A comparison of early-life-history traits in Atlantic menhaden *Brevoortia tyrannus* and gulf menhaden *B. patronus*

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Abstract.–Atlantic menhaden *Brevoortia tyrannus* and gulf menhaden *B. patronus* expressed significant differences in their early-life-history traits under laboratory conditions. Eggs of Atlantic menhaden were larger and contained more yolk. Their larvae were larger at hatching, and contained more yolk. A suite of developmental events (yolk depletion, age at first feeding, and, possibly, age at metamorphosis) was achieved earlier in Atlantic menhaden. The expression of these early-life-history traits in each species may reflect adaptations to the contrasting environments that these species occupy.

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Progeny size is a key life-history trait that has evolved in response to the predictability of the reproductive environment (Stearns 1976). The influence of progeny size on early-life-history characteristics has received considerable attention (Blaxter & Hempel 1963; see reviews or summaries by Miller et al. 1988, Hinckley 1990, Pepin 1991); however, comparative early-life-history studies between congeners are sparse and largely restricted to salmonids (e.g., Beacham & Murray 1990). A preliminary study suggested differences between early life histories of the Atlantic and gulf menhadens (Powell & Phonlor 1986). Here, a more extended and detailed documentation of differences between these menhadens is provided.

Atlantic menhaden *Brevoortia tyrannus* and gulf menhaden *B. patronus* are morphologically-similar allopatric clupeids. Both are schooling, filter-feeding clupeids that use estuaries during their first year of life. Individuals of Atlantic menhaden range from Nova Scotia to Florida and thus encounter variable environmental conditions during their lifetime. The distribution of Atlantic menhaden is stratified by age and size, with older and larger fish ranging further north (Nicholson 1971). Spawning is protracted and occurs throughout its range, in inshore waters during summer and early fall in Long Island Sound and New England. From Long Island to Chesapeake Bay, spawning occurs offshore during October–December and March–May (Higham & Nicholson 1964).

Gulf menhaden, in contrast, are restricted to the Gulf of Mexico, distributed from Cape Sable, FL to Vera Cruz, Mexico (Reintjes 1969). Spawning occurs October through March in nearshore and offshore coastal waters (Christmas & Waller 1975).

The specific objective of this study was an interspecific comparison of egg size, yolk volume, and the characteristics they may influence: size-at-hatching, first-feeding and metamorphosis, resistance to starvation, development (yolk and oil depletion, age-at-first-feeding), growth, and mouth size. In addition, for Atlantic menhaden, relationship between egg size and latitude of capture was evaluated.

Methods and materials

Spawning and rearing

Adult gulf menhaden (179–201 mmTL) were captured by cast net in Pensacola Bay, FL in the fall of 1983–85 and transported to Beaufort, NC (methods followed Hettler 1983). Adult Atlantic menhaden (204–212 mmTL) were collected from commercial purse seines in Core Sound, NC in the summers of 1983 and 1985. Menhaden were held at the laboratory in Beaufort at ambient temperatures until water temperatures fell below 20°C. Thereafter, temperatures were maintained at ca. 20°C. Ten menhaden were induced to spawn at each spawning (methods followed Hettler 1981, 1983). Generally, spawning occurred in 20°C water at night, and eggs were collected in the morning. Eggs were held either in 10 L black-sided tanks with static water immersed in a temperature-controlled water bath or in 100 L black-sided rearing tanks with static water. Temperatures in the 100 L tanks varied with slight changes in room temperature (19–20°C). Salinities ranged from approximately 30 to 35‰. Two 40 W fluorescent lamps were placed 90 cm above each large rearing tank and 40 cm above each small tank. The tanks were illuminated for a 12 h dark:12 h light cycle. Rotifers *Brachionus plicatilis* were the sole source of food. Experimental temperatures were 16°, 20°, and 24°C. These temperatures were chosen because 20°C approximates the average temperature of most intensive spawning for both species (Shaw et al. 1985, Checkley et al. 1988). The 16° and 24°C temperatures were arbitrarily chosen to bracket the 20°C temperature and were in accord with a previous study (Powell & Phonlor 1986).

Eggs

Egg, yolk, and oil globule diameters were measured on approximately 50 live eggs per spawning for each species. Yolk and oil diameters were used to calculate volumes. Because the spheroidal oil globule is embedded in the prolate spheroidal yolk mass, oil volumes were subtracted from initial yolk volume estimates to give a more accurate measurement of yolk volume.

