

# EFFECTS OF FOOD CONCENTRATION AND TEMPERATURE ON DEVELOPMENT, GROWTH, AND SURVIVAL OF WHITE PERCH, *MORONE AMERICANA*, EGGS AND LARVAE

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## ABSTRACT

Growth and mortality during the egg and early larval stages of white perch, *Morone americana*, were examined in relation to food concentration and temperature. Laboratory experiments were conducted utilizing variable food conditions (high, low, and initially delayed rotifer levels) and temperatures (13°, 17°, and 21°C). Egg and yolk-sac larva stage durations were inversely related to temperature, and optimum hatch of eggs occurred at 17°C or lower. Larvae fed initially at low food levels for as little as 2 days exhibited significantly reduced survival and growth after 8 days of feeding at all temperatures. Survival rates of well-fed larvae after 8 days of feeding ranged from 43 to 55%. Feeding delays of 4–8 days resulted in markedly reduced survival at 17° and 21°C. Growth was slow under any food conditions at 13°C (<0.05 mm/d in length, <5%/d in dry weight). At 17° and 21°C, well-fed larvae grew at significantly higher rates (>0.20 mm/d in length, >15%/d in dry weight). Based on these laboratory data and on seasonal abundance of food in Chesapeake tributaries, it was estimated that optimum temperatures for growth and survival of first-feeding white perch larvae are 15°–20°C. Results suggest that the estimation of variability in growth rates of larval white perch in Chesapeake tributaries would make a major contribution to our understanding of white perch recruitment.

The white perch, *Morone americana*, is an important recreational and commercial fish species in the Chesapeake Bay drainage. Fluctuations in relative abundance of white perch are most likely related to survivorship during the early life history, yet surprisingly little is known about the effects of varying environmental factors on growth, development, and survival of white perch eggs and larvae.

Past studies on the early life history of white perch have focused on distribution patterns (Mansueti 1961), descriptions of egg and larval development (Mansueti 1964), electrophoretic (Morgan 1975), and biochemical (Sidell and Otto 1978) characterizations of larvae and temperature effects on hatching (Morgan and Rasin 1982). The interacting effects of temperature and food on the development, growth, and survival of white perch eggs and larvae had not been studied previously.

Fecundity of white perch, which usually are 100–250 mm SL, is high (50,000–300,000 ova per female),

thus larval mortality rates are expected to be high (Ware 1975). For most high-fecundity species, if large numbers of larvae are produced in a cohort, small changes in growth or mortality rates during the larval stages may produce large variations in recruitment (Houde 1987). White perch juveniles are large relative to reproductive size, with the greatest relative weight increases occurring in the larval stage. This growth pattern indicates a strong potential for regulation of numbers through variable larval growth (Houde 1987).

In this study, I examined the effects of two variable environmental factors, food concentration and temperature, on the development, growth, and survival of first-feeding white perch larvae. White perch spawn in Chesapeake tributaries over a temperature range of 10°–20°C (Hardy 1978). Thus, first-feeding larvae can encounter a wide range of developmental temperatures. Microzooplankton, which forms the bulk of the diet for first-feeding white perch larvae, can fluctuate in Chesapeake tidal freshwaters during spring months from <50 to >1,000/L (Heinle and Flemer 1975; Lipson et al. 1980). By examining the interacting effects of temperature and food, the scope for growth and survival potential of white perch larvae were studied.

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## METHODS

### Experimental Design

White perch adults were collected by otter trawl from the Potomac and Patuxent Rivers, MD during April and May 1982. Eggs were collected from at least four females and milt from four males from each river system. Gametes were stripped into 8 L polycarbonate containers. Fertilized eggs were then transported to the laboratory and placed in well-aerated, 38 L tanks divided into three temperature groups: 13°, 17°, and 21°C. Salinity was maintained at 1‰. After hatching, yolk-sac larvae were transferred to 38 L culture tanks. Feeding studies were initiated with larvae that had some yolk remaining and which had pigmented eyes, indicating readiness to initiate feeding (Blaxter 1969).

All feeding experiments were conducted for a period of 8 days. Partial water changes of 25% were made in each feeding tank every other day to minimize buildup of metabolites. Fluorescent lighting provided constant 200–300 lux, with photoperiod maintained on a 13 h light: 11 h dark cycle. Temperature was controlled to the nearest 0.5°C by maintaining aquaria in water baths of ambient Patuxent River water and regulating individual tanks by aquarium heaters.

Food for larvae consisted of rotifers (*Brachionus plicatilis*) cultured in the laboratory on the green alga *Chlorella* sp. Field studies demonstrated that *Brachionus* constitutes the bulk of the diet of first-feeding white perch larvae (Martin and Setzler-Hamilton 1983). Based on a size analysis of zooplankton prey consumed by Potomac River larvae, rotifers were graded as follows: Day 1 to day 3: 100–150 µm in breadth provided; and day 4 to day 8: all sizes (100–180 µm) provided. Food levels were measured in the feeding tanks by calculating the mean values of three 100 mL aliquots taken four times daily. Food concentrations subsequently were adjusted to nominal levels.

Four food groups were established, representative of high, low, and delayed-high food conditions. Group 1 was a well-fed group maintained at 800 rotifers/L; group 2 was maintained at 50 rotifers/L concentrations for 2 days and then fed at 800 rotifers/L levels for 6 days; group 3 was fed at 50 rotifers/L levels for 4 days and then fed at 800 rotifers/L concentrations for 4 days; group 4 was maintained at low levels of 50 rotifers/L for the entire study period. The food levels of 800 and 50 rotifers/L were representative of high and low microzooplankton levels that typically occur in tidal

freshwaters of the Chesapeake (Lippson et al. 1980).

