EARLY LIFE HISTORY OF ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*, AND GULF MENHADEN, *B. PATRONUS*

Atlantic menhaden, *Brevoortia tyrannus*, and gulf menhaden, *B. patronus*, are allopatric, morphologically similar clupeids with contrasting distributional patterns and reproductive traits. The Atlantic menhaden has a meridional distribution and encounters variable environmental conditions during its lifetime. It occurs along the eastern coast of North America from Nova Scotia to Florida, and its distribution is stratified by age and size, with the older and larger fish ranging farther north (Nicholson 1978). Atlantic menhaden are a relatively long-lived clupeid. Their maximum reported age is approximately 10 yr, and they may spawn for approximately 7 yr (Higham and Nicholson 1964; Nicholson 1975). The spatial and temporal spawning habits of Atlantic menhaden are more complex than those of its congener. In Long Island Sound and New England waters, limited spawning occurs in inshore waters during the summer and early fall. From Long Island to Chesapeake Bay, spawning occurs in offshore coastal waters from October to December and from March to May. From North Carolina to Florida, spawning occurs in offshore coastal waters from October through March and this spawning population consists of fish that have migrated from the north and contains all age groups (Nicholson 1978). The gulf menhaden, which is distributed zonally, is restricted to the Gulf of Mexico and ranges from Cape Sable, FL, to Vera Cruz, Mexico (Reintjes 1969). Their maximum reported age is approximately 4 yr, and they may spawn for approximately 2 yr (Lewis and Roithmayr 1981). They spawn from October through March in nearshore and offshore waters within the 110 m depth contour (Christmas and Waller 1975). Both species use estuaries as nursery areas for more than half their first year of life.

The major objectives of this study were to examine and compare early life history characteristics of these two menhadens and to investigate the effects of temperature on developmental processes. Characteristics examined were egg size, size at hatching, yolk utilization rates, yolk volume at first feeding, size and age at first feeding, and growth.

Methods

Atlantic menhaden were collected with a commercial purse seine from the Newport River, NC, during the summer. Fish were held in the laboratory at ambient temperatures for approximately 4 mo before spawning. Gulf menhaden were collected in late September by cast net near Gulf Breeze, FL, and transported to the laboratory by methods developed by Hettler (1983). They were held in the laboratory at ambient temperatures for about 1 mo before spawning. For each spawning, about 10 menhaden were induced to spawn by methods described by Hettler (1981, 1983). Eggs were spawned in approximately 20°C water during the night and collected the following morning. All experiments except those dealing specifically with growth were conducted in 10 L rearing tanks; growth experiments were conducted in 60 L rearing tanks. Tanks were set in a temperature controlled water bath with two 40-W fluorescent lamps positioned 40 cm above each tank, and the tanks were illuminated for 12 h daily. Temperatures were controlled to approximately ±0.5°C. Salinities ranged from 28‰ to 32‰. Rotifers, *Brachionus plicatilis*, were used as food for about the first 10 d, and *Artemia* nauplii and rotifers were used thereafter. Feeding levels were not controlled, but, based on experience, we pro-

vided food in densities we felt would not limit growth.

Growth in standard length (SL) from the time larvae begin feeding to age 21 d at 20°C was modeled by an exponential equation. All measurements were made on eggs and larvae that were preserved in 5% sodium acetate buffered Formalin[1]. Volumes (V) of the elliptically shaped yolk mass were calculated using the formula for a prolate spheroid

$$V = (\pi/6)\ lh^2,$$

where l is the length and h is the height of the yolk mass (Blaxter and Hempel 1963).

We were unable to treat the two species the same in most experiments. The gulf menhaden was subjected to a greater number of treatments than the Atlantic menhaden. Experiments dealing with starvation and yolk utilization rates were conducted only on the gulf menhaden. In addition, the lack of replications for some experiments limited the application of statistical tests (e.g., ANOVA) and, as a result the differences or similarities between the two menhadens, should be considered tentative.

Results and Discussion

Based on a sample of eggs from the single spawn of a group of approximately five females from each species, Atlantic menhaden had significantly ($P < 0.001$) larger eggs (1.6 mm diameter, $N = 20$) than gulf menhaden (1.3 mm diameter, $N = 20$). Egg sizes for both these species that have been reported (Houde and Fore 1973; Jones et al. 1978; Hettler 1984) support our observations that Atlantic menhaden eggs are larger than gulf menhaden eggs. Atlantic menhaden larvae measured at hatching also were larger than gulf menhaden (Fig. 1) and supports Blaxter and Hunter's (1982) view that egg size greatly influences the size of larvae at hatching.

Temperature did not affect the size at hatching of gulf menhaden (Fig. 1), but the rate of yolk utilization was affected by temperature and was roughly 2.5 times faster at the highest temperature (24°C) than at the lowest temperature (14°C) (Table 1). The instantaneous rate of yolk utilization increased linearly with increasing temperature (Fig. 2). The volume of yolk at the onset of exogenous feeding (first feeding) was approximately similar at all temperatures (Table 1) and was not affected by temperature (ANOVA, $P = 0.13$).

