EMBRYONIC DEVELOPMENT OF ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*, AND A FISH EMBRYO AGE ESTIMATION METHOD

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ABSTRACT

Eggs of Atlantic menhaden, *Brevoortia tyrannus*, were artificially fertilized and embryos were reared in the laboratory at 12 temperature-salinity combinations (temperature: 10°, 15°, 20°, and 25° C; salinity: 10, 20, 30‰). Salinity between 10 and 30‰ had no significant effect on embryonic mortality and no noticeable effect on rate of development. Temperature had a significant effect on embryonic mortality and rate of development. Embryonic mortality was significantly greater at 10° C than at 15°, 20°, and 25° C, and significantly greater before than after blastopore closure at 15°, 20°, and 25° C. The temperature coefficient for embryonic development of *B. tyrannus* from fertilization to hatching at temperatures between 10° and 25° C is 3.89.

Age of *B. tyrannus* embryos can be estimated by the regression of age on developmental stages when incubated at constant temperature.

The Atlantic menhaden, *Brevoortia tyrannus*, is an important commerical and forage fish of the east coast of North America (geographic range: lat. 27°-46° N). Atlantic menhaden spawn in Continental Shelf waters and in bays and estuaries in the northern part of its range during a northward spring and southward fall-winter migration (Reintjes 1961, 1969; Higham and Nicholson 1964; Kendall and Reintjes 1975; Chapoton[2]). *Brevoortia tyrannus* embryos were first described by Kuntz and Radcliffe (1917), and *B. tyrannus* embryos captured at sea have been reared in the laboratory by Reintjes (1968) and Hettler (1970), but rearing conditions were not well controlled and details on development were not published.

Rapid growth and low natural survival characterize the early life history of many marine fishes. Presented in this paper are results of a laboratory experiment to determine effects of temperatures between 10° and 25° C and salinities between 10 and 30‰ on survival and development rates of *B. tyrannus* embryos. Also presented is a useful method for estimating fish embryo age from empirical relations between embryo age, stage of development, and temperature. This fish embryo age estimation method is simple and has broader practical applications than other methods. It was developed for use in ichthyoplankton research to identify cohorts, construct embryonic stage life tables, and back calculate the time of day of spawning.

MATERIALS AND METHODS

Adult Atlantic menhaden were captured by gill nets off the Shoreham Power Plant, Long Island, N.Y., at 2300 h on 14 June 1973 (lat. 40°58′ N, long. 72°52′ W; water temperature 20.5° C; salinity 23.5‰). Eggs from a sexually mature female *B. tyrannus* were artificially fertilized on shipboard with milt from five adult males. Fertilized eggs were carried in four 1 l glass jars in an insulated box to the laboratory at the Marine Sciences Research Center, State University of New York at Stony Brook, N.Y.

Laboratory rearing experiments were two-factor, 4 × 3 (temperature × salinity) factorial designs with two replicates per treatment. Twenty-five embryos were transferred to each culture dish containing 85 ml water with salinities 10, 20, or 30‰, and temperature 20° C. Distilled water or artificial sea salts were added to filtered seawater to produce the desired salinities, and loose fitting plastic covers on the culture dishes reduced evaporation. Culture dishes with embryos were placed in thermostatically controlled constant temperature Hotpoint (#535)[3] incubators

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[2]R. B. Chapoton. 1972. On the distribution of Atlantic menhaden eggs, larvae, and adults. Unpubl. manuscr., 69 p. Atlantic Estuarine Fisheries Center, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

[3]Reference to trade names does not imply endorsement by the State University of New York at Stony Brook, or the National Marine Fisheries Service, NOAA.

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which maintained temperatures within ±0.5° C of 10°, 15°, 20°, and 25° C. Before the experiments began the embryos had been reared for 5 h at 20.5° C and 23.5‰, and had reached the early blastodisc stage of development. By the time of the next observations, about 5 h later, water temperature in the culture dishes had reached the desired incubation temperatures. Development data were mathematically adjusted for the delay in attaining experimental temperatures—see Results.