Each food group was tested at three temperatures: 13°, 17°, and 21°C. At each temperature, 10 eggs and 10 newly hatched larvae were sampled from the rearing tanks and fixed in 4% formalin to test for possible incubation temperature or parental stock effects on egg and newly hatched larva sizes. Just prior to feeding, 10 larvae were removed from each temperature stock tank and preserved for initial length and dry weight measurements.

At each temperature, 150 larvae were assigned to each of two replicates for each food group (with four food groups per temperature). Once feeding was initiated, at 2 d intervals, subsamples of 3 or 4 larvae were removed from each tank and preserved in 4% formalin for growth analyses.

### Sample Analyses

Mean egg diameter, larval hatching length, and length at first-feeding were measured and compared among temperatures. Yolk and oil globule dimensions of eggs and larvae were measured by ocular micrometer and converted to yolk and oil volumes (mm<sup>3</sup>); the stage-specific volumes were then compared among temperatures. Regressions also were developed predicting the duration of the egg and yolk-sac stages in relation to temperature.

Expected mean survival after 8 days of feeding was calculated based on the relationship:  $N_t = N_0 e^{-Zt}$ , where  $N_t$  = number of survivors at  $t$  days after first-feeding (8 days),  $N_0$  = initial number of larvae (150),  $t$  = number of days of feeding (8), and  $Z$  = instantaneous total mortality rate. Also,  $Z = F + M$ , where  $F$  = sampling mortality and  $M$  = natural mortality rate. The number of larvae preserved for analyses was considered sampling mortality ( $F$ ), and all other mortality was  $M$ . Thus, when  $N_0$ ,  $N_t$ ,  $t$ ,  $Z$ , and  $F$  were known, it was possible to solve for  $M$ , from which expected number of survivors was calculated as  $N_t$  (Expected) =  $N_0 e^{-Mt}$  (Ricker 1975).

Growth rates were calculated from the subsamples of preserved larvae. Lengths were measured after three weeks of preservation using a Wild<sup>2</sup> dissecting microscope fitted with an ocular micrometer. Lengths were recorded to the nearest 0.1 mm. Dry weight was obtained by drying larvae at 60°C for 48 hours, desiccating, and weighing to the nearest 0.1 µg on a Cahn electrobalance. Growth in length was estimated by linear regression:  $L_t = a$

<sup>2</sup>Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

+  $bt$ , where  $L_t$  is length at time " $t$ " days and  $b$  is daily growth rate (mm per day). Growth in weight for the 8 d period was determined from the exponential regression of dry weight on days after first-feeding:  $W_t = W_0 e^{Gt}$ , where  $W_t$  = dry weight at time " $t$ " days,  $G$  = instantaneous daily growth coefficient, and  $W_0$  = dry weight at first-feeding. Specific growth rate (percent per day) was calculated as  $100(e^G - 1)$ . In addition, mean incremental growth coefficients (i.e., between sampling days 2, 4, 6, and 8) also were calculated (Ricker 1975).

Data were analyzed by regression analysis, analysis of variance (ANOVA), and analysis of covariance (ANCOVA) followed by the Student-Newman-Kuels (SNK) multiple comparison test (Sokal and Rohlf 1981). The probability level for rejecting null hypotheses was  $P = 0.05$ .

## RESULTS

### Development

Preserved white perch eggs ranged from 0.76 to 1.03 mm in diameter. Mean diameters of eggs hatched at 13°, 17°, and 21°C were 0.91, 0.87, and

0.92 mm, respectively (Table 1). Each egg contained a large volume of yolk (0.14–0.16 mm<sup>3</sup>), and a prominent, amber-colored oil globule (0.0070–0.0081 mm<sup>3</sup>). There were no significant differences (ANOVA,  $P > 0.10$ ) among incubation temperatures for mean egg diameter, yolk volume, or oil globule volume (Table 1).

Mean larval size at hatch ranged from 2.37 to 2.81 mm SL and averaged 2.50 mm (Table 1). Dry weight of hatchlings was approximately 35 µg. Newly hatched larvae had unpigmented eyes, with the head deflected downward over the yolk sac. Mean lengths and weights of newly hatched larvae at the three temperatures did not differ significantly (ANOVA,  $P > 0.10$ ).

At the first-feeding stage, larvae averaged 3.45 mm SL and weighed approximately 19 µg (Table 1). First-feeding larvae had utilized at least 98% of their yolk reserves and from 55 to 75% of their oil. At the first-feeding stage no significant temperature effects were apparent for size of larvae, percentage of yolk remaining or percentage of oil volume remaining (ANOVA,  $P > 0.10$ ). Although not significant, there was a trend for larvae to retain more yolk and oil at lower temperatures.

Temperature had a pronounced effect on the duration of the egg and yolk-sac larval stages (Fig. 1). The relationships between the durations of these stages and temperature were best described by decreasing exponential functions. Although effect of temperature on hatching success was not measured precisely, rough estimates based on removals of dead eggs were made. Percentage hatch was near 80% at 13°C, approximately 60% at 17°C, and near 20% at 21°C.

### Survival

Expected survival after 8 days of feeding ranged from 4.0 to 55.0%, depending on temperature and food conditions (Fig. 2). As expected, survival at each temperature was highest for the well-fed larvae in food group 1. Larvae fed at low food levels for as little as 2 days (groups 2, 3, and 4) exhibited significantly reduced survival at all temperatures (ANOVA and SNK procedure,  $P < 0.05$ ). In particular, larvae fed at low food concentrations for 4–8 days (groups 3 and 4) displayed markedly reduced survival at 17° and 21°C.

### Growth

At 13°C, growth in length was slow under all food conditions—all larvae were <4.0 mm SL after 8 days

TABLE 1.—Characteristics of fertilized white perch eggs, newly hatched larvae and first-feeding larvae cultured at three temperatures.