Relationship between egg size and latitude was investigated by using collections of preserved (5% formalin) Atlantic menhaden eggs from eight cruises during 1979–81 by the Sandy Hook Laboratory, NMFS Northeast Fisheries Science Center, Highlands, NJ.

Larvae

Starvation experiments were conducted at 16°, 20°, and 24°C. Approximately 20–25 larvae were removed from the rearing tanks and randomly placed in each 1L fingerbowl at each experimental temperature on the day prior to initiation of feeding by the larvae. Food was withheld from all larvae. Mortalities were recorded at 24 h intervals. Results from repeated independent experiments (n=6 and 3 for Atlantic and gulf menhaden, respectively) were averaged.

Mean standard lengths (SL) and mean dry weights of menhaden larvae at hatching and at first-feeding were determined from larvae reared at 16°, 20°, and 24°C in 10 L tanks. Mean lengths and mean dry weights were obtained from approximately 10 preserved larvae (5% buffered formalin) per experiment. To determine when first-feeding occurred, 10 larvae at each experimental temperature were removed daily, preserved, and inspected for the presence or absence of rotifers. The presence of rotifers in the guts of any of the 10 larvae was considered to be first-feeding. Observations on development were also made (e.g., fully-pigmented eyes, functional mouth, and differentiated foregut and midgut). All observations were made at 50× magnification.

Mean rate of yolk absorption was determined from approximately 10 larvae sampled daily at 16°, 20°, and 24°C, from time of hatching until the time when yolk and oil were completely used. Because preservation had a significant effect (P<0.01, n=50) on size and condition of the yolksac (preserved yolk diameters were smaller than those measured live), measurements were made only on live material. Yolk volumes were calculated using the formula for a prolate spheroid,

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

where l is length and h is the height of the yolk mass (Blaxter & Hempel 1963). As with the measurement of eggs, oil volumes were calculated and subtracted from the calculated yolk volumes to give a better estimate of yolk volume.

Two series of growth experiments were conducted on each species. One examined the relationship between growth and survival of menhaden larvae in relation to temperature and food density. Groups of 50 larvae, approximately 6 d old, were removed from 100 L rearing tanks and transferred to each 10 L experimental tank. The larvae were slowly acclimated (~4 h) to 16°, 20°, or 24°C. Food levels were designed to reflect high, moderate, and low food availabilities. Food levels the first year (1984) were 50, 25, and 5 rotifers/mL, and two replicates were performed at each food level for each species. These food levels did not limit growth. Food levels of 10.0, 1.0, 0.1, and 0.025 rotifers/mL were employed the following years (1985 and 1986) and three replicates were performed. Over the course of a 7 d experiment, food densities were monitored daily and adjusted on the basis of the average of three samples from each rearing tank. Growth was determined as the difference between mean size of the preserved survivors at the end of the experiment and mean size of 50 preserved larvae removed from the 100 L tank at the beginning of the experiment. Larvae for each tank were combined, dry weights obtained, and values expressed as mean dry weight. The gain in biomass over a 7 d period was calculated to weight the number of survivors, which varied markedly. Growth and survival between species were compared using this index.

Gain in biomass (B) for each tank was calculated as

$$B = (W_t - W_{t-7})(S),$$

where W = mean dry weight/fish, t = age in days, and S = number of survivors.

A second series of growth experiments was conducted to examine instantaneous daily growth rates and size of larvae 10 d past first-feeding. Eggs and larvae were reared in 10 L tanks at 16°, 20°, and 24°C. Larvae were maintained on high food densities (~ >25 rotifers/mL). For each experimental temperature, 10 larvae were sampled 10 d past first-feeding. Length (SL), dry weight, and mouth width (an estimate of gape size) were obtained from preserved larvae. Daily instantaneous rates of increase in length and weight were calculated according to Ricker (1975:207).

Length-weight relationships were used to estimate sizes separating early-life-history periods (Balon 1984). Larvae were measured live, and dry weights were obtained from larvae that were preserved by freezing. For each species, an iterative process was used to determine the break point (SL) between two regressions that described the length/weight relationship. Iterations were done with break point values of 8–14 mm SL at 1 mm intervals. The two regressions that resulted in the minimal mean square error were chosen. An ANCOVA was used to compare the biphasic regressions.