The size of gulf menhaden at first feeding was independent of temperature (Fig. 3) (ANOVA $P = 0.15$) and, although data are limited, the size of Atlantic menhaden also was independent of temperature. The age at first feeding, however, was dependent on temperature (Fig. 3). An ANCOVA (log transformed ages on temperature) revealed that the regression slopes were similar ($P = 0.37$), in-

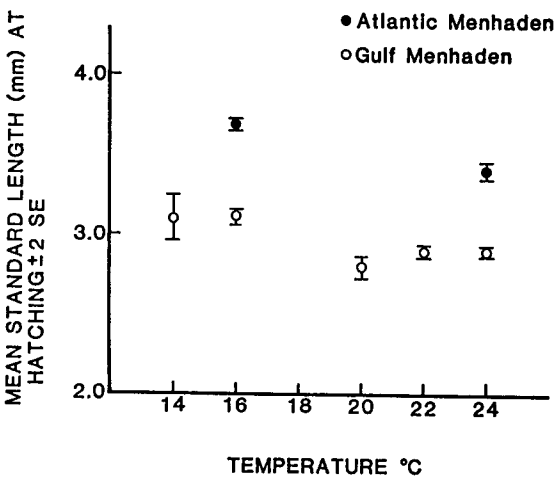

FIGURE 1.—The size at hatching of Atlantic gulf menhadens at different temperatures. Each point represents the mean of 10 fish.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—The effects of temperature on yolk utilization of gulf menhaden. For regression equations, $Y = \log_e$ preserved yolk volume (mm^3) and X = age (d). The equations were derived from the means of approximately 10 fish per sample. S is the number of samples; N is the number of larvae.

Temperature (°C)	S No.	Regression equation	r^2	Mean volume of yolk at hatching (mm^3)	N	Mean volume of yolk at first feeding (mm^3)	N
14	15	$Y = -1.189 - 0.96446(x)$	0.93	0.130482	10	0.000340	20
16				0.133397	10	0.000335	10
18	5	$Y = -0.803 - 1.67066(x)$	0.98			0.000211	10
20	10	$Y = -1.375 - 1.61365(x)$	0.91	0.169317	10	0.000549	20
22	7	$Y = -1.447 - 2.04386(x)$	0.96	0.110202	10	0.000506	20
24	8	$Y = -1.509 - 2.22355(x)$	0.95	0.123148	10	0.000289	19

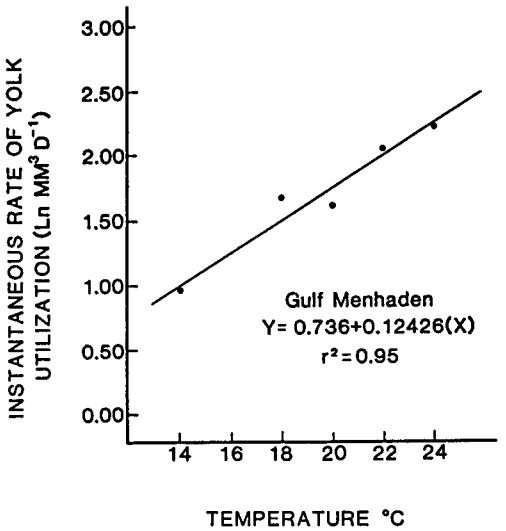

FIGURE 2.—The effects of temperature on the instantaneous rate of yolk utilization for gulf menhaden.

dicating a similar response to temperature by both species. But the Y-intercepts differed significantly (P = 0.02) indicating that, over the range of temperatures tested, the Atlantic menhaden fed at a significantly earlier age than gulf menhaden. For both species the age at first feeding declined exponentially with increasing temperatures. Atlantic menhaden were larger than the gulf menhaden at first feeding (Fig. 3). At 20°C, Atlantic and gulf menhaden growth rates were similar (ANCOVA, P = 0.36), but Atlantic menhaden maintained a size advantage during the early larval period (Table 2). This difference was attributed to differential size and age at first feeding.