Parameter	n:	Temperature (°C)		
		13	17	21
		10	10	10
<b>Eggs</b>				
$\bar{x}$ diameter (mm)		0.91	0.87	0.92
SE $_{\bar{x}}$		0.02	0.02	0.03
$\bar{x}$ yolk vol (mm <sup>3</sup> )		0.14	0.15	0.16
SE $_{\bar{x}}$		0.01	0.01	0.01
$\bar{x}$ oil glob. vol (mm <sup>3</sup> )		0.0081	0.0070	0.0080
SE $_{\bar{x}}$		0.0005	0.0004	0.0004
<b>Newly hatched larvae</b>				
$\bar{x}$ SL (mm)		2.52	2.46	2.53
SE $_{\bar{x}}$		0.03	0.03	0.02
$\bar{x}$ dry wt (µg)		35.2	34.0	36.4
SE $_{\bar{x}}$		1.3	1.1	1.2
<b>First-feeding larvae</b>				
$\bar{x}$ SL (mm)		3.48	3.43	3.49
SE $_{\bar{x}}$		0.06	0.05	0.05
$\bar{x}$ dry wt (µg)		18.8	18.4	19.4
SE $_{\bar{x}}$		0.5	0.4	0.6
$\bar{x}$ yolk vol (mm <sup>3</sup> )		0.0026	0.0018	0.0014
SE $_{\bar{x}}$		0.0005	0.0004	0.0004
$\bar{x}$ % yolk remaining		1.87	1.53	0.75
SE $_{\bar{x}}$		0.36	0.33	0.23
$\bar{x}$ oil glob. vol (mm <sup>3</sup> )		0.0036	0.0023	0.0022
SE $_{\bar{x}}$		0.0007	0.0003	0.0006
$\bar{x}$ % oil remaining		44.1	32.1	27.6
SE $_{\bar{x}}$		7.8	4.6	7.0

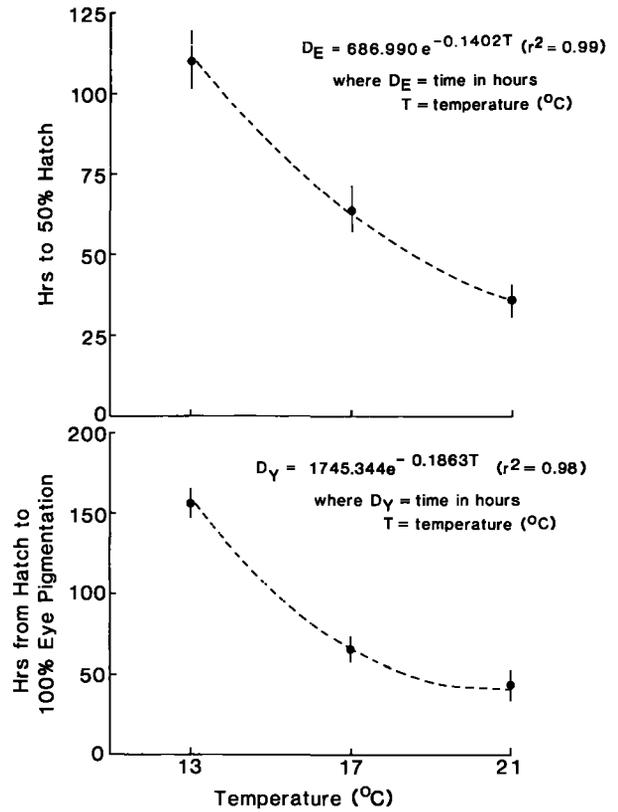


FIGURE 1.—The effect of temperature on egg and yolk-sac stage duration of white perch. Plotted values are means  $\pm$  2 SE.

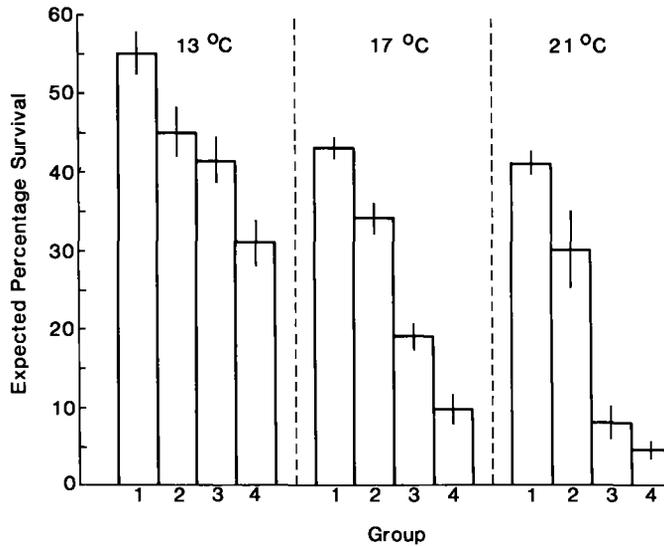


FIGURE 2.—Mean expected survival of white perch larvae after eight days of feeding. Error bars are  $\pm$  2 SE.

(Fig. 3). At 17° and 21°C, food level effects were clearly demonstrated and the final lengths attained by larvae in all food groups differed significantly from each other (SNK procedure,  $P < 0.05$ ). The well-fed larvae in groups 1 and 2 were significantly longer after 8 days of feeding at 17° and 21° than they were at 13° (SNK procedure,  $P < 0.05$ ).

