DESCRIPTION OF EGGS, LARVAE, AND EARLY JUVENILES OF GULF MENHADEN, *BREVOORTIA PATRONUS*, AND COMPARISONS WITH ATLANTIC MENHADEN, *B. TYRANNUS*, AND YELLOWFIN MENHADEN, *B. SMITHI*[1]

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ABSTRACT

Morphometric, meristic, and pigmentation descriptions of laboratory-reared gulf menhaden, *Brevoortia patronus*, and Atlantic menhaden, *B. tyrannus*, indicate that larvae of these species can be distinguished from each other by the number of myomeres and vertebrae; that Atlantic menhaden can be distinguished from yellowfin menhaden, *B. smithi*, by the number of myomeres and vertebrae, by pigmentation, and by morphometrics; and that gulf menhaden can be separated from yellowfin menhaden by pigmentation and morphometrics. Unlike yellowfin menhaden, gulf and Atlantic menhaden lacked paired melanophores along the dorsal midline forward of the dorsal fin and along the ventral midline between the paired fins. Compared with yellowfin menhaden larvae of equal lengths, gulf menhaden had less body depth, shorter heads and snouts, smaller eyes, and longer prepelvic and predorsal distances. Gulf menhaden eggs averaged 1.29 mm in total diameter, 0.95 mm in yolk diameter, and 0.20 mm in oil droplet diameter. Twelve-hour-old larvae had a snout-notochord tip length of 3.3 mm. Their growth rate averaged 0.30 mm/day through 90 days of rearing at 20°C. On specimens 6-17 mm the mean number of myomeres was 44.6; on specimens >15 mm the mean number of vertebrae was 45.3. Postdorsal-preanal myomeres decreased from 5.3 to 1.8 as the dorsal fin grew and the gut shortened during development. Transformation from larva to juvenile in laboratory-reared gulf menhaden was completed at a smaller size than reported for field-caught fish (25 vs. 28 mm SL).

Eggs and larvae of gulf menhaden, *Brevoortia patronus* Goode, have not been described, even though this species is the most economically important clupeid in the United States. The gulf menhaden purse seine fishery landed an average of 660,368 t annually from 1977 to 1981, making it the largest fishery in the United States (U.S. National Marine Fisheries Service 1982). Gulf menhaden, one of three species of *Brevoortia* in the Gulf of Mexico, are found from Florida Bay to the Gulf of Campeche, Mexico. They spawn in the northern gulf at least as far offshore as the 80 m isobath between mid-October and late March, with a peak in December (Christmas and Waller 1975[3]); juveniles are estuarine dependent. Yellowfin menhaden, *B. smithi*, and finescale menhaden, *B. gunteri*, co-occur with gulf menhaden, but contribute <1% to the landings. The Atlantic menhaden, *B. tyrannus*, which supports a large purse seine fishery along the U.S. Atlantic coast, is a large-scaled cognate of the gulf menhaden, but does not occur in the Gulf of Mexico (Hildebrand 1963). Distribution of yellowfin menhaden is continuous around Florida to as far north as North Carolina.

Menhaden larvae superfically resemble the larvae of other clupeids with which they co-occur and can be distinguished from them (Houde and Fore 1973; Houde and Swanson 1975), but current descriptions (Suttkus 1956; Houde and Fore 1973; Houde and Swanson 1975; Jones et al. 1978) are not adequate to separate sympatric *Brevoortia* larvae. Eggs, larvae, and juveniles of yellowfin menhaden have been described (Houde and Swanson 1975), whereas the early development of finescale menhaden has not. Gulf and yellowfin menhaden hybrids in the eastern Gulf of Mexico (Hettler 1968; Turner 1969; Dahlberg 1970) further complicate separation by species. Although gulf and Atlantic menhaden larvae cannot be confused in ichthyoplankton collections because of their allopatric separation by the Florida Peninsula, Atlantic and yellowfin menhaden larvae may be confused in collections from the east coast of Florida, where both species are known to spawn during the winter (Dahlberg 1970).

In this paper, I describe the eggs, larvae, and early

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[3]Christmas, J. Y., and R.S. Waller. 1975. Location and time of menhaden spawning in the Gulf of Mexico. Unpubl. manuscr., 20 p. Gulf Coast Research Laboratory, Ocean Springs, MS 39564.

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juveniles of gulf menhaden spawned and reared in the laboratory using morphometrics, meristics, and pigmentation features, and I compare gulf menhaden larvae with yellowfin menhaden larvae described by Houde and Swanson (1975). Morphometric and meristic data on laboratory-spawned and reared Atlantic menhaden are also presented to supplement the composite description of this species by Jones et al. (1978) and to aid in the separation of Atlantic menhaden and yellowfin menhaden larvae. Characters for separating *Brevoortia* from other clupeids are reviewed.

METHODS

Gulf menhaden were collected as mature adults in September 1981 near Gulf Breeze, Fla., tranported to the Beaufort Laboratory, and induced to spawn with human chorionic gonadotropin (HCG) and carp pituitary (Hettler 1983). Spawnings that occurred in November 1981 and February 1982 provided a developmental series of eggs, larvae, and juveniles up to 90 d old, reared at a temperature of 20° ± 2°C and a salinity of 30‰. One hundred eggs, preserved during the early embryo stage, and 100 live eggs were measured.

Atlantic menhaden were captured as juveniles in September 1978 near Beaufort, N.C., and reared to sexual maturity in the laboratory for 19 mo. They were induced to spawn in April 1980, and the larvae were reared at temperatures that began at 15°C and increased to 25°C during development (Hettler 1981). This spawning resulted in a developmental series of larvae and juveniles up to 130 d old.

All specimens were preserved in 2% buffered formaldehyde in seawater before being measured. The following morphometic measurements were taken with an ocular micrometer in a dissecting microscope on 123 gulf menhaden and 196 Atlantic menhaden.

Standard length (SL)—tip of snout to tip of notochord before and during notchord flexion; in postflexion larvae, tip of snout to posterior margin of hypural bones. All references to length in this paper are standard length unless otherwise stated.

Preanus length—tip of snout to posterior end of anus, measured along midline.

Predorsal length—tip of snout to anterior edge of dorsal fin base, measured along midline.