Statistical testing was done by using the General Linear Model procedure (SAS 1985). Unless otherwise noted, ANOVA was used to test differences. Each treatment consisted of a group of larvae in a common tank. The mean measurement (e.g., mean length or mean weight of the group) was used in the statistical analysis. Each experiental replicate was treated as an independent observation. Differences between main effects were considered significant at $\alpha=0.05$. For interaction between factors, differences were considered significant at $\alpha=0.10$ to reduce the chance of a type-II error.

Results

Atlantic menhaden eggs were larger in diameter and nearly two-fold heavier than gulf menhaden eggs (Table 1, 2). The volume of yolk was greater for Atlantic menhaden, but oil globule volumes were similar (Table 1, 2).

There was no discernible change in egg size during the laboratory spawning season (Fig. 1), and the level of variability throughout the season was smaller for gulf (SD=0.02–0.04) than Atlantic (SD=0.04–08) menhaden. There was a trend for field-collected Atlantic menhaden eggs to be larger at higher latitudes ($P<0.01$), but there was a considerable amount of variability in egg size for any given latitude (Fig. 2).

Table 1

Summary of analysis of variance results expressed as *P*-values (Pr>F) for gulf and Atlantic menhaden. S = species, T = temperatures, S×T = species × temperature interactions, F = food, S×F = species × food interaction, T×F = temperature × food interaction, and S×F×T = species × food × temperature interaction.

	Class		
Factor	S	T	S×T
Egg diameter	<0.01		
Egg yolk volume	0.01		
Egg oil volume	0.24		
Size at hatching	<0.01	0.01	0.51
Weight at hatching	<0.01	0.08	0.65
Yolk volume at hatching	<0.01	0.14	0.62
Oil volume at hatching	0.01	0.94	0.83
Yolk utilization rate	<0.01	<0.01	0.14
Oil utilization rate	0.33	<0.01	0.12
Yolk volume at first-feeding	0.80	0.87	0.80
Oil volume at first-feeding	0.23	0.22	0.44
Age at first-feeding	<0.01	<0.01	0.32
Length at first-feeding	0.00	0.24	0.77
Weight at first-feeding	0.19	0.51	0.26
Growth rate (10 d) in length	0.53	0.03	0.07
Growth rate (10 d) in weight	0.03	0.06	0.08
Length 10 d past first-feeding	<0.01	0.16	0.06
Weight 10 d past first-feeding	<0.01	0.01	0.03
Mouth gape 10 d past first-feeding	0.90	0.02	0.13

	S	T	S×T	F	S×F	T×F	S×T×F
Growth in biomass	0.79	<0.01	0.97	<0.01	0.99	0.10	0.97

Table 2

Summary of Atlantic and gulf menhaden egg data. Values in parentheses indicate the number of replicates. For each experiment ~50 eggs were measured or weighed.

	Eggs		Yolk	Oil Globule
Species	Mean diameter (mm±SD)	Mean dry weight (µg)	Mean volume (mm³±SD)	Mean volume (mm³±SD)
Atlantic menhaden	1.61+0.08 (9)	78 (2)	0.583±0.0561 (6)	0.003±0.0006 (6)
Gulf menhaden	1.22±0.04 (7)	43 (2)	0.483±0.0359 (4)	0.003±0.0003 (4)

Newly-hatched, laboratory-reared Atlantic menhaden were longer and heavier than gulf menhaden (Table 1, 3). Temperature affected length-at-hatching, in that larvae (especially gulf menhaden larvae) were longer

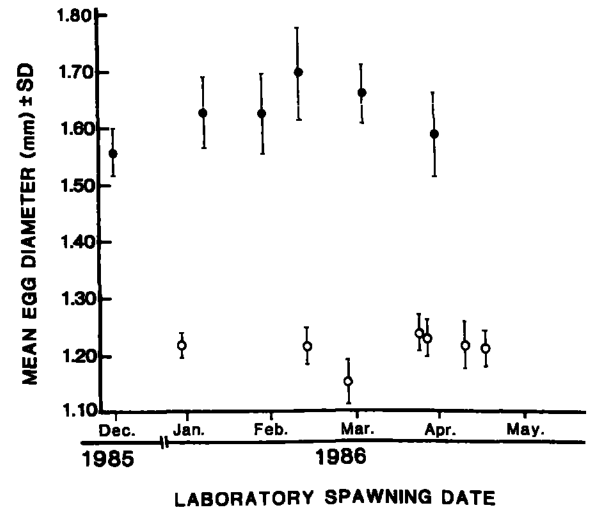

Figure 1

Relationship between mean egg size and laboratory spawning date for *Brevoortia tyrannus* (●) and *B. patronus* (○). Observations ($\bar{x}$±SD) are derived from approximately 50 eggs.

at lower incubation temperatures. On the other hand, incubation temperatures in the laboratory did not affect the weight of larvae at hatching (Table 1, 3).

