44$, $P = 0{\cdot}0008$), (c) <5 mm, $y = -0{\cdot}0125 + 0{\cdot}0116x$ ($n = 22$, $r^2 = 0{\cdot}31$, $P = 0{\cdot}0073$), >5 mm, $y = -0{\cdot}0206 + 0{\cdot}0094x$ ($n = 22$, $r^2 = 0{\cdot}22$, $P = 0{\cdot}0372$). The significant linear regressions do not account for possible covariance among samples and thus are only suggestive of positive relationships between gut fullness and prey abundance.

encounter rate with prey because of their poor swimming ability and visual acuity (Margulies 1990). In laboratory experiments, Sirois & Dodson (2000*b*) found that growth of larval rainbow smelt *Osmerus mordax* (Mitchill) was

enhanced at high turbidities and high prey concentrations. In the field, Sirois & Dodson (2000*b*) reported that larval rainbow smelt fed primarily during the coincidence of daylight hours and flooding tide in the St Lawrence ETM. The present results suggest that prey concentrations, rather than light, turbidity or tidal currents, was the most important factor that influenced the feeding success of white perch larvae.

FEEDING IN DARKNESS

The present results also suggest that white perch larvae can feed successfully in darkness. Many fish larvae are visual feeders (Hunter, 1981; Blaxter, 1986) and light level is considered one of the most important factors affecting behaviour and feeding success of visual larval feeders. Light penetration, however, is limited due to high turbidity (50–150 mg l^{-1}) in the upper Chesapeake Bay and its tributaries (Herman *et al.*, 1968; Schubel *et al.*, 1977). E.W. North & E.D. Houde (unpubl. data) estimated that light levels during day at the depth where most white perch larvae were located in the present study (mid-depth and bottom waters) were often below the minimum threshold (0·008 μmol photon m^{-2} s^{-1}) at which striped bass, a congener of white perch, could feed visually in laboratory experiments (J. Duston, pers. comm.). Mean growth rate of white perch larvae collected within the ETM during the study ranged from 0·23 to 0·34 mm day^{-1} (unpubl. data) and are similar to those of white perch larvae from the Hudson River estuary (0·16–0·41 mm day^{-1}; Limburg *et al.*, 1999). In the upper Chesapeake Bay, white perch larvae fed successfully and obtained adequate food for growth despite the dark conditions in the ETM. This supports Mansueti's (1961) suggestion that white perch larvae are well adapted to the highly turbid conditions of Chesapeake Bay tributaries.

Feeding in darkness is uncommon in larval fishes (Hunter, 1981; Blaxter, 1986) although it is reported to occur in several taxa (Rao 2003). There is evidence suggesting that larval striped bass feeds in very low light or total darkness (McHugh & Heidinger, 1977; Eldridge *et al.*, 1981; Chesney, 1989). Although the specific mechanism is unknown, Chesney (1989) hypothesized that striped bass larvae utilize a mechano- or possibly chemo-sensory feeding strategy based on detailed laboratory experiments and results. White perch larvae may also feed successfully under dark conditions using a mechano- or chemosensory feeding mode.

ANNUAL VARIABILITY IN FEEDING

The gut contents analysis demonstrated variability in larval feeding incidence between years. Feeding incidence was lower in 1999 than in 1998. In spring 1999, which experienced the lowest Susquehanna River discharge into upper Chesapeake Bay in 30 years, the salt front was located 15 km up-stream of its location in 1998. Salinity stratification was less intense and turbidity was lower in the ETM in spring 1999 (North & Houde, 2003). The ETM in 1999 probably had lower retention efficiency of zooplankton than in 1998, when it exhibited a well-developed convergence zone. *Eurytemora affinis* abundances based on pump sample collections were significantly lower in 1999 than in 1998 (E.W. North & E.D. Houde, unpubl. data). Annual variability in physical conditions

may influence feeding intensity of white perch larvae by controlling concentration and aggregation of *E. affinis* in the ETM region of the upper Chesapeake Bay.

There was a significant correlation between summer YOY white perch abundance (2 to 4 months post-hatch) in the upper Chesapeake Bay and mean daily discharge of the Susquehanna River during spring months from 1977 to 1999 (North & Houde, 2001). Variability in freshwater flow may influence the survival and recruitment of white perch larvae by: 1) controlling retention of larvae and prey *via* flow-induced changes in convergence zone strength, 2) affecting overlap of larval preferred temperature and salinity zones with the areas of highest prey concentrations or predation refuge (North & Houde, 2001) and 3) controlling prey productivity through delivery of organic matter to the ETM region (Turner & Chadwick, 1972; Boynton *et al*., 1977). In addition to indicating that more larvae fed successfully in a high-flow year than in a low-flow year, the results support the contention that physical factors acting to affect prey concentrations (retention and production) influence larval feeding success. Margulies (1988) reported that short-term variations in feeding conditions for first-feeding white perch larvae caused significant variability in their growth under experimental conditions. Growth rates of larval white perch collected in and near the ETM during early May were higher in 1998 than in 1999 (unpubl. data). Larval growth-rate variability can affect recruitment by governing the duration of early-life stages when they are most vulnerable to predation (Houde, 1996).

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