Prepelvic length—tip of snout to anterior insertion of pelvic fin, measured along midline.

Body depth—vertical depth at symphysis of the cleithra, exclusive of the finfold.

Dorsal and anal fin base lengths—distance from anterior to posterior edges of fin base; in larvae with incomplete fins, distance from origin of first ray to the insertion of the last ray.

Head length—tip of snout to posterior margin of otic capsules in yolk-sac larvae; tip of snout to opercular margin in older larvae and juveniles.

Snout length—tip of snout to anterior margin of eye.

Eye diameter—horizontal distance between anterior and posterior edges of fleshy orbit.

Myomeres were counted on semidry specimens (not completely immersed) up to 17 mm with transmitted unpolarized light by adjusting the microscope mirror to give maximum contrast between myosepta and myomeres. Myomeres were classified as follows:

Total myomeres—all myomeres between the most anterior myoseptum and the most posterior myoseptum.

Preanal myomeres—number anterior to the myomere in which the anterior ray of the anal fin is inserted or to the myomere in contact with the downward curve of the dorsal margin of the anus in larvae without anal fin rays.

Postanal myomeres—number posterior to the anterior insertion of the anal fin.

Predorsal myomeres—number anterior to the myomere containing the origin of the first dorsal fin ray.

Postdorsal-preanal myomeres—number between the myomere connected to the last dorsal fin ray and the most posterior preanal myomere.

Following morphometric measurements on all specimens and myomere counts on specimens with visible myomeres, the pigment pattern was recorded and specimens of gulf menhaden were illustrated with a camera lucida. Atlantic menhaden were not illustrated as the figures in Jones et al. (1978) are adequate.

Specimens were then used for counts of fin rays, pterygiophores, predorsal bones, vertebrae, and scutes. Specimens were transferred to 95% ethanol, stained with alcian blue for cartilage, cleared with trypsin, stained with alizarin red S for bone, and stored in 100% glycerin[4].

[4]Taylor, W. R., and G. C. Van Dyke. 1978. Staining and clearing small vertebrates for bone and cartilage study. Unpubl. manuscr., 19 p. National Museum of Natural History, Washington, DC 20560.

DESCRIPTION

Embryos

Gulf menhaden eggs were spherical, and had an unsculptured chorion, a faintly segmented yolk, and a single oil droplet. Living eggs were buoyant in salinities >26‰. Twenty-seven percent had both an outer and inner chorionic membrane. This has not been reported in wild-caught *Brevoortia* eggs. This inner chorion was not an artifact of preservation, since live eggs also contained a double chorion, but may have been a result of induced ovulation by HCG and carp pituitary. Dimensions of preserved and live eggs were the same as maximum sizes given by Houde and Fore (1973) for gulf menhaden eggs taken in plankton collections (Table 1). At its widest point the perivitelline space was 24-28% of the egg diameter. Eggs produced during December 1982 by another spawning group of gulf menhaden were smaller than gulf menhaden eggs produced the year before; total diameter was 1.18-1.22 mm; the yolk diameter was 0.66-0.79 mm; the oil droplet was 0.16 mm. The adults producing these eggs were smaller (17.8 cm mean length, 90 g mean weight) than the spawners that produced the larger eggs (20 cm, 135 g) (Table 1). Small adult size may be responsible for the small eggs as well as the reduced fecundity. Only a few hundred fertilized eggs were collected from the December 1982 group of 20 fish.

TABLE 1.—Mean diameter (mm) of gulf menhaden, *Brevoortia patronus*, eggs. Numbers in parentheses are equal to one standard deviation of the mean.

Eggs	*N*	Total diameter	Inner chorion diameter (if present)	Yolk diameter (along axis)	Oil droplet diameter
Preserved	100	1.29 (0.04)	1.23 (0.04)	0.95 (0.05)	0.20 (0.02)
Live	100	1.30 (0.05)	1.25 (0.03)	0.97 (0.04)	0.19 (0.01)

Advanced embryos had 30-40 small melanophores on each side along the dorsal surface from the posterior end of the head to the notochord tip (Fig. 1A).