Depending on food and temperature conditions, larvae grew in length at rates ranging from 0.01 to 0.28 mm/d (Table 2). The larvae in group 1 exhibited the highest growth rate at all temperatures, grow-

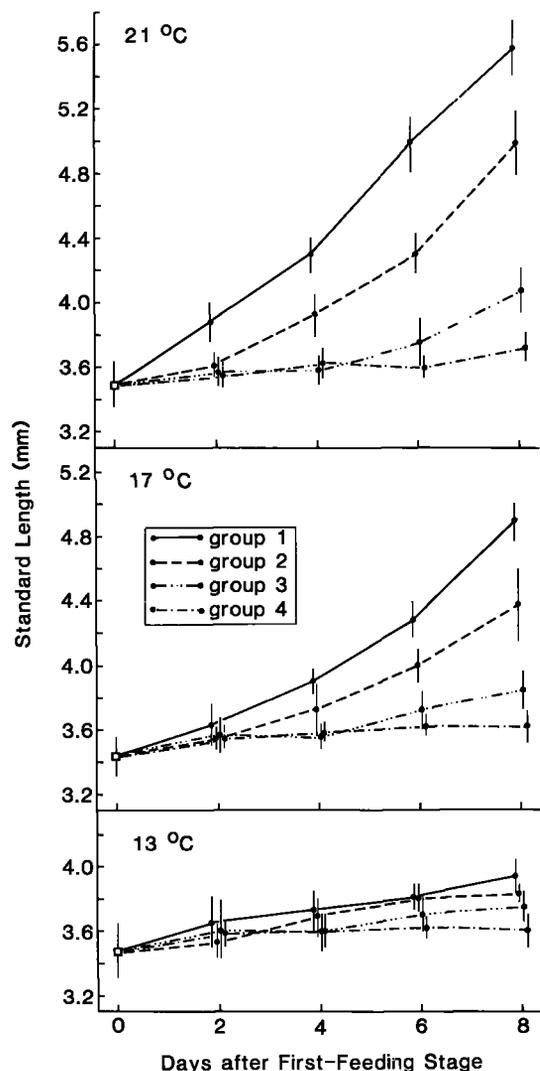


FIGURE 3.—Growth in standard length of white perch larvae tested under four food availability conditions and at three temperatures. Plotted values are means  $\pm 2$  SE.

ing at 0.05 mm/d at 13°C, 0.20 mm/d at 17°C, and 0.28 mm/d at 21°C. At 17° and 21°C, larvae in groups 1 and 2 grew significantly faster than those in groups 3 or 4 (ANCOVA and SNK procedure,  $P < 0.05$ ). For either group 1 or 2, an increase in temperature resulted in a significantly higher growth rate compared to 13°C (SNK procedure,  $P < 0.05$ ). The linear regressions gave good fits to the growth-in-length data, although there was some indication that growth at 17° and 21°C for groups 1 and 2 was becoming more curvilinear after day 4 (Table 2, Fig. 3).

Well-fed larvae (group 1) were significantly heavier at all three temperatures (ANOVA and SNK procedure,  $P < 0.05$ ). At 17° and 21°C, final mean weights of larvae from all food groups differed significantly from each other (SNK procedure,  $P < 0.05$ ). As temperature increased, weight increases were most pronounced for groups 1 and 2 (Fig. 4).

The well-fed group 1 larvae had the highest

TABLE 2.—Regression equations describing growth in length of white perch larvae tested under four food availability conditions and at three temperatures. Feeding duration was 8 days. In the regression equation,  $L$  is standard length in mm,  $t$  equals days after first-feeding,  $b$  is growth rate in mm, and  $a$  is the  $y$ -intercept. Results of ANCOVA and multiple comparison procedures (SNK) also are given.

T (°C)	Food group	$n$	Regression equation	SE <sub>b</sub>	$r^2$
13	1	40	$L = 3.546 + 0.054t$	0.004	0.97
	2	42	$L = 3.465 + 0.049t$	0.005	0.96
	3	41	$L = 3.511 + 0.029t$	0.006	0.91
	4	41	$L = 3.550 + 0.013t$	0.007	0.57
17	1	39	$L = 3.176 + 0.202t$	0.024	0.95
	2	39	$L = 3.250 + 0.133t$	0.015	0.95
	3	37	$L = 3.418 + 0.050t$	0.007	0.94
	4	40	$L = 3.521 + 0.014t$	0.006	0.77
21	1	38	$L = 3.293 + 0.276t$	0.019	0.97
	2	40	$L = 3.143 + 0.216t$	0.029	0.93
	3	35	$L = 3.381 + 0.073t$	0.011	0.94
	4	38	$L = 3.523 + 0.020t$	0.006	0.86

ANCOVA result: The growth rates differ significantly ( $P < 0.001$ ).

SNK summary (different superscript numbers on each line indicate significant differences among growth rates ( $P < 0.05$ )):

Among food groups (FG):

(°C)	FG1	FG2	FG3	FG4
13	0.054 <sup>1</sup>	0.049 <sup>1,2</sup>	0.029 <sup>2,3</sup>	0.013 <sup>3</sup>
17	0.202 <sup>1</sup>	0.133 <sup>2</sup>	0.050 <sup>3</sup>	0.014 <sup>4</sup>
21	0.276 <sup>1</sup>	0.216 <sup>1</sup>	0.073 <sup>2</sup>	0.020 <sup>3</sup>

Among temperatures:

Food group	13°	17°	21°
1	0.054 <sup>1</sup>	0.202 <sup>2</sup>	0.276 <sup>3</sup>
2	0.049 <sup>1</sup>	0.133 <sup>2</sup>	0.216 <sup>3</sup>
3	0.029 <sup>1</sup>	0.050 <sup>1,2</sup>	0.073 <sup>2</sup>
4	0.013 <sup>1</sup>	0.014 <sup>1</sup>	0.020 <sup>1</sup>