Developing embryos were observed with a stereomicroscope at intervals of about 4-6 h. Dead embryos were counted and removed, and stage of development of most live embryos was recorded. The basic nine-stage staging classification (Table 1) used in this research was similar to that used by Farris (1958, 1961). I refined this staging scheme by distinguishing among an early, middle, and two late periods within the nine stages. Early and late periods within a stage of development were quantified by subtracting 0.2 from, and adding 0.3, and 0.5, respectively, to the stage number.

TABLE 1.—Fish embryo stages of development used for *Brevoortia tyrannus*.

Stage	Description
1	Fertilized eggs prior to cell division to 8-cell stage
2	Eight-cell stage to completion of blastodisc formation
3	Blastodisc formation to germ ring halfway around egg
4	Germ ring halfway around egg to just prior to blastopore closure
5	Blastopore closure to tail bud beginning to separate from the yolk
6	Tail bud free of yolk to caudal one-eighth of body free of the yolk
7	Caudal one-eighth of body free of yolk to caudal one-fourth of body free of yolk
8	Caudal one-fourth of body free of yolk to fin fold moderately wide and tail portion of embryo rotated out of embryonic axis and tail approaching head
9	Tip of tail approaching head to hatching

RESULTS

Survival to hatching in the *B. tyrannus* rearing experiments was low, particularly at the 10° C incubation temperature. Temperature but not salinity had a significant effect on embryonic mortality in these experiments (Table 2). Testing by a posteriori sum of squares simultaneous test procedure (SS-STP) (Sokal and Rohlf 1969) revealed that embryonic mortality was significantly greater ($P<0.05$) at the 10° C incubation temperature, and not significantly different ($P>0.05$) at 15°, 20°, and 25° C.

During the experiments it became clear that most embryo deaths occurred during the first half of embryogenesis, and in particular, just prior to blastopore closure (prior to stage 5 in the staging classification used in this research) (Table 3).

TABLE 2.—Data on mortality (upper) and two-way ANOVA (lower) with replication to determine the effect of temperature and salinity on *Brevoortia tyrannus* embryos. Mortality data are the proportion of dead embryos (p). ANOVA performed on angular transformed (arc sine $p^{-0.5}$) data.

	Temperature			
Salinity	10° C	15° C	20° C	25° C
10‰	0.96	0.64	0.68	0.56
	.92	.60	.92	.72
20‰	1.00	.72	.76	.64
	1.00	.56	.60	.80
30‰	1.00	.48	.56	.68
	1.00	.48	.52	.68

Source of variation	df	SS	MS	F_s
Subgroups	11	5,327.935	484.358	
Temperature	3	4,640.063	1,546.688	49.6**
Salinity	2	106.056	53.028	1.7 ns
Temp. × Salinity	6	581.816	96.969	3.1 ns
Within subgroups (error)	12	373.950	31.162	
Total	23	5,701.885		

** = $P<0.01$; ns = $P>0.05$.

TABLE 3.—Percent (cumulative) mortality of *Brevoortia tyrannus* embryos prior to and after blastopore closure (stage 5) reared at four temperatures in the laboratory.

Temperature (° C)	Mortality to stage 5 (%)	Mortality to stage 9 (%)
10	94	98
15	49	58
20	59	67
25	63	68

When the difference in frequency of embryo deaths prior to stage 5 and from stage 5 to stage 9 was tested at each of the four incubation temperatures, mortality was not significantly different throughout development at 10° C, but was significantly greater prior to stage 5 at the 15°, 20°, and 25° C incubation temperatures (Table 4).

Data on embryonic age and stage of development were virtually identical in replicate culture dishes and for embryos reared at the same temperature but different salinity. Therefore, analysis was restricted to temperature effects on development rate.