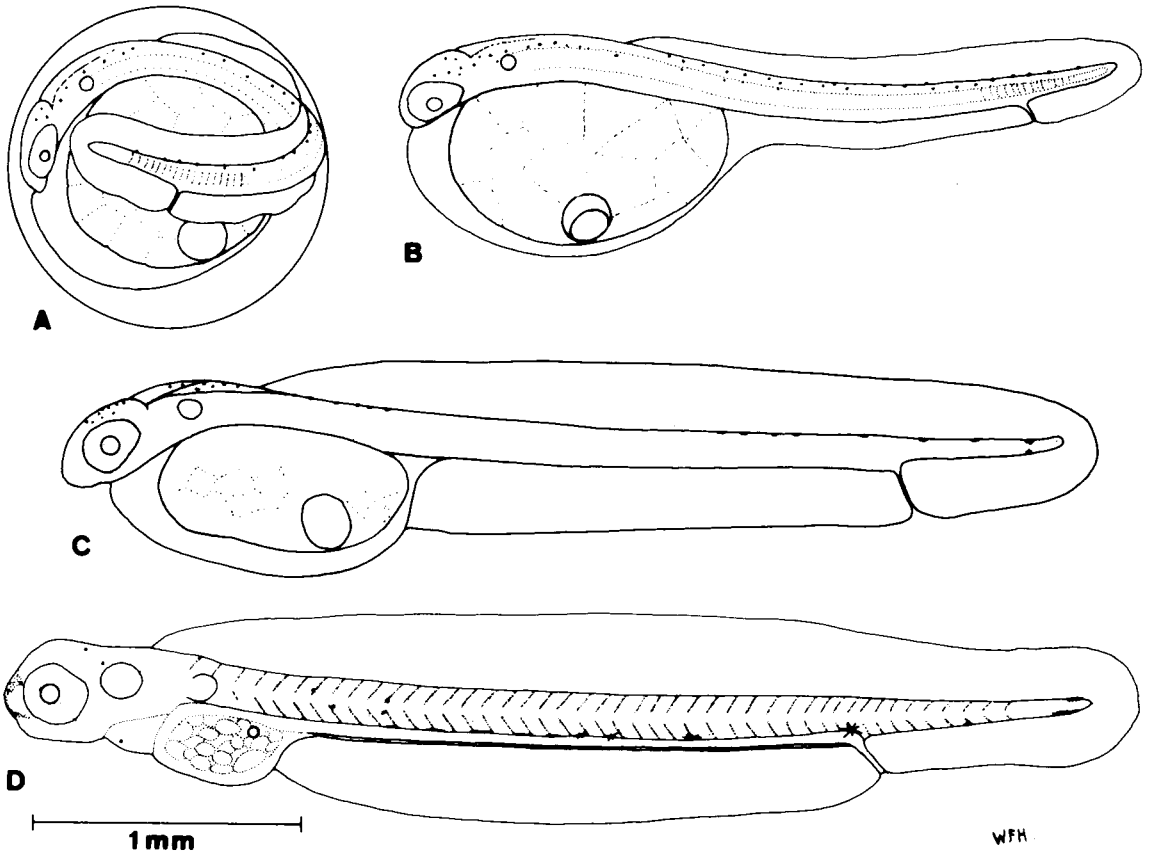

FIGURE 1.—Early stages of *Brevoortia patronus*. A. Embryo 40 h after fertilization. B. 2.6 mm larva, 5 min after hatching. c. 3.5 mm larva, 1 d after hatching. D. 3.9 mm larva, 2 d after hatching.

About 15-20 myomeres were visible in the caudal region. The yolk was faintly segmented into irregular globules. Eggs hatched in 40-42 h at a water temperature of 19°-20°C.

Atlantic menhaden eggs spawned in the laboratory were larger than gulf menhaden eggs in total diameter (1.54-1.64 mm) but similar in yolk diameter (0.82-0.95 mm) and oil droplet diameter (0.20-0.23).

Larvae

Growth

Gulf menhaden larvae were 2.6-3.0 mm SL immediately after hatching (Fig. 1B), but within 6 h had a mean length of 3.3 mm. The yolk and oil droplet were absorbed, the eyes were pigmented, and the mouth was functional at a length of 4.5 mm, 4 d after hatching. The growth rate of larvae at 20° ± 2°C averaged 0.30 ± 0.03 mm/d through 90 d of rearing (Fig. 2). Yellowfin menhaden reared for 32 d at 20°C grew 0.36 mm/d (Hettler 1970). Yellowfin menhaden reared at 26°C grew 0.45 mm/d until the 20th day (Houde and Swanson 1975).

Body Proportions

For 123 gulf menhaden, 3.1-34.9 mm, body depth, head length, prepelvic length, dorsal fin base length, anal fin base length, snout length, and eye diameter all increased relative to standard length as larvae grew, while preanus length and predorsal length decreased (Table 2). The decrease in predorsal length resulted from the forward movement of the dorsal fin, and the decrease in preanus length reflected the transformation from an elongate clupeiform larva shape to the laterally flattened fusiform shape of the juvenile. Transformation from the larval to the juvenile form in gulf menhaden began at about 19 mm (Fig. 3C) and was completed at about 25 mm. Atlantic menhaden larvae completed transformation at about 27 mm.

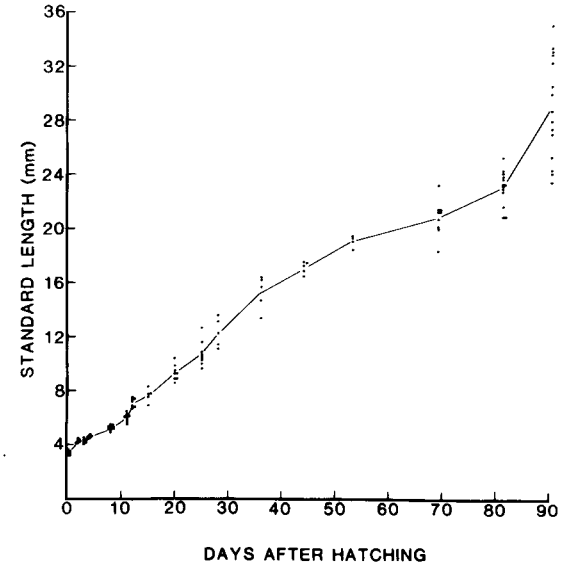

FIGURE 2.—Growth of laboratory-reared larvae of *Brevoortia patronus*. Lines connect means of each age group.

TABLE 2.—Proportions of head and body parts of gulf menhaden, *Brevoortia patronus*, expressed as a percent of standard length. Characters were not developed at lengths marked with a dash.

Length class (mm, SL)	Number of specimens	Preanus length	Predorsal length	Prepelvic length	Body depth	Dorsal fin base length	Anal fin base length	Head length	Snout length	Eye diameter
3.0-3.9	6	84.0	—	—	—	—	—	14.1	2.3	5.2
4.0-4.9	19	80.2	—	—	9.7	—	—	13.5	1.7	5.4
5.0-5.9	12	81.4	—	—	9.6	—	—	15.8	3.0	5.2
6.0-6.9	8	82.4	69.3	—	8.4	4.4	—	15.5	3.1	5.0
7.0-7.9	7	83.0	70.2	—	8.2	5.0	—	15.4	2.9	4.9
8.0-8.9	4	83.2	67.6	—	7.9	8.2	—	15.5	3.1	4.8
9.0-9.9	5	83.9	65.8	—	8.3	10.0	3.8	16.2	3.6	5.0
10.0-10.9	6	85.5	65.6	—	8.3	11.5	4.9	16.9	3.7	5.0
11.0-11.9	3	85.5	65.2	—	8.9	13.2	5.6	17.7	3.9	5.2
12.0-12.9	2	83.1	63.0	—	8.6	13.3	6.0	16.9	3.6	4.8
13.0-13.9	3	84.2	62.8	—	9.9	15.1	6.8	17.8	3.7	4.9
14.0-14.9	1	81.0	62.0	41.5	10.0	14.5	7.5	17.0	3.5	5.0
15.0-15.9	1	82.2	61.2	—	10.7	15.4	7.5	18.2	3.7	5.1
16.0-16.9	4	79.8	60.8	44.2	10.8	15.3	9.4	18.9	4.0	5.5
17.0-17.9	3	79.0	61.0	44.3	12.4	14.8	11.0	19.4	4.1	5.5
18.0-18.9	2	76.0	57.0	47.6	18.1	16.8	12.3	24.1	5.0	7.3
19.0-19.9	4	76.2	56.4	46.9	17.8	16.6	12.8	24.0	5.1	6.8
20.0-21.9	8	71.4	51.8	50.0	25.8	18.6	16.0	28.1	6.0	8.1
22.0-23.9	8	70.2	48.6	49.2	28.0	18.4	15.7	28.9	6.1	8.4
24.0-25.9	6	70.7	47.9	49.6	29.1	19.3	16.0	29.3	6.6	8.5
26.0-27.9	3	70.6	44.7	50.0	31.6	19.2	17.0	29.7	6.9	8.6
28.0-29.9	1	70.2	43.5	49.4	30.1	20.1	16.4	27.7	6.4	7.7
30.0-34.9	7	72.7	47.7	51.3	36.0	19.4	17.1	31.5	7.2	7.8