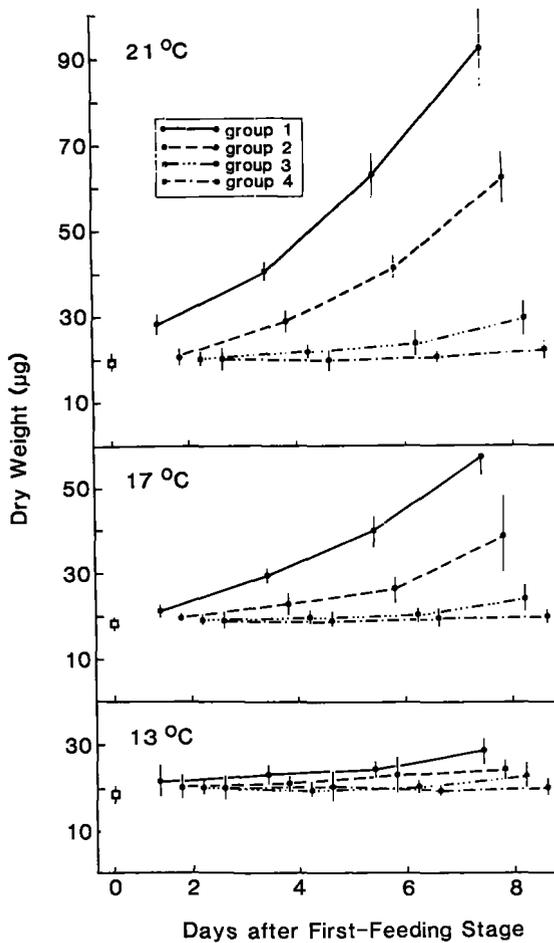


FIGURE 4.—Growth in dry weight of white perch larvae tested under four food availability conditions and at three temperatures. Plotted values are means  $\pm$  2 SE.

growth rates at all temperatures (Table 3). At 17° and 21°C group 2 larvae, delayed only 2 days, had significantly reduced overall weight gains compared to group 1 larvae (ANCOVA and SNK procedure,  $P < 0.05$ ). Weight gains after 8 days for groups 3 and 4 were significantly lower at all temperatures (SNK procedure,  $P < 0.05$ ) (Table 3).

The mean instantaneous growth rates attained by larvae at 2 d intervals showed several important patterns (Fig. 5). At all temperatures, feeding at 800 versus 50 rotifer/L food levels produced significantly different growth rates in 2 days or less (ANOVA,  $P < 0.05$ ). At 13°C, growth differences among food groups were established after 2 days but became inconsistent, while food group differences became more pronounced at higher temperatures. At 17° and 21°C, larvae that had 2 d delays before being

TABLE 3.—Regression equations describing growth in weight of white perch tested under four food availability conditions and at three temperatures. Feeding duration was 8 days. In the regression equation,  $W$  is dry weight in  $\mu\text{g}$ ,  $t$  equals days after first-feeding,  $G$  is the instantaneous growth coefficient, and  $W_0$  is dry weight at time 0. Results of ANCOVA and multiple comparison procedures (SNK) also are given.

T (°C)	Food group	n	Regression equation	SE <sub>G</sub>	r <sup>2</sup>	Percent gain (% d <sup>-1</sup> )
13	1	40	$W = 19.029 e^{0.0481t}$	0.0062	0.96	4.9
	2	42	$W = 18.774 e^{0.0328t}$	0.0020	0.98	3.3
	3	41	$W = 18.911 e^{0.0196t}$	0.0076	0.68	2.0
	4	41	$W = 19.433 e^{0.0058t}$	0.0054	0.24	0.6
17	1	39	$W = 18.938 e^{0.1413t}$	0.0095	0.98	15.2
	2	39	$W = 16.910 e^{0.1084t}$	0.0178	0.91	11.4
	3	37	$W = 18.099 e^{0.0317t}$	0.0068	0.88	3.2
	4	40	$W = 18.858 e^{0.0089t}$	0.0037	0.66	0.9
21	1	38	$W = 19.254 e^{0.1973t}$	0.0101	0.99	21.8
	2	40	$W = 19.298 e^{0.1436t}$	0.0158	0.96	15.4
	3	35	$W = 18.216 e^{0.0538t}$	0.0106	0.89	5.5
	4	38	$W = 19.497 e^{0.0147t}$	0.0050	0.73	1.5

ANCOVA result: The growth rates differ significantly ( $P < 0.001$ ).

SNK summary (different superscript numbers on each line indicate significant differences among growth rates ( $P < 0.05$ )):

Among food groups (FG):

(°C)	FG1	FG2	FG3	FG4
13	0.0481 <sup>1</sup>	0.0328 <sup>1,2</sup>	0.0196 <sup>2,3</sup>	0.0058 <sup>3</sup>
17	0.1413 <sup>1</sup>	0.1084 <sup>2</sup>	0.0317 <sup>3</sup>	0.0089 <sup>3</sup>
21	0.1973 <sup>1</sup>	0.1436 <sup>2</sup>	0.0538 <sup>3</sup>	0.0147 <sup>4</sup>

Among temperatures:

Food group	13°	17°	21°
1	0.0481 <sup>1</sup>	0.1413 <sup>2</sup>	0.1973 <sup>3</sup>
2	0.0328 <sup>1</sup>	0.1084 <sup>2</sup>	0.1436 <sup>2</sup>
3	0.0196 <sup>1</sup>	0.0317 <sup>1,2</sup>	0.0538 <sup>2</sup>
4	0.0058 <sup>1</sup>	0.0089 <sup>1</sup>	0.0147 <sup>1</sup>

offered the high food level (group 2) equalled group 1 growth rates after lag times of 2–4 days. Growth recovers from 4 d delays were slower and incomplete, but there were strong indications that group 3 larvae were initiating substantial growth during the last 2 days of feeding. Group 4 larvae lost weight from day 2 to day 4 and grew slowly throughout the study.

Instantaneous growth coefficient also was regressed on temperature for each food group (Fig. 6). All four regression coefficients (slopes) differed significantly among food groups (ANCOVA with SNK procedure,  $P < 0.05$ ). Growth rates of all food groups diverged at a faster rate in the upper half of the temperature range. Growth coefficients for groups 1 and 2 larvae increased by factors of 3.5–4.0 within the temperature range tested (13°–21°C).