TABLE 4.—Significance of difference in deaths of *Breevortia tyrannus* embryos prior to and after blastopore closure (stage 5) at four temperatures. Test is 2 × 2 test of independence using the G-statistic with Yates' correction.

Temperature	Development stage	Alive	Dead	Sum	% dead	G_{adj}
10° C	Prior to stage 5	9	141	150	94.0	
	Stage 5-stage 9	3	6	9	66.7	3.639 ns
15° C	Prior to stage 5	77	73	150	48.7	
	Stage 5-stage 9	63	14	77	18.2	19.922**
20° C	Prior to stage 5	62	88	150	58.7	
	Stage 5-stage 9	49	13	62	21.0	24.684**
25° C	Prior to stage 5	55	95	150	63.3	
	Stage 5-stage 9	48	7	55	12.7	42.685**

ns = $P>0.05$; ** = $P<0.01$.

Brevoortia tyrannus embryos used in the experiments were fertilized and reared at 20.5° C and 23.5‰ for the first 5 h of embryogenesis. To adjust development data for the delay in attaining experimental temperatures, correction factors were calculated to estimate the age embryos would have been at the beginning of the experiment had the embryos been incubated at experimental temperatures from fertilization. Since at 20°±0.5° C incubation temperature was constant throughout development, the correction factor used was the ratio of development time to stage 9 for embryos reared at 10°, 15°, and 25° C relative to development time to stage 9 at 20° C. Correction factors should be approximately proportional to development rates at different temperatures if the effect of delay in attaining experimental temperatures is small relative to incubation time to stage 9, and development rates are linear, as they appear to be (experimental (unadjusted) data points in Figure 1). When the experiments began, embryos had reached the early blastodisc stage of development; the age at that stage, therefore, for each incubation temperature, was estimated by multiplying the appropriate correction factor by 5 h. Development data were adjusted by adding to or subtracting from experimental data the difference between the expected age at the early blastodisc stage at 10°, 15°, and 25° C from the age observed at 20° C. Derivations of correction factors are presented in Table 5, and adjusted data on embryonic development in Table 6.

Age was regressed on embryonic stage of development (S) by least-squares linear regression.

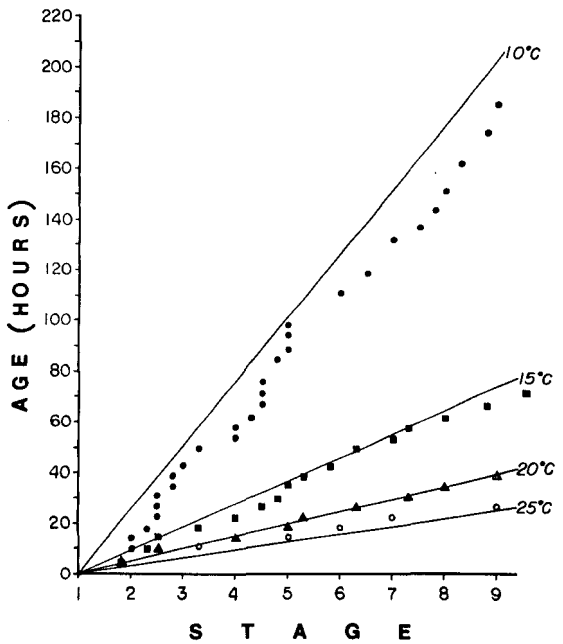

FIGURE 1.—Symbols represent age-stage relations of most *Brevoortia tyrannus* embryos in experiments (unadjusted data) at 10° C, 15° C, 20° C, and 25° C. Solid lines are regression lines of embryo age (A) on developmental stage (S) with experimental data adjusted for preexperimental time and temperature. Regression equation at 10° C is $A = 25.476(S - 1)$; 15° C, $A = 9.295(S - 1)$; 20° C, $A = 4.948(S - 1)$; 25° C, $A = 3.311(S - 1)$.