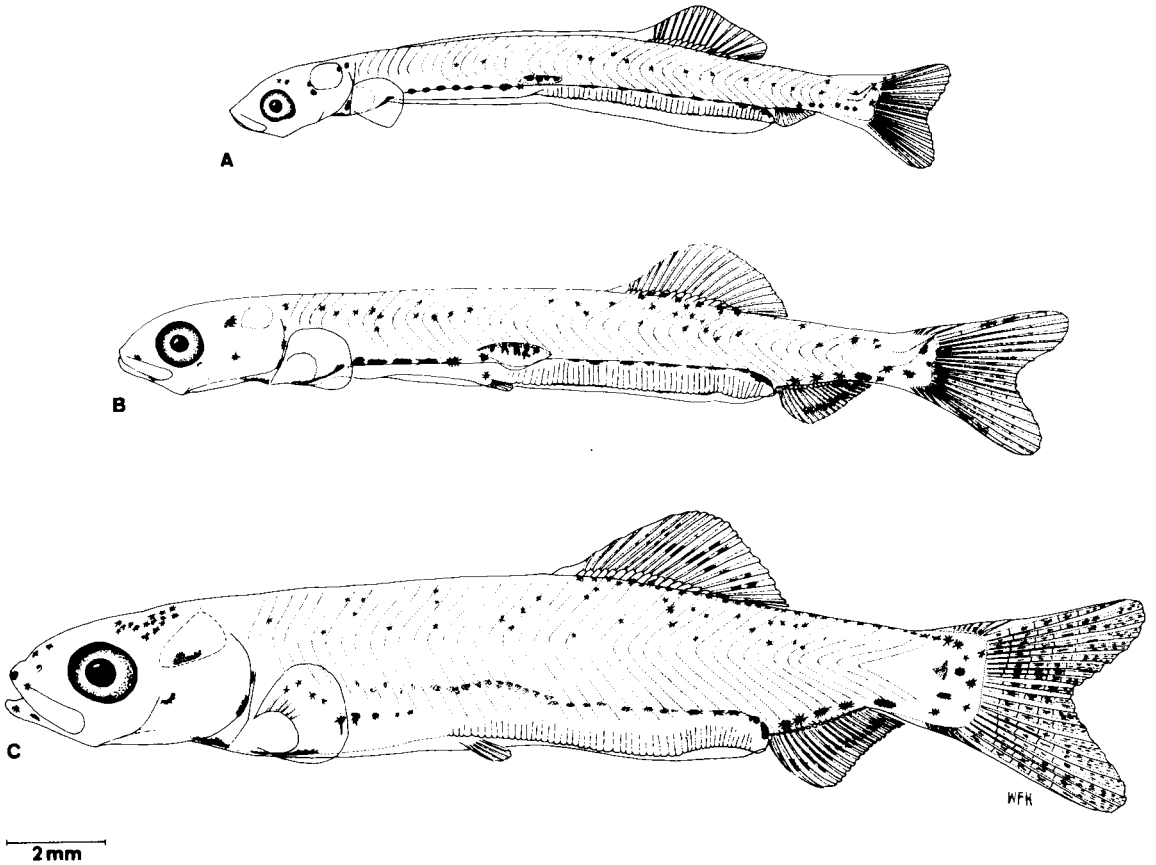

FIGURE 3.—Larval *Brevoortia patronus*: (A) 13.0 mm (28 d after hatching). (B) 16.5 mm (44 d after hatching). (C) 18.9 mm (53 d after hatching).

Gulf menhaden larvae and Atlantic menhaden larvae could not be separated morphometrically (Table 3, Fig. 4), but both could be separated from yellowfin menhaden larvae between 10 and 20 mm (Houde and Swanson 1975) by body depth, prepelvic length, and head length. Snout length and eye diameter may be useful to distinguish 15-25 mm specimens; snouts ≥7% of SL and eye diameter ≥9% of SL probably identify yellowfin menhaden.

Myomeres

The total number of myomeres could be counted only on specimens under 17 mm in length. Although the preanal myomeres could be easily counted on larger specimens, the last few postanal myomeres on the peduncle became indistinguishable. The number of myomeres (mean = 44.6) did not change significantly with length in gulf menhaden and corresponds with the number of adult vertebrae (44-46; mean = 44.7 not counting the hypural bones) reported by Dahlberg (1970). Radiographs of 20 adult gulf menhaden spawners used in my study showed that all fish had either 45 or 46 vertebrae (counting hypurals), with a mean of 45.6. During development the dorsal and anal fins moved in relation to the myomeres (Table 4). The anterior end of the dorsal fin moved from myomere 30 forward to myomere 23, numbered from head to tail. The posterior end of the dorsal fin remained fixed at myomere 32. The anus and the anterior end of the anal fin moved forward from myomere 37 to myomere 34. The postdorsal-preanal myomere count of 2 or 3 is diagnostic for *Brevoortia* at lengths >14 mm. Atlantic menhaden larvae 6-16 mm SL had a mean of 47.2 myomeres, with about two more predorsal myomeres and one more postanal myomere than gulf menhaden. Myomere number and distribution for gulf menhaden and yellowfin menhaden (Houde and Swanson 1975) were so similar that neither were useful for

TABLE 3.—Proportions of head and body parts of Atlantic menhaden, *Brevoortia tyrannus*, expressed as a percent of standard length. Characters were not developed at lengths marked with a dash.