Yolk reserves were larger for Atlantic menhaden at hatching, but oil reserves were greater for gulf menhaden (Table 1, 3). Temperature did not affect the amount of oil or yolk reserves for recently-hatched Atlantic or gulf menhadens. After hatching, both species utilized yolk and oil reserves at an exponential rate (Table 4). Atlantic menhaden utilized yolk reserves at a higher rate than gulf menhaden, but rates of oil depletion did not differ (Table 1, 4). Temperature affected rates of yolk and oil utilization. At first-feeding, the oil globule and yolk were virtually depleted (Table 3). Yolk reserves at this time were similar for the two species and were independent of rearing temperature. The age at which anatomical features associated with first-feeding appeared (eye pigment, fore- and midgut, and functional mouth) did not differ, but the interval between the appearance of these features and first-feeding was shorter for Atlantic menhaden (Table 5).

At first-feeding, Atlantic menhaden were significantly longer and younger than, but of similar weight to, gulf menhaden (Table 1, 3). Although length-at-hatching increased with decreasing temperature, temperature did not influence length of larvae at first-feeding. Age-at-first-feeding decreased with increasing temperatures for both species (Table 1, 3).

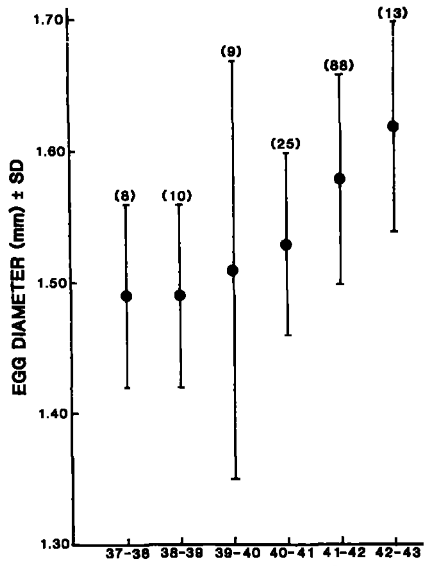

Figure 2

Relationship between egg size ($\bar{x}$±SD) and latitude of capture for *Brevoortia tyrannus*. Numbers in parentheses indicate number of eggs measured.

First-feeding Atlantic menhaden, which are longer than first-feeding gulf menhaden, may be slightly more resistant to starvation (Fig. 3). Atlantic menhaden lived 1–2 d longer than gulf menhaden. The survivorship curves of the two species were similarly shaped at the same temperature. At the highest temperature (24°C) survivorship declined rapidly after the third day, while at the lowest temperature (16°C) it was nearly linear with time.

The amount of biomass gained during the early stages did not differ between species (Table 1, Fig. 4). Population biomass of both menhadens was relatively low at 16°C, as compared with 20°C and 24°C when food was not limiting. Food concentrations of ≤1.0 rotifer/mL similarly limited the growth and survival of both species. Low temperature (i.e., 16°C) affected biomass gained by larvae of both species during this 7 d feeding and growth study.

Interactions between species and temperature were observed for all growth experiments (Table 1, Fig. 4). Atlantic menhaden growth was lower at 16°C than at 20° and 24°C. Gulf menhaden growth did not appear to differ between temperatures. Atlantic menhaden exhibited higher growth rates at 20° and 24°C, and, in like manner, were larger than gulf menhaden 10 d past first-feeding; however, mouth gape at this time did not differ between species (Table 1, 3).

Atlantic menhaden may attain its size-threshold for metamorphosis (i.e., Balon's 1984 concept) earlier than gulf menhaden (Figs. 5, 6). Length-weight relationships expressed during early-

Table 3

Summary of data ($\bar{x}\pm$SD) for larval Atlantic and gulf menhaden. Values for specific temperatures are given only when temperature had a statistically-significant (α=0.05) influence on the trait. An asterisk (*) preceding the trait indicates a statistically-significant (α=0.05) difference between species. Values in parentheses indicate the number of replicates. Means are calculated from replicate means.