The ability of early larvae to withstand the deprivation of food was influenced by temperature (Table 3). Although at 20°C mortalities may be attributed to causes other than starvation (compare control and starved), at progressively higher temperatures larvae are less able to withstand the deprivation of food. For example, at 24°C, gulf menhaden must find food within three days after the onset of first

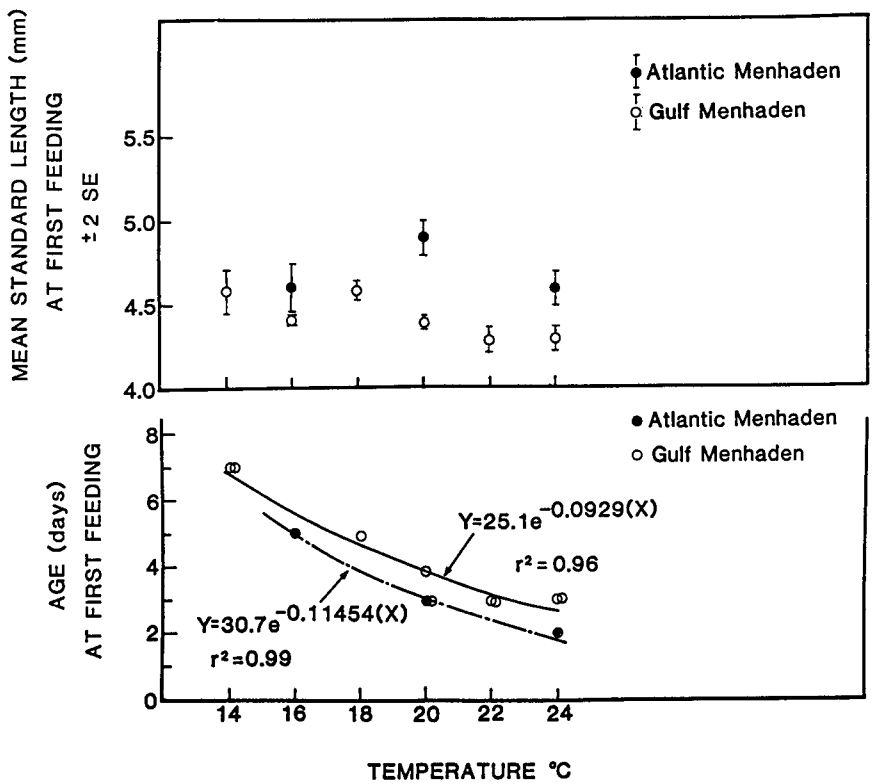

FIGURE 3.—The size and age when gulf and Atlantic menhadens begin feeding on exogenous food sources at different temperatures. Each point represents a sample of about 10 fish. Replicate experiments were only conducted for gulf menhaden and only at 14°, 20°, 22°, and 24°C.

TABLE 2.—Growth of larval gulf and Atlantic menhadens from time of first feeding to age 21 d at 20°C.

Species	N[1]	Growth parameters[2] a	b	r^2	Estimated SL (mm) First feeding	Age 21 d
Gulf menhaden	11	3.36	0.04640	0.97	4.0	8.9
Atlantic menhaden	16	4.38	0.04267	0.95	5.0	10.7

[1]Number of samples; about 10 fish per sample.
[2]SL (mm) = $a \times \exp b$ (age in d).

TABLE 3.—The survival (%) of first-feeding gulf menhaden larvae deprived of food (starved) in relation to temperature. The fed treatment represents the control group.

Temperature (°C)	Treatment	N	Days past time of first feeding 1	2	3	4	5	6	7
18	Starved	25	100	100	100	100	92	32	0
	Fed	25	100	100	100	100	96	92	92
20	Starved	25	92	76	72	48	8	4	0
	Fed	25	88	84	84	84	72	68	68
22	Starved	20	100	100	80	75	0		
	Fed	20	100	100	100	100	100		
24	Starved	25	56	40	40	4	0		
	Fed	25	96	96	96	96	96		

feeding or high mortalities will occur; whereas at 18°C they can survive without food for 5 d without incurring high mortalities (Table 3). The gulf menhaden's response to starvation in relation to temperature is comparable to numerous temperate zone, pelagic fish larvae (McGurk 1984).

In conclusion, although temperature is an important factor in controlling the development of marine fish larvae (Blaxter 1970), we observe that temperature was not a determinant of size at hatching, size at first feeding, and yolk volume remaining at first feeding. These data suggest that age is not a good correlate of these developmental events. On the other hand, temperature had an effect on the rate of yolk utilization, the time between hatching and exogenous feeding, and the ability of larvae to withstand the deprivation of food.

Our observations, although limited by a lack of rigorous statistical testing, suggest that, relative to gulf menhaden, Atlantic menhaden produced larger eggs, were larger at hatching, were larger and younger at time of first feeding, and appeared to maintain a larger size throughout the early larval period. We tried to interpret these differences in the context of their entire life history. Relative to gulf menhaden, Atlantic menhaden exhibit life history traits (later maturity, longer life, and more reproductive years) that may be adapted to a more fluctuating environment producing more reproductive uncertainty (Murphy 1968; Stearns 1976). This information suggests to us that the subtle differences we observed may indicate a fine tuning of reproductive strategies that allow these menhadens to persist in their particular environments. A more rigorous comparative study is required before we can understand how menhaden life history characteristics are adapted to their particular environments. Such a study is presently underway by the senior author.

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