TABLE 6.—Adjusted data on the embryonic development of *Brevoortia tyrannus* incubated at four temperatures.

Temperature	Age (h)	Embryonic stage	Temperature	Age (h)	Embryonic stage
10° C	24.0	1.8	15° C	8.6	1.8
	28.5	2.0		13.0	2.3
	33.0	2.0		17.5	2.5
	36.5	2.3		21.5	3.3
	41.5	2.5		25.5	4.0
	45.5	2.5		30.0	4.5
	49.5	2.5		33.0	4.8
	53.5	2.8		38.5	5.0
	57.5	2.8		42.0	5.3
	61.5	3.0		46.0	5.8
	68.5	3.3		53.0	6.3
	72.5	4.0		57.0	7.0
	76.5	4.0		61.0	7.3
	80.5	4.3		65.0	8.0
	85.5	4.5		70.0	8.8
	89.5	4.5		74.0	9.3
	94.5	4.5	20° C	5.0	1.8
	103.0	4.8		10.0	2.5
	107.0	5.0		14.0	4.0
	113.0	5.0		18.5	5.0
	117.0	5.0		22.5	5.3
	129.5	6.0		27.0	6.3
	137.5	6.5		30.5	7.3
	151.0	7.0		35.0	8.0
	156.0	7.5		39.0	9.0
	163.0	7.8	25° C	3.5	1.8
	170.5	8.0		9.0	3.3
	181.5	8.3		13.0	5.0
	194.0	8.8		17.0	6.0
	205.0	9.0		21.0	7.0
				25.0	9.0

TABLE 5.— Derivation of correction factors to adjust development data for differences between experimental and preexperimental temperatures during the first 5 h of embryogenesis in *Brevoortia tyrannus*.

Item	10 ° C	15° C	20° C	25°
Hours to stage 9 in experiment (unadjusted data)	186	67	39	27
Ratio of hours to stage 9 relative to 39 h to stage 9 at 20° C	4.77	1.72	1.00	0.69
Expected age (h) at early blastodisc stage. Line 2 × 5 h	24.0	8.6	5.0	3.5
Correction factor to unadjusted data. Line 3 − 5 h	+19.0	+3.6	0	−1.5

$$\text{Age} = B\ (S - 1). \quad (1)$$

The results (Table 7; Figure 1) showed that age stage relations were nearly perfectly linear as a function of incubation temperature, and the regressions were highly significant (Table 7). Analysis of variance of the regression coefficients showed that development rates were highly significantly different among temperatures ($F(3, 57) = 1{,}405.0; P<0.001$). (Regression coefficients (B's) of Table 7 represent the "stage" development rate (units: hours/stage) of embryogensis in *B. tyrannus* and are only meaningful when used in context with the embryo staging classification in Table 1.)

The linear relationship between the logrithm of the stage development rate of *B. tyrannus* (B) and temperature (T in degrees Celsius) (Figure 2) is expressed by the following:

$$\log_{10} B = 1.923 - 0.059\ T. \quad (2)$$

The temperature coefficient (Q_{10}) for *B. tyrannus* embryonic development from fertilization to hatching at 10° to 25° C determined by Equation (2) is 3.89. The relation between the logarithm of the embryonic development rate of fish and temperature, though, is not necessarily linear (Kinne and Kinne 1962; Fonds et al. 1974), and, therefore, best predictions of stage development rates of *B. tyrannus* embryos (B) incubated at constant temperature (T in degrees Celsius) are obtained from the explicit empirical equation:

$$\log_{10} B = -0.193 + 17.193\ T^{-1} + 34.090\ T^{-2} - 461.276\ T^{-3}. \quad (3)$$

TABLE 7.—Linear regression of *Brevoortia tyrannus* embryo age (A) in hours since fertilization on morphological stage of development (S).