Trait	Temperature (°C)	Atlantic menhaden	Gulf menhaden
*Size at hatching (mmSL)	16	3.4 ± 0.2 (4)	3.1 ± 0.2 (4)
	20	3.2 ± 0.2 (4)	2.6 ± 0.1 (4)
	24	3.2 ± 0.1 (3)	2.8 ± 0.2 (4)
*Dry weight at hatching (µg)	—	49.8 ± 5.0 (11)	39.3 ± 5.9 (12)
*Yolk volume at hatching (mm^3)	—	0.1512 ± 0.0220 (15)	0.1205 ± 0.0259 (11)
*Oil volume at hatching (mm^3)	—	0.0023 ± 0.0005 (15)	0.0029 ± 0.0004 (11)
Yolk volume at first-feeding (mm^3)	—	0.0002 ± 0.0000 (15)	0.0002 ± 0.0000 (11)
Oil volume at first-feeding (mm^3)	—	0.00 (15)	0.00 (11)
*Age at first-feeding (d)	16	5.2 ± 0.4 (8)	5.7 ± 0.1 (6)
	20	3.0 ± 0.3 (8)	3.9 ± 0.1 (7)
	24	2.4 ± 0.3 (8)	2.9 ± 0.1 (7)
*Size at first-feeding (mmSL)	—	4.8 ± 0.2 (9)	4.3 ± 0.3 (10)
Dry weight at first-feeding (µg)	—	37.8 ± 2.6 (9)	35.1 ± 1.6 (10)
Growth rate (10 d) in length (ln mm/d)**	16	0.027 ± 0.010 (3)	0.038 ± 0.013 (3)
	20	0.047 ± 0.000 (3)	0.037 ± 0.005 (3)
	24	0.049 ± 0.006 (3)	0.042 ± 0.004 (3)
*Growth rate (10 d) in weight (ln mg/d)**	16	0.051 ± 0.029 (3)	0.061 ± 0.029 (3)
	20	0.103 ± 0.016 (3)	0.062 ± 0.013 (3)
	24	0.102 ± 0.013 (3)	0.062 ± 0.005 (3)
*Length 10 d past first-feeding (mmSL)**	16	6.6 ± 0.7 (3)	6.5 ± 0.8 (3)
	20	7.9 ± 0.1 (3)	6.2 ± 0.3 (3)
	24	7.7 ± 0.0 (3)	6.4 ± 0.3 (3)
*Dry Weight 10 d past first-feeding (µg)**	16	62.0 ± 19.2 (3)	60.3 ± 15.8 (3)
	20	115.3 ± 19.6 (3)	63.3 ± 8.1 (3)
	24	100.7 ± 13.4 (3)	71.0 ± 3.5 (3)
Mouth gape 10 d past first-feeding (mm)	16	0.3 ± 0.02 (3)	0.3 ± 0.01 (3)
	20	0.3 ± 0.01 (3)	0.3 ± 0.01 (3)
	24	0.3 ± 0.02 (3)	0.3 ± 0.03 (3)

**A species × temperature interaction was observed.

Table 4

Linear regression equations ($Y=B_0+B_1X_1$) between $\log_e$ yolk and oil volume in mm^3 (Y) and age in days (X_1) for gulf and Atlantic menhaden. *N* = number of replicates.

Species	°C	*N*	Slope (B_1)	Intercept (B_0)	r^2
Yolk					
Gulf menhaden	16	4	−1.220	−2.089	0.96
	20	4	−1.734	−1.733	0.97
	24	4	−2.228	−2.118	0.98
Atlantic menhaden	16	5	−1.270	−1.765	0.97
	20	5	−2.065	−1.712	0.96
	24	5	−2.595	−1.723	0.97
Oil					
Gulf menhaden	16	4	−1.432	−5.082	0.81
	20	4	−1.819	−4.985	0.86
	24	4	−2.834	−4.814	0.81
Atlantic menhaden	16	5	−1.222	−5.392	0.92
	20	5	−2.041	−5.232	0.83
	24	5	−2.017	−5.714	0.84

Table 5

The mean time (d) before first-feeding when ≥80% of gulf and Atlantic menhaden larvae attained eye pigment (EYE), fore-and midgut (FG/MG), and a functional mouth (MOUTH) in relation to temperature. Values are the means of three replicates. Values in parentheses indicate average age (days post-hatch).