Length class (mm, SL)	Number of specimens	Preanus length	Predorsal length	Prepelvic length	Body depth	Dorsal fin base length	Anal fin base length	Head length	Snout length	Eye diameter
3.0-3.9	4	85.4	—	—	—	—	—	14.5	1.9	6.7
4.0-4.9	10	82.8	—	—	8.3	—	—	12.0	1.9	5.4
5.0-5.9	15	81.0	—	—	8.4	—	—	12.1	2.2	5.0
6.0-6.9	7	81.4	—	—	8.4	—	—	13.3	2.5	4.8
7.0-7.9	18	82.3	71.0	—	8.0	2.6	—	13.7	2.6	4.8
8.0-8.9	12	82.7	69.6	—	7.9	4.3	—	13.9	2.6	4.8
9.0-9.9	13	82.8	67.3	—	8.3	6.5	2.4	15.0	3.0	5.2
10.0-10.9	13	85.6	66.9	—	8.6	9.5	4.2	16.4	3.4	5.3
11.0-11.9	8	85.9	66.4	—	8.7	10.1	5.0	16.6	3.5	5.4
12.0-12.9	10	84.7	64.6	—	9.1	11.5	5.5	17.6	3.7	5.6
13.0-13.9	10	83.2	63.6	—	9.4	13.0	6.7	18.2	4.0	6.0
14.0-14.9	7	82.9	62.7	45.8	9.8	13.6	7.1	18.3	4.0	6.2
15.0-15.9	7	81.7	61.9	45.3	10.0	14.0	7.8	18.3	4.0	6.2
16.0-16.9	9	80.8	62.5	45.5	11.4	14.0	8.8	20.2	4.1	6.8
17.0-17.9	8	79.9	60.2	47.6	12.8	15.2	10.0	22.9	4.5	7.3
18.0-18.9	6	77.9	58.6	47.0	14.2	15.7	10.6	23.2	4.4	7.4
19.0-19.9	9	76.9	57.3	48.0	16.1	16.0	11.8	23.8	4.6	7.8
20.0-21.9	7	74.2	53.8	48.6	19.8	17.1	14.2	27.2	4.8	8.0
22.0-23.9	3	73.4	50.4	50.9	24.7	17.7	16.1	29.8	5.5	8.0
24.0-25.9	2	72.7	51.4	51.3	25.4	17.6	15.9	31.0	5.7	7.6
26.0-27.9	3	74.7	49.6	52.8	29.1	19.6	18.0	31.1	7.0	8.3
28.0-29.9	1	72.6	48.9	51.5	29.0	17.3	16.3	31.3	6.8	7.8
30.0-34.9	4	75.4	49.6	52.4	32.6	20.0	15.6	33.0	8.2	8.8
35.0-39.9	3	76.0	49.9	53.2	36.5	20.4	16.6	33.6	7.6	7.8
40.0-49.9	4	74.9	49.6	52.2	33.5	20.5	17.1	32.2	7.6	8.3
60.0-69.9	3	74.8	48.9	52.2	33.4	19.5	16.8	32.4	7.0	5.3

TABLE 4.—Number of myomeres relative to dorsal fin and anal locations on gulf menhaden, *Brevoortia patronus*, larvae.

Length class (mm, SL)	Preanal			Postanal			Predorsal			Postdorsal-Preanal		
	N	Range	Mean	*N*	Range	Mean	*N*	Range	Mean	*N*	Range	Mean
<6.0	4	36-37	36.7	4	9	8.0	—	—	—	—	—	—
6.1-8.0	16	36-37	36.7	3	7-9	7.7	9	28-30	28.9	9	4-6	5.3
8.1-10.0	9	35-38	36.3	9	8-10	8.6	9	26-28	27.3	9	3-5	4.4
10.1-12.0	10	33-37	35.4	10	8-10	9.1	10	23-27	25.2	10	3-4	3.3
12.1-14.0	4	33-35	34.0	4	8-10	9.5	4	23-25	23.7	4	2-3	2.2
14.1-17.0	4	32-33	32.5	—	—	—	4	22-23	22.2	5	1-2	1.8

separating small larvae of these species. Yellowfin menhaden had a mean of 45.7, about one less predorsal myomere, and about one to two more postanal myomeres than gulf menhaden. Atlantic menhaden had about two more preanal myomeres and about one more postanal myomere than gulf menhaden at each size class (Table 5).

Meristics

In gulf menhaden the caudal and dorsal fins were the first fins to initiate development and the pectoral fins were the last fins to complete development, even though they were the first fins to form as nonrayed buds (Table 6, Fig. 1C). Two specimens had an extra principal ray in both the upper and lower group of caudal rays. Vertebrae centra did not first stain with alcian blue as did other bony structures. At 13 mm, vertebrae first stained with alizarin red S, with the staining reaction progressing from the middle of the column towards each end as length increased. The neural and haemel spines initially stained blue, beginning at each end of the column and progressing towards the middle. The mean number of vertebrae,

TABLE 5.—Number of myomeres relative to dorsal fin and anal locations on Atlantic menhaden larvae, *Brevoortia tyrannus*. Myomeres on specimens <6 mm could not be accurately counted.