Temperature	Regression equation	F ratio	P	r^2
10° C	$A = 25.476\ (S - 1)$	$F(1, 29) = 7{,}110.8$	***	0.996
15° C	$A = 9.295\ (S - 1)$	$F(1, 15) = 6{,}427.6$	***	.998
20° C	$A = 4.948\ (S - 1)$	$F(1, 8) = 3{,}386.8$	***	.998
25° C	$A = 3.311\ (S - 1)$	$F(1, 5) = 1{,}258.6$	***	.996

*** = $P<0.001$.

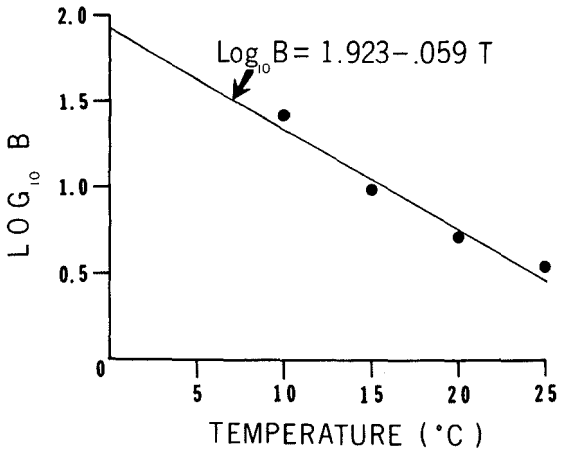

FIGURE 2.—Linear regression of the $\log_{10}$ of the "stage" development rate of *Brevoortia tyrannus* embryos (B) on temperature (T). Coefficient of determination = 0.96; SE regression coefficient = 0.0084.

DISCUSSION

The *B. tyrannus* embryo rearing experiments were mainly designed to determine effects of temperature and salinity on development rate; however, the results also have a bearing on temperature and salinity effects on embryonic survival.

Wide salinity tolerances have been reported for many marine fish embryos (Holliday 1969). *Brevoortia tyrannus* embryos have a salinity tolerance range >10-30‰, and they are, therefore, euryhaline by Kinne's (1964) criteria. Atlantic menhaden embryos have been collected in water with salinity as low as 18.15‰ (Wheatland 1956), but according to Reintjes (1967) most spawning occurs ". . . in the ocean or in inshore waters with salinities similar to those of the ocean." It would appear, therefore, that *B. tyrannus* embryos can tolerate low salinity conditions not normally encountered in nature.

Details of the salinity-development rate relation are species dependent, and they may be complicated by the influence of salinity on dissolved oxygen (Kinne and Kinne 1962; Forrester and Alderdice 1966), and the hatching process (Kinne and Kinne 1962; Alderdice and Velsen 1971); but, within limits, salinity effects on embryonic development rates tend to be small or insignificant for most marine fishes studied (e.g., McMynn and Hoar 1953; Alderdice and Forrester 1968, 1971a, b). Slight but apparently significant positive relations between embryonic development rate and salinity have been reported in some oceanic species (Forrester and Alderdice 1966; Laurence and Rogers 1976). Embryos of oceanic species are probably more sensitive to low salinity and changes in salinity than estuarine species. In the experiments presented in this paper, salinity between 10 and 30‰ had no noticeable effect on the embryonic development rate of *B. tyrannus*.

Brevoortia tyrannus embryo mortality was high at the 10° C incubation temperature. In a preliminary laboratory experiment, naturally fertilized *B. tyrannus* embryos at the blastodisc stage of development (stage 2) from field plankton collections (14.7° C, 24‰) failed to develop beyond stage 4 when the incubation temperature was lowered to 6°±1° C. The lowest temperatures at which Atlantic menhaden embryos have been collected in the field generally range between 10° and 13° C (Perlmutter 1939; Wheatland 1956; Richards 1959; Herman 1963), but they have been reported in water as low as 7.7° C (Mundy[4]). The available information, therefore, indicates that while spawning rarely occurs in water <10° C, the low lethal temperature of *B. tyrannus* embryos is probably about 7° C.