	16°C			20°C			24°C		
Species	FG/ MG	Eye	Mouth	FG/ MG	Eye	Mouth	FG/ MG	Eye	Mouth
Gulf menhaden	1.0 (4.7)	1.3 (4.4)	1.3 (4.4)	0.7 (3.2)	0.7 (3.2)	0.7 (3.2)	0.3 (2.6)	0.3 (2.6)	0.7 (2.2)
Atlantic menhaden	0.3 (4.9)	0.7 (4.5)	0.7 (4.5)	0.3 (2.9)	0.3 (2.9)	0.3 (2.9)	0 (2.4)	0 (2.4)	0 (2.4)

life-history stages of these two menhadens suggest that Atlantic menhaden reaches a size-threshold at a smaller size than gulf menhaden. For regression lines that described the length-weight relationship for Atlantic menhaden >10 mmSL and gulf menhaden >12 mmSL, there were no differences between slopes or intercepts. For Atlantic menhaden ≤10 mmSL and gulf menhaden ≤12 mmSL, there were no differences in slopes between the two species, although their intercepts differed. Beginning at the size-threshold in both species (>10 mmSL for Atlantic menhaden, >12 mmSL for gulf menhaden), there is a larger change in weight in relation to a given change in length, reflecting morphogenic changes.

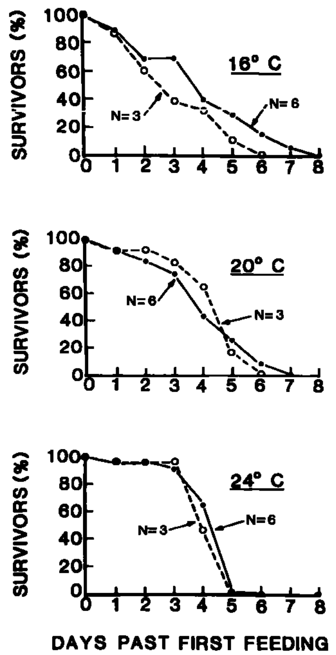

Figure 3

Time to starvation of unfed *Brevoortia tyrannus* (●) and *B. patronus* (○) in relation to temperature. Approximately 25 larvae were used at each experimental temperature. N denotes number of replicates.

Discussion

Egg size and its influence on early-life-history characteristics have received considerable attention. My results, in general, are in accord with other studies of diverse fishes and other organisms. Larger eggs are positively correlated with size of larvae at hatching, yolk reserves, resistance to starvation, and size-at-first-feeding, e.g., Blaxter & Hempel 1963 (clupeoid stocks), Crump 1984 (amphibia), Wallace & Aasjord 1984 (salmonids), Knutsen &

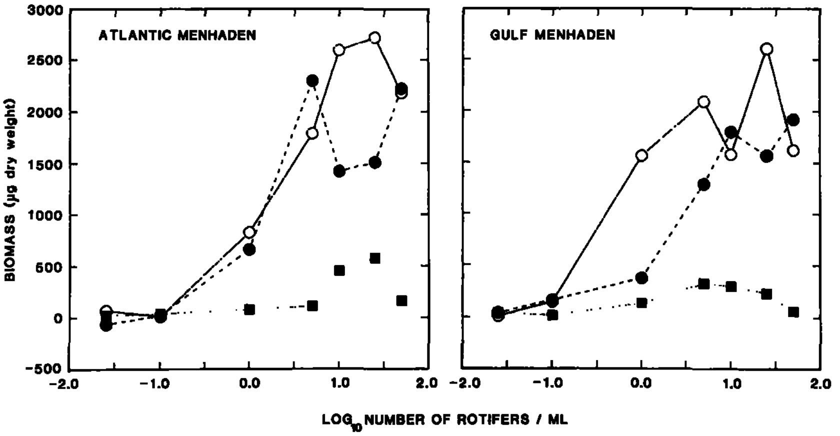

Figure 4

Amount of biomass gained (mean dry weight gained/larvae × number of survivors) over a 7 d period for early-larval *Brevoortia tyrannus* and *B. patronus* at 16 (■), 20 (●) and 24°C (○). Values are means of two replicates for food levels of 5, 25, and 50 rotifers/mL and means of three replicates for all other food levels.