Length class (mm, SL)	Preanal			Postanal			Predorsal			Postdorsal-Preanal		
	N	Range	Mean	*N*	Range	Mean	*N*	Range	Mean	*N*	Range	Mean
6.1-8.0	13	38-40	38.7	13	8-10	9.0	10	30-31	30.7	10	5-6	5.7
8.1-10.0	16	37-40	38.4	16	8-11	9.9	16	27-30	29.0	10	4-6	5.2
10.1-12.0	16	36-37	36.1	16	10-11	10.8	16	25-28	26.2	16	3-5	4.0
12.1-14.0	14	35-37	35.6	10	10-11	10.7	14	24-26	25.1	14	3-4	3.2
14.1-16.0	2	35-36	35.5	—	—	—	2	24-25	24.5	3	3	3.0

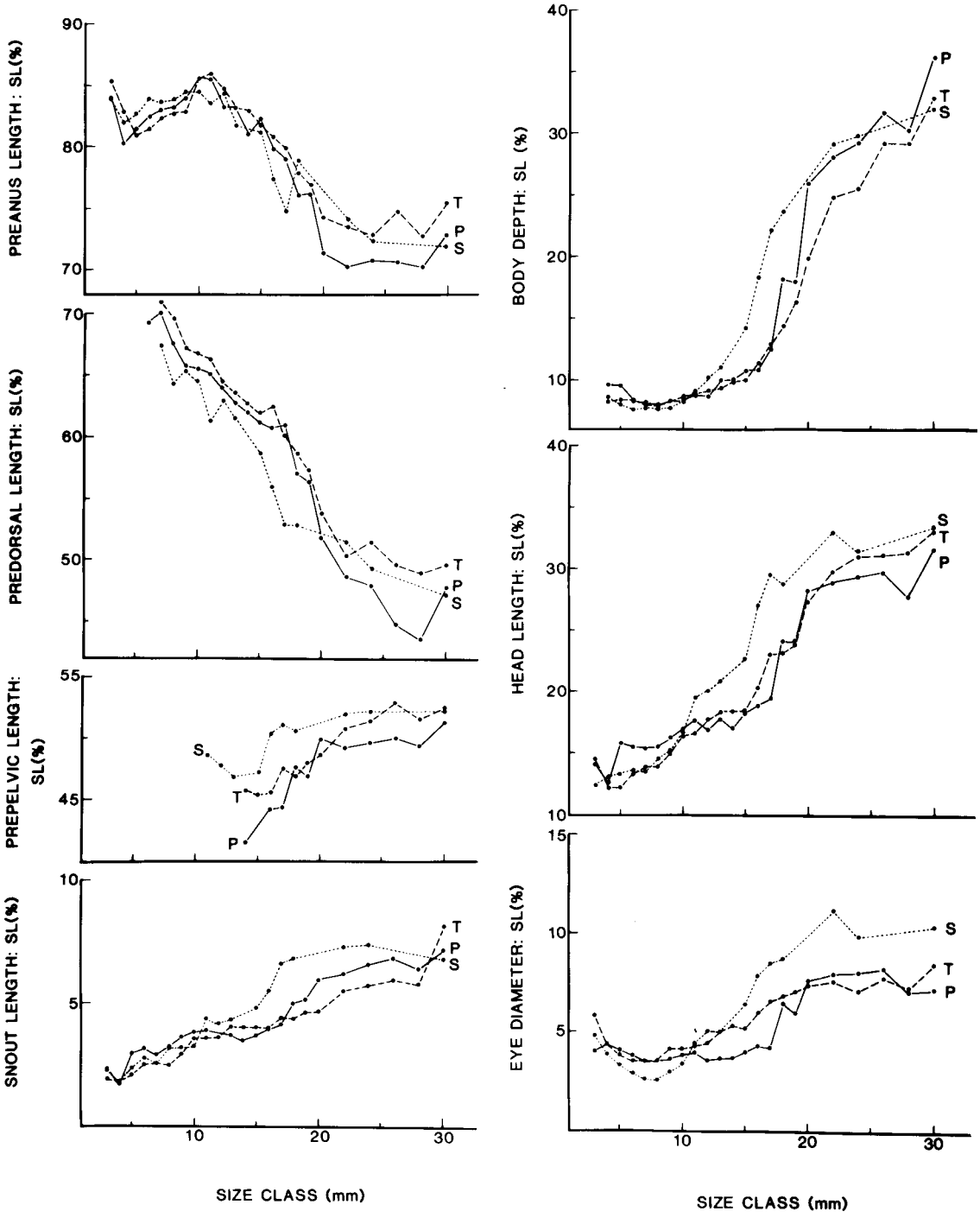

FIGURE 4.—Morphometric comparisons as a percentage of standard length of laboratory-reared *Brevoortia patronus* (P), *B. tyrannus* (T), and *B. smithi* (S). Yellowfin menhaden data from Houde and Swanson (1975).

TABLE 6.—Meristics in gulf menhaden, *Brevoortia patronus*, (35 specimens) and in Atlantic menhaden, *B. tyrannus*, (34 specimens).

Meristic	Size (mm SL) when first stained		Size (mm SL) when all are stained		Number in full complement	
	B. patronus	*B. tyrannus*	*B. patronus*	*B. tyrannus*	*B. patronus*	*B. tyrannus*
Caudal fin rays						
Principal	8	9	9	12	10-11 (dorsal)	10 (dorsal)
	16	13	18	20	9-10 (ventral)	9 (ventral)
Procurrent					8-9 (dorsal)	7-8 (dorsal)
					7-8 (ventral)	6-7 (ventral)
Dorsal fin						
Pterygiophores	8	8	16	16	19-21	18-19
Rays	8	9	19	17	21-23	20-22
Anal fin						
Pterygiophores	9	10	16	15	17-20	17-20
Rays	10	12	17	15	18-22	19-21
Pelvin fin rays	16	15	18	18	7	7
Pectoral fin rays	18	18	21	21	13-15	15-17
Predorsal bones	19	17	21	21	9-11	10-12
Vertebrae	13	14	16	15	45-46	48-49
Ventral scutes	21	21	31	27	29-31	32-33

including the hypural bones, was 45.3 counted in 21 specimens longer than 16 mm SL. The first bones to stain with alizarin red S were the dentaries, the maxillaries, and the cleithra which occurred in 9 mm specimens.

Only vertebrae and ventral scute counts were useful in separating gulf menhaden and Atlantic menhaden; other meristics overlapped (Table 6). Yellowfin menhaden larvae could not be separated from the two large-scaled menhaden by meristics, with the possible exception of Atlantic menhaden that had 47-48 vertebrae and yellowfin menhaden that had 45-47 (including the hypural bones) (Dahlberg 1970).