The temperature range in the experiments (10°-25° C) was not sufficiently wide to determine the upper temperature tolerance of *B. tyrannus* embryos, which survived equally well at 15°, 20°, and 25° C. There are no references in the literature of Atlantic menhaden embryos in nature in water >25° C.

A number of investigators have noted that high fish embryo mortalities tend to occur during gastrulation and just prior to or during hatching (McMynn and Hoar 1953; Alderdice and Forrester 1971a; Laurence and Rogers 1976; and others). High mortalities of *B. tyrannus* embryos occurred only during gastrulation.

Generally there is a linear or slightly curvilinear relationship between the logarithm of the development rate of fish embryos and temperature (see Blaxter 1969, fig. 4; Williams 1975; and others). The embryonic development rate of *B. tyrannus* followed this general rule (Figure 2).

Brevoortia tyrannus embryo age-stage relations at each of the four incubation temperatures were nearly perfectly linear (Figure 1; Table 7). These results imply a) the durations of the stages (Table 1) are approximately equal, b) the effect of the four incubation temperatures on rate of development of *B. tyrannus* embryos was relatively the same in all stages, and c) the stages of development can be used to estimate the age of embryos if the incubation temperature is known and constant.

A simple method of predicting the age of a *B. tyrannus* embryo at any stage of development from Table 1, incubated at any constant temperature (degrees Celsius) is to solve Equations (3) and (1), in succession for B and age. At low temperatures precision of the age estimate decreases because duration of stages increases. At temperatures in which menhaden commonly spawn (15°-20° C), this method yields an estimate of embryo age with an average expected error from stage duration of between 1.3 and 2.3 h (average error = ¼ × stage development rate).

Kuntz and Radcliffe (1917) and Hettler (1970) gave the incubation time of *B. tyrannus* embryos, but Kuntz and Radcliffe did not specify the incubation temperature. Hettler (1970) observed hatching within 66-74 h at an average incubation temperature of about 15.5° C (range 11.5°-19.5° C). The embryo age calculated for stage 9 at 15.5° C from the age prediction equations is 68.8 h, which compares well with Hettler's observation.

Other methods have been developed which estimate age of fish embryos. Simpson (1959) and Brown and Hassler (1973) constructed nomographs recording the influence of temperature on durations of embryonic stages of *Pleuronectes platessa* and *Morone saxatilis*, respectively. Ahlstrom (1943) and Talbot (1977) used regression analysis to describe the relationship between temperature and durations of fish egg stages, but their methods require calculating separate regressions for each development stage and temperature and does not allow interpolation of development rates between temperatures. Zweifel and Lasker (1976) applied the Laird-Gompertz growth equation to incubation times and embryonic growth (extrapolated from early posthatch growth) of fish embryos. The Laird-Gompertz equation appears to give good predictions of fish embryo growth, but its computation requires solving a multiparameter equation by iteration for each incubation temperature. The fish embryo age estimation method described in this paper is simple and has broader practical applications than the methods above. Together Equations (3) and (1) accurately describe the age-stage-temperature relations of *B. tyrannus* embryos at easily identifiable stages, during the entire embryonic development, and over a wide range of temperatures. Embryo age prediction equations can be calculated for other species in the manner described

[4]Mundy, B. C. 1974. Order Clupeiformes Family Clupeidae *Brevoortia tyrannus* (Latrobe), Atlantic menhaden. *In* H. M. Austin (editor), Preoperational ecological monitoring program of the marine environs at the Long Island Lighting Company (LILCO) nuclear power generating facility, Shoreham, Long Island, N.Y., vol. 2, sect. 5, p. 15-20. Contract SR-72-32. LILCO Community Relations, 250 Old Country Road, Mineola, NY 11501.

here for *B. tyrannus*, and, if necessary, the precision of embryo age estimates by this method can be improved by increasing the number of development stages of approximately equal duration in the embryo stage classification scheme.

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