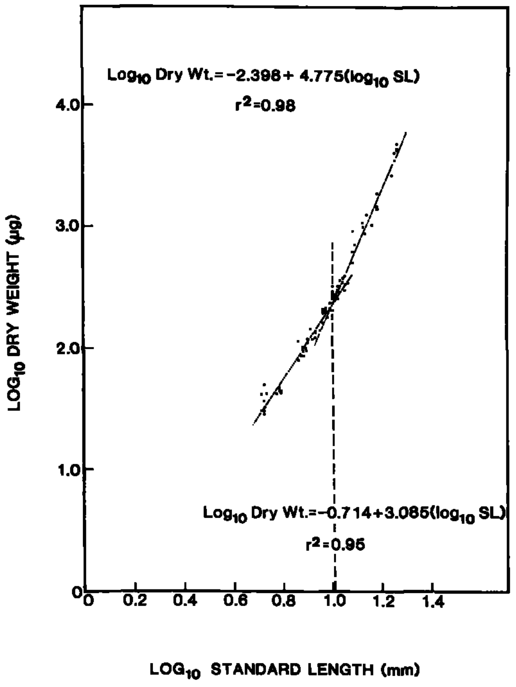

Figure 5

Length-weight relationship of larval *Brevoortia tyrannus* showing a change in body morphology. Breakpoint occurs at 10 mmSL.

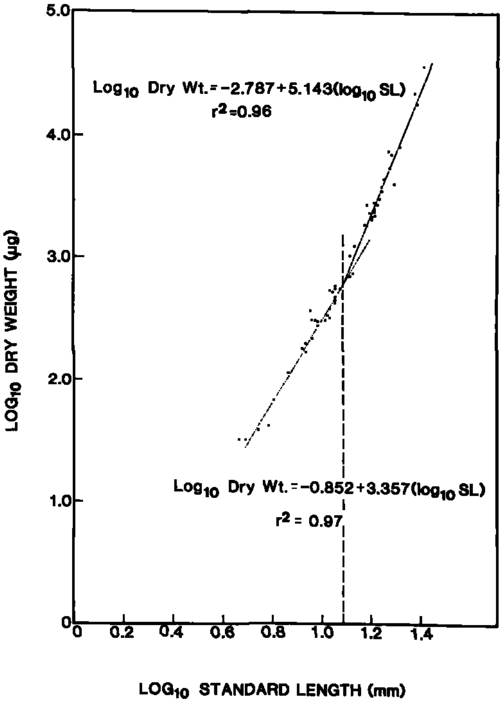

Figure 6

Length-weight relationship of larval *Brevoortia patronus* showing a change in body morphology. Breakpoint occurs at 12 mmSL.

Tilseth 1985 (gadoids), Marsh 1986 (percids), and Goulden et al. 1987 (cladocerans). Relatively larger larvae have been reported to have increased mobility, enhanced encounter rates with prey, and, because of these features, should be better able to detect food (Miller et al. 1988). Large eggs, then, would appear to be more fit in environments where the food supply is relatively poor or variable (Hempel & Blaxter 1967, Goulden et al. 1987). This suggests that the Atlantic menhaden is responding to a more variable or unpredictable reproductive environment than its congener. Because larger eggs appear to confer an advantage over smaller eggs, early survival of larvae from larger eggs should be less variable (Miller et al. 1988). This was not apparent in this study. Although growth rate of early Atlantic menhaden was greater than gulf menhaden at moderate to high temperatures (Table 2), the gain in population biomass of larvae did not differ between species (Table 1, Fig. 4). Pepin (1991) also was unable to support the prediction that larval survival is less variable for species that spawn large eggs.

The cumulative effects of egg size through the early-larval stage may influence menhaden stage duration. Atlantic menhaden not only produce larger eggs and larger larvae at the onset of feeding than do gulf menhaden, but they also have higher rates of yolk utilization and, apparently, higher rates of development (i.e., digestive and sensory systems). Hence, Atlantic menhaden larvae are not only larger, but also younger, than gulf menhaden at first-feeding. This could result in larger larval size shortly after first-feeding (e.g., 10 d), if larvae encounter suitable prey and temperatures. Moreover, Atlantic menhaden appear to undergo transformation of development (based on the relationship between length and weight) at a relatively smaller size, thus spending relatively less time in the early-larval stage. Chambers et al. (1988) showed that winter flounder *Psuedopleuronectes americanus* larvae that metamorphosed early were growing faster than their cohorts despite their small size at metamorphosis. Furthermore, the size advantage acquired during the larval period was maintained during the early-juvenile period. Williams (1966) argued that acceleration of development will occur in those developmental stages in which mortality rates are high. Comparatively, Atlantic menhaden reproduce in an environment that is unpredictable, and the suite of traits exhibited by this menhaden species mediates the unpredictability of the environment. Further, Atlantic menhaden spawn over a wide range of locations throughout most of the year. This may minimize reproductive failure, because the effects of extreme environmental conditions in one place or time will be dampened by less-extreme environmental conditions in others (Den Boer 1968).