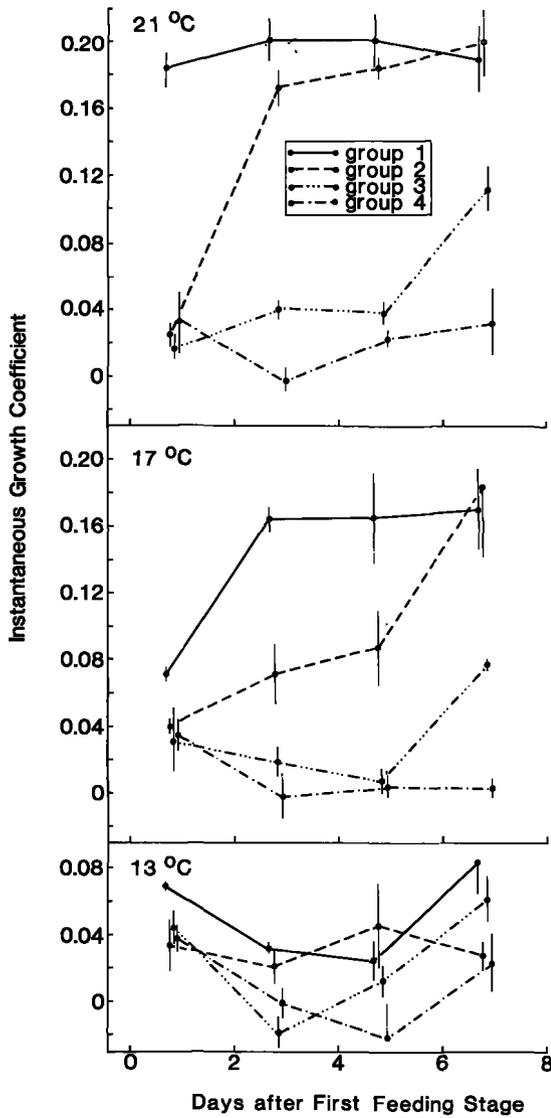


FIGURE 5.—Mean instantaneous growth coefficients attained by white perch larvae at 2 d intervals. Error bars are  $\pm 2$  SE.

**DISCUSSION**

White perch produce large numbers of eggs, hatch at small sizes (<3 mm) and undergo pronounced differences in development, growth, and survival in relation to variable food and temperature conditions. Egg stage duration decreased by a factor of three over the temperature range of 13°–21°C, but the reduced duration at higher temperatures was offset by a decline in percent hatch of nearly 60%. Morgan and Rasin (1982) reported that optimum hatch of white perch eggs in the laboratory occurred

at 14°–16°C, and believed that greater percent hatch occurred in the estuary at these temperatures. Hardy (1978) reported that peak spawning activity for Chesapeake Bay white perch occurs at 12°–16°C. My results indicate that optimum temperatures for hatch occur at  $\leq 17^\circ\text{C}$ .

The effect of temperature on yolk-sac stage duration may be important. Prolongation of this stage could have significant effects on cohort survival. Predation by planktivorous fishes on yolk-sac larvae is probably substantial in tidal freshwaters, based on the results of laboratory predation experiments (Margulies 1986). Results reported here indicate that a short-term decrease in temperature of 4°C during the spawning season, which is not unusual in tidal freshwaters (James et al. 1984<sup>3</sup>), could prolong the yolk-sac stage by at least 3 days, which could

<sup>3</sup>James, R. W., R. H. Simmons, and B. F. Strain. 1984. Water resources data, Maryland and Delaware, Water Year 1983. U.S. Geol. Surv. Water-Data Rep. MD-DE-83-1.

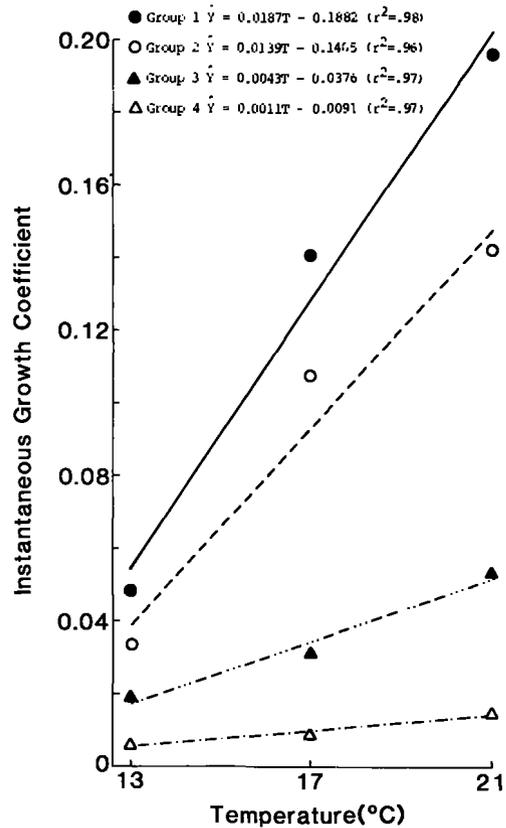


FIGURE 6.—Relationship between temperature and instantaneous growth coefficient for each food group.

substantially increase larval mortality due to fish predation.

Survival of white perch larvae is strongly dependent upon food availability and temperature. At 13°C, larvae were vulnerable to low food conditions, but survival differences after 8 days among malnourished and well-fed larvae were much more pronounced at higher temperatures. The metabolic demands of larvae are reduced at low temperatures, allowing relatively low caloric intake to sustain larvae. The food levels of 800 and 50 rotifers/L used in the study correspond to caloric values of 0.64 and 0.04 cal/L, respectively (Theilacker and McMaster 1971). It was apparent from survival data, particularly at 17° and 21°C, that 0.04 cal/L was inadequate for white perch survival, and that critical levels for survival fall in the range of 0.04–0.64 cal/L. This estimate falls within the broad range of 0.01 to 10.0 cal/L that Houde (1978) summarized as reported critical caloric concentrations for marine fish larvae.