Pigmentation

Pigmentation of gulf menhaden larvae (Figs. 1, 3, 5, 6) was similar, but not identical, to the pigmentation described for yellowfin menhaden (Houde and Swanson 1975) and Atlantic menhaden (Jones et al. 1978). Gulf menhaden up to 8 mm had 1 melanophore on the dorsal side of the notochord tip and 1 or 2 melanophores on the ventral side of the notochord tip, which is diagnostic for the genus *Brevoortia* (Figs. 1C, D, 5A). Lateral pigmentation, although found on the trunk of specimens as small as 4.9 mm, was not found on all small specimens. At 10 mm, all specimens had 5-20 melanophores scattered the length of the trunk. Larvae 4-5 mm had 10-20 tiny melanophores on top of the head. One 7.8 mm larva had a single stellate melanophore on top of the head behind the eyes. One single medial melanophore, which enlarged into additional melanophores as larvae grew, was present along the isthmus (ventral midline forward of the cleithrum) on 6 mm and larger larvae. On 8-20 mm larvae, 1 or more melanophores occurred along the

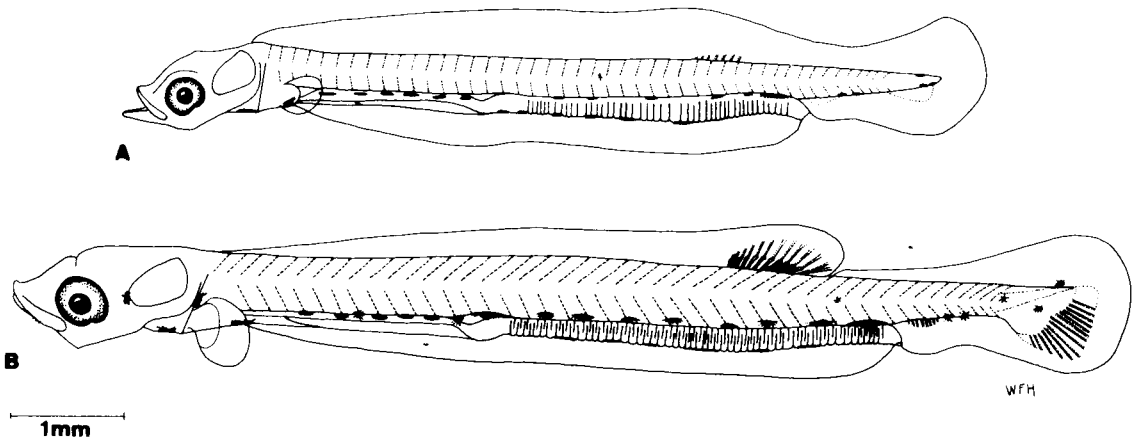

FIGURE 5.—Larval *Brevoortia patronus*: (A) 7.2 mm (12 d after hatching). (B) 9.2 mm (20 d after hatching).

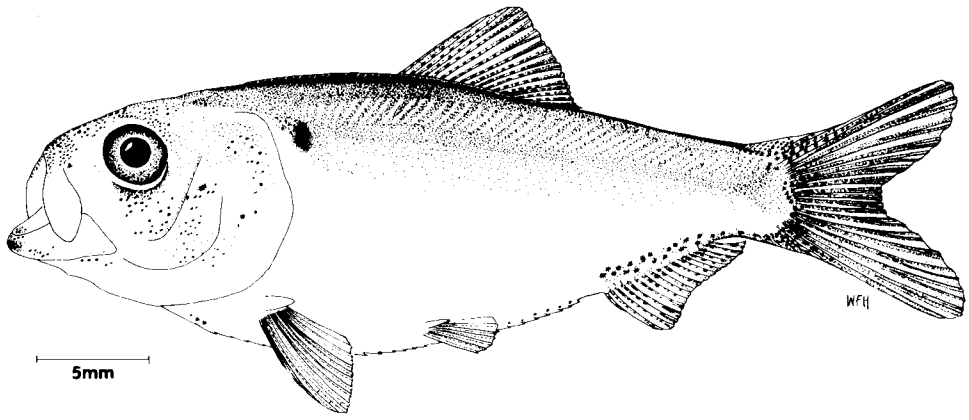

FIGURE 6.—Juvenile *Brevoortia patronus* 33.8 mm (90 d after hatching).

cleithrum axis on each side. Along the surface, lateral and parallel with the dorsal surface of the foregut, there were usually 6-10, but sometimes up to 20, rectangular melanophores on each side. These paired melanophores were positioned anteriad to 2 or 3 stellate melanophores covering the dorsal surface of the gas bladder. A series of 10-18 medial, unpaired melanophores occurred between the trunk musculature and the dorsal surface of the gut. This series merged into 1-3 stellate melanophores projecting ventrally over the end of the gut towards the anus. A medial string of nearly continuous, thin melanophores traced the junction of the finfold along the ventral surface of the hindgut. Dorsal to the base of the anal fin 2 or more melanophores were always present in larvae >5 mm. The caudal fin was pigmented by 10 mm, whereas the medial fins, lower jaw tip, snout, and nape acquired pigment by 18 mm (Fig. 3C). Pigment was absent on the surface lateral to the ventral portion of the foregut between the distal end of the pectoral fin rays and the pelvic fin. Melanophores were present on specimens >17 mm along the base of the dorsal fin and along the dorsal midline between the dorsal and caudal fins. Paired melanophores were absent between the head and dorsal fin. For pigment descriptions of gulf menhaden larvae and juveniles >19 mm, see Suttkus (1956).

Other Structures

By 4.5 mm, the dentaries, maxillaries, branchial arches, cleithra, and hypurals were stained with alcian blue, but the first bones to accept alizarin red S stain, and thus indicate ossification, were the cleithra in 8.5 mm specimens. Flexion of the notochord upward to initiate caudal fin development began at 7 mm. Ossification of the hypural bones began at 10 mm and was completed at 15 mm. Eight maxillary teeth and three dentary teeth on each side were observed on 10 mm larvae. Fourteen teeth on each maxillary and three teeth on each dentary were still visible on 25 mm juveniles. In the oral cavity of 16-24 mm larvae, one or two teeth projected downward from each endopterygoid bone and one or two teeth projected upward from the second basibranchial cartilage. These teeth were absent in fully transformed juveniles. Scales were first visible along the dorsolateral margin of the caudal peduncle and along the midline on each side of the trunk at the beginning of transformation, which occurred at 19 mm.

COMPARISON AMONG *BREVOORTIA* AND WITH OTHER CLUPEIDS

Of the *Brevoortia* species, eggs and larvae of gulf menhaden were the most difficult to distinguish from yellowfin menhaden. Gulf menhaden had 44-46 myomeres, whereas yellowfin menhaden had 45-47 (Houde and Swanson 1975). Morphometrics may be useful to distinguish 10-25 mm specimens of gulf menhaden from yellowfin menhaden. At equal lengths, gulf menhaden had less body depth, a shorter head length, a longer prepelvic distance, a longer predorsal distance, a shorter snout, and a smaller eye. Yellowfin menhaden >17 mm had paired melanophores between the head and the dorsal fin (Houde and Swanson 1975), whereas gulf menhaden did not. Wild specimens of yellowfin menhaden from southern Florida also had a double row of melanophores along the ventral midline between the pectoral and pelvic fins, but neither laboratory-

reared gulf menhaden or wild specimens of gulf menhaden collected from four locations along the northern Gulf of Mexico had ventral midline pigment. Gulf menhaden had more dorsal fin rays, but both species had an equal number of anal rays. Fertilized eggs of the two species had the same diameter, but gulf menhaden had a larger oil droplet (0.20 vs. 0.15 mm) than yellowfin menhaden. No description of finescale menhaden larvae exists, but presumably they have 42-43 myomeres, based on the number of vertebrae reported for this species (Dahlberg 1970). Although gulf menhaden larvae are geographically separated from Atlantic menhaden larvae, they can be separated by counting myomeres or vertabrae; gulf menhaden, 44-46; and Atlantic menhaden, 47-48. Atlantic menhaden and yellowfin menhaden had nearly equal dorsal and anal fin ray numbers, but Atlantic menhaden had one to four more myomeres and lacked dorsal and ventral midline paired melanophores anterior to the dorsal and pelvic fins. Mophometric differences between Atlantic menhaden and yellowfin menhaden are similar to differences between gulf menhaden and yellowfin menhaden.

There are some differences in egg and larval meristics and morphology data between my study and the literature, which may be due to differences between laboratory-reared and wild specimens. Houde and Fore (1973) reported that gulf menhaden had 45-48 myomeres (vs. 44-46 that I found for gulf menhaden), 20-23 anal rays (vs. 19-21), 17-21 dorsal rays (vs. 20-22), and reported that pelvic fins in northern gulf specimens were not developed until 20 mm (vs. 18 mm). They also reported that gulf menhaden eggs had a diameter of 1.04-1.30 mm (vs. 1.18-1.34 mm), an oil droplet of 0.08-0.20 mm (vs. 0.16-0.22 mm), and a wide perivitelline space of about 33% (vs. 24-28%). Jones et al (1978) reported that Atlantic menhaden egg diameter was 1.30-1.95 mm (vs. 1.54-1.64 mm that I found for Atlantic menhaden), that yolk diameter was 0.90-1.20 (vs. 0.82-.095 mm), and that the oil droplet diameter was 0.11-0.17 (vs. 0.20-0.23). For Atlantic menhaden larvae of unspecified lengths they reported 16-18 dorsal rays (vs. 20-22), 18-20 anal rays (vs. 19-21), and a body depth:standard length ratio of about 0.05 at 23 mm total length (vs. about 0.20 I found at the same length); however, the body depth ratio is undoubtedly a typographical error.

Laboratory-reared gulf menhaden and Atlantic menhaden both appeared to transform into juveniles at a smaller size than wild fish. Morphometric data and photographs of specimens of gulf menhaden from Louisiana indicated that the juvenile form was not reached until about 30 mm SL (Suttkus 1956). Lewis et al. (1972) indicated that Atlantic menhaden from North Carolina did not complete "prejuvenile" growth until about 33 mm SL. Houde and Swanson (1975) suggested that tank-reared yellowfin menhaden transformed at smaller sizes than did wild fish, and I concur.

Characters useful for separating eggs and larvae of *Brevoortia* from other clupeids have been identified (Houde and Fore 1973; Richards et al. 1974; Houde and Swanson 1975; Powles 1977). *Sardinella* and *Opisthonema* have about the same total myomere counts as *Brevoortia*, but usually have 6-9 post-dorsal-preanal myomeres. *Etrumeus* has the same or more total myomeres than *Brevoortia*, but about 10 fewer anal rays. The smaller larvae of *Sardinella*, *Opisthonema*, and *Etrumeus* have no pigment on the dorsal side of the notochord tip, whereas *Brevoortia*, *Harengula*, and *Jenkinsia* have this pigment. However, *Jenkinsia* and *Harengula* have 42 or fewer myomeres. The spawning seasons of all these genera overlap with the spawning season of *Brevoortia* species (Houde and Fore 1973; Powles 1977; Jones et al. 1978). Larvae of *Dorosoma* and *Alosa* are not normally found in marine waters with *Brevoortia*.

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LITERATURE CITED

DAHLBERG, M. D.
1970. Atlantic and Gulf of Mexico menhadens, Genus *Brevoortia* (Pisces: Clupidae). Bull. Fla. State Mus., Biol. Sci. 15:91-162.

HETTLER, W. F., JR.
1968. Artificial fertilization among yellowfin and Gulf menhaden (*Brevoortia*) and their hybrid. Trans. Am. Fish. Soc. 97:119-123.
1970. Rearing larvae of yellowfin menhaden, *Brevoortia smithi*. Copeia 1970:775-776.
1981. Spawning and rearing Atlantic menhaden. Prog. Fish-Cult. 43:80-84.
1983. Transporting adult and larval gulf menhaden and techniques for spawning in the laboratory. Prog. Fish-

Cult. 45:45-48.

HILDEBRAND, S. F.
1963. Family Clupeidae. *In* H. B. Bigelow (editor), Fishes of the western North Atlantic. Part Three, p. 257-454. Mem. Sears found. Mar. Res. Yale Univ. 1.

HOUDE, E. D., AND P. L. FORE.
1973. Guide to identity of eggs and larvae of some Gulf of Mexico clupeid fishes. Fla. Dep