Differences in life-history characteristics between Atlantic and gulf menhadens observed in this study generally are in agreement with previous studies. Reported egg sizes support the observation that Atlantic menhaden eggs are larger than gulf menhaden eggs (Hettler 1984, Powell & Phonlor 1986). The influence of temperature on early-life-history characteristics, interspecific differences in size-at-hatching, and size- and age-at-first-feeding are in accord with findings of Powell & Phonlor (1986). An exception was interspecific differences in growth rate, which were found to differ between species in this study. Interspecific differences between the two menhadens in the wild have been reported by Maillet & Checkley (1991). Although Powell & Phonlor (1986) found no differences in growth rates between species (growth rates were determined at 20°C only), they found a difference in size at age 21d past first-feeding (Atlantic menhaden 10.7 mmSL, gulf menhaden 8.9 mmSL). This supports observations in the present study that age- and size-at-first-feeding are subtle but important early-life-history characteristics that can influence future size if larvae encounter suitable prey and temperatures.

The influence of temperature on hatching size, as observed in this study, has been linked to larval survivorship. Buckley et al. (1990) reported that recently-hatched and first-feeding winter flounder *Psuedopleuronectes americanus* larvae were longer and displayed greater amounts of protein and nucleic acids at low temperatures, thus maximizing size and condition during the cold winter spawning period. Bengston et al. (1987) observed that recently-hatched Atlantic silverside *Menidia menidia* were larger at low temperatures. They suggested that this conferred a survival advantage to larvae hatched early in the season (colder temperatures), because they are larger at any given age than those hatched later in the season (warmer temperatures). I was unable to detect a survival advantage in this study. Although gulf and Atlantic menhaden were relatively larger at low incubation temperatures (Table 3), incubation temperatures had no influence on size-at-first-feeding.

Certain early-life-history characteristics do not appear to be correlated with egg size. Egg oil volume, oil utilization rates, oil volume at hatching, and weight-at-first-feeding were not related to egg size (Tables 1–3). Egg oil volume has been correlated with resistance to starvation (Chambers et al. 1989). In the present study, there were no differences between menhadens in egg oil volume, and recently-hatched gulf menhaden larvae had a greater volume of oil than Atlantic menhaden, yet still appeared to be least resistant to starvation. This is not surprising, since oil was depleted in both species at first feeding.

A major constraint of this study, and in comparison with previous studies (Hettler 1984, Powell & Phonlor 1986), is that adults from all studies were collected from similar areas and may not be representative of the entire population. Intraspecific latitudinal variation in field-collected Atlantic menhaden egg size has been observed in this study, and variation in egg size has been reported for gulf menhaden (Hettler 1984). Evidence in both studies shows that egg size is related to fish size. Hettler (1984) found that larger laboratory-spawned gulf menhaden (20 cm mean length) produced larger eggs than smaller gulf menhaden (18 cm mean length). Because Atlantic menhaden are distributed by size and age, differences in egg size with latitude might be related to female size. If so, values for the early-life-history variables (e.g., egg size, size-at-hatching, etc.), especially for Atlantic menhaden as reported here, should be viewed with caution because intraspecific and latitudinal variation in life-history variables was not evaluated in this study.

With the exception of salmonids, there are few studies that relate interspecific differences in early-life-history traits to the environments that the species occupy. Beacham & Murray (1990) clearly related variation of early-life-history traits of five species of Pacific salmon to their different spawning environments. As in the present study, alevin and fry weight were greatly influenced by egg size. Given the constraints and limitations of the present study, the differences in egg size which influenced larval size, along with differences in a suite of developmental events observed between the two menhadens, may reflect life-history selection processes that have occurred in their different environments.

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