White perch resemble many small marine and estuarine larvae (e.g., northern anchovy, *Engraulis mordax*; jack mackerel, *Trachurus symmetricus*; spot, *Leiostomus xanthurus*) in having relatively low survival potential at low food levels (Theilacker and Dorsey 1980; Powell and Chester 1985). For example, at 17° and 21°C, 8 d survival values for white perch decreased by 60–80% with a 4 d delay in high food levels. At those same temperatures, an 8 d delay resulted in 80–90% decreases in survival. Larger larvae such as sand lance, *Ammodytes americanus*, (Buckley et al. 1984); Atlantic herring, *Clupea harengus harengus*, (Rosenthal and Hempel 1970); Kiorboe and Munk 1986); and striped bass, *Morone saxatilis*, (Houde and Lubbers 1986) are less vulnerable to starvation under low-food conditions. When food is scarce, smaller larvae such as white perch are often more vulnerable to starvation because of low frequency of prey contact (Laurence 1982). However, comparisons among species should be done with caution because survival potential is species-specific. For example, sea bream, *Archosargus rhomboidalis*, (Houde 1978); plaice, *Pleuronectes platessa*, (Blaxter and Staines 1971); and cod, *Gadus morhua*, (Ellertsen et al. 1981), all relatively small at first-feeding, are efficient feeders and exhibit significant survival at low prey levels (<50/L).

For most species, larval growth variability and stage durations are important aspects of prerecruit survival (Cushing 1976; Houde 1987). Temperature variability resulted in more than fourfold differences in mean weights of white perch larvae after 8 days

of feeding. Thus, the effect of temperature on feeding stage duration would be even more pronounced than its effects on yolk-sac stage duration. Under good feeding conditions, a drop in temperature of 2° (from 17° to 15°, for example) would result in a 30% reduction in growth after 8 days (see Figure 6). The magnitude of the prolongation of stage duration would be similar. The effects of reduced food on stage duration would be even more pronounced. At 17° or 21°C, food levels need only be reduced for 2 days upon initiation of feeding to produce the same 30% reduction in growth after 8 days (Fig. 6).

The growth potential of white perch is intermediate between that reported for temperate and subtropical marine and estuarine species (Houde and Schekter 1981). White perch growth at 17°C and higher exceeded that reported for most temperate latitude species, which usually grow at rates of 10%/d or less (Houde and Schekter 1981). However, white perch growth rates were less than that of most subtropical species, such as bay anchovy, *Anchoa mitchilli*, (Florida populations); lined sole, *Archirus lineatus*; sea bream (Houde and Schekter 1981); and tidewater silverside, *Menidia peninsulae*, (McMullen and Middaugh 1985), which may grow at ≥20%/d. The specific growth rates of white perch larvae also appear to be slightly lower than those of the larger larvae of congeneric striped bass (Chesney 1986; Houde and Lubbers 1986).

Springtime densities of microzooplankton in Chesapeake tidal freshwaters usually begin to increase when temperatures reach 14° and peak at 20°–22°C (Lippson et al. 1980; Martin and Setzler-Hamilton 1981). Temperature and food concentration have important interacting effects on white perch during the first 2–3 weeks of life, with an apparent balance struck between hatching success, growth rate, and survival potential. Based on my results and historical patterns of zooplankton abundance, the optimum temperatures for white perch development and growth are in the range 15°–20°C. Hatching success was optimal at ≤17°C. Larvae hatched at 13°C were not as vulnerable to starvation, but they grew at <5%/d regardless of food level. At temperatures above 17°C, larvae could grow at ≥20%/d if high food levels were available at first-feeding. However, at 21°C (and presumably at higher temperatures), hatching success declined and there was greater likelihood of starvation under suboptimum food conditions.

Ultimate survival of white perch larvae and potential for recruitment will depend on environmental conditions in the estuary and how they effect subtle changes in growth and mortality rates of prerecruit

stages. A study of larval growth patterns in Chesapeake tributaries would be useful to understand early survivorship and establishment of year-class strength in white perch. Field estimates of growth rates of white perch larvae could be compared with indices of juvenile abundance that are now obtained in Chesapeake tributaries by the Maryland Department of Natural Resources. Results of the current study indicate that even short-term variations in food and temperature can result in significant changes in survival and growth of white perch eggs and larvae.

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## LITERATURE CITED

- BLAXTER, J. H. S.  
1969. Development: Eggs and larvae. In W. S. Hoar and D. J. Randall (editors), *Fish physiology*, Vol. III, p. 177-252. Acad. Press, N.Y.
- BLAXTER, J. H. S., AND M. E. STAINES.  
1971. Food searching potential in marine fish larvae. In D. J. Crisp (editor), *Fourth European Marine Biology Symposium*, p. 467-485. Cambridge Univ. Press.
- BUCKLEY, L. J., S. I. TURNER, T. A. HALAVIK, A. S. SMIGIELSKI, S. M. DREW, AND G. C. LAURENCE.  
1984. Effects of temperature and food availability on growth, survival, and RNA-DNA ratio of larval sand lance (*Ammodytes americanus*). *Mar. Ecol. Prog. Ser.* 15:91-97.
- CHESNEY, E. J., JR.  
1986. Multiple environmental factors as determinants of survival and growth in larval striped bass, *Morone saxatilis*. *Int. Counc. Explor. Sea C. M.* 1986/M:26.
- CUSHING, D. H.  
1976. Biology of fishes in the pelagic community. In D. H. Cushing and J. H. Walsh (editors), *The ecology of the seas*, p. 317-340. W.B. Saunders Co., Philadelphia, PA.
- ELLERTSEN, B., E. MOKSNESS, P. SOLEMDAL, S. TILSETH, T. WESTGARD, AND V. OESTAD.  
1981. Growth and survival of cod larvae in an enclosure. Experiments and a mathematical model. *Rapp. P.-v. Réun. Cons. int. Explor. Mer* 178:45-57.
- HARDY, J. D., JR.  
1978. Development of fishes of the mid-Atlantic Bight, an atlas of egg, larval and juvenile stages, Vol. III, Aphredoderidae through Rachycentridae. U.S. Fish Wildl. Serv., FWS/OBS-78/12, 394 p. Ann Arbor, MI.
- HEINLE, D. R., AND D. A. FLEMER.  
1975. Carbon requirements of a population of the estuarine copepod *Eurytemora affinis*. *Mar. Biol. (Berl.)* 31:235-247.
- HOUDE, E. D.  
1978. Critical food concentrations for larvae of three species of subtropical marine fishes. *Bull. Mar. Sci.* 28:395-411.  
1987. Fish early life dynamics and recruitment variability. *Am. Fish. Soc., Symp.* 2:17-29.
- HOUDE, E. D., AND L. LUBBERS III.  
1986. Survival and growth of striped bass, *Morone saxatilis*, and *Morone* larvae: laboratory and pond enclosure experiments. *Fish. Bull.*, U.S. 84:904-914.
- HOUDE, E. D., AND R. C. SCHEKTER.  
1981. Growth rates, rations and cohort consumption of marine fish larvae in relation to prey concentration. *Rapp. P.-v. Réun. Cons. int. Explor. Mer* 178:441-453.
- KIORBOE, T., AND P. MUNK.  
1986. Feeding and growth of larval herring, *Clupea harengus*, in relation to density of copepod nauplii. *Environ. Biol. Fishes* 17:133-139.
- LAURENCE, G. C.  
1982. Nutrition and trophodynamics of larval fish - review, concepts, strategic recommendations and opinions. In B. J. Rothschild and C. Rooth (convenors), *Fish ecology III. A foundation for REX, a recruitment experiment*. Univ. Miami Tech. Rep. No. 82008.
- LIPPSON, A. J., M. S. HAIRE, A. F. HOLLAND, F. JACOBS, J. JENSEN, R. L. MORAN-JOHNSON, T. T. POLGAR, AND W. A. RICHKUS.  
1980. Environmental atlas of the Potomac estuary. *Environ. Cent.*, Martin Marietta Corp., Baltimore, 135 p.
- MANSUETI, R. J.  
1961. Movements, reproduction, and mortality of the white perch, *Roccus americanus*, in the Patuxent estuary, Maryland. *Chesapeake Sci.* 2:142-204.  
1964. Eggs, larvae and young of the white perch, *Roccus americanus*, with comments on its ecology in the estuary. *Chesapeake Sci.* 5:3-45.
- MARGULIES, D.  
1986. Effects of food concentration and temperature on development, growth, survival, and susceptibility to predation of larval white perch (*Morone americana*). Ph.D. Thesis, Univ. Maryland, College Park, 168 p.
- MARTIN, F. D., AND E. M. SETZLER-HAMILTON.  
1981. Assessment of larval striped bass stocks in the Potomac estuary for 1980. Annual report to the U.S. National Marine Fisheries Service. UMCEES Ref. No. 81-65-CBL, Chesapeake Biol. Lab., Solomons, MD.  
1983. Assessment of larval striped bass stocks in the Potomac estuary for years 1980, 1981, and 1982. Final report to the U.S. National Marine Fisheries Service. UMCEES Ref. No. 83-55-CBL, Chesapeake Biol. Lab., Solomons, MD.
- McMULLEN, D. M., AND D. P. MIDDAGH.  
1985. The effect of temperature and food density on survival and growth of *Menidia peninsulae* larvae (Pisces: Atherinidae). *Estuaries* 8:39-47.
- MORGAN, R. P., II.  
1975. Distinguishing larval white perch and striped bass by electrophoresis. *Chesapeake Sci.* 16:68-70.
- MORGAN, R. P., II, AND V. RASIN, JR.  
1982. Influence of temperature and salinity on development

- of white perch eggs. *Trans. Am. Fish. Soc.* 111:396-398.
- POWELL, A. B., AND A. J. CHESTER.  
1985. Morphometric indices of nutritional condition and sensitivity to starvation of spot larvae. *Trans. Am. Fish. Soc.* 114:338-347.
- RICKER, W. E.  
1975. Computation and interpretation of biological statistics of fish populations. *Fish. Res. Board Can., Bull.* 191, 382 p.
- ROSENTHAL, H., AND G. HEMPEL.  
1970. Experimental studies in feeding and food requirements of herring larvae (*Clupea harengus* L.) In J. H. Steele (editor), *Marine food chains*, p. 344-364. Univ. Calif. Press, Berkeley.
- SIDELL, B. D., AND R. G. OTTO.  
1978. A biochemical method for distinction of striped bass and white perch larvae. *Copeia* 1978:340-342.
- SOKAL, R. R., AND F. J. ROHLF.  
1981. *Biometry. The principles and practice of statistics in biological research.* W. H. Freeman and Co., San Franc., 776 p.
- THEILACKER, G. H., AND K. DORSEY.  
1980. Larval fish diversity, a summary of laboratory and field research. In G. D. Sharp (rapporteur), *Workshop on the effects of environmental variation on the survival of larval pelagic fishes*, p. 105-142. UNESCO, Int. Oceanogr. Comm. Workshop Rep. 28.
- THEILACKER, G. H., AND M. F. MCMASTER.  
1971. Mass culture of the rotifer *Brachionus plicatilis* and its evaluation as a food for larval anchovies. *Mar. Biol. (Berl.)* 10:183-188.
- WARE, D. M.  
1975. Relation between egg size, growth and natural mortality of larval fish. *J. Fish. Res. Board Can.* 32:2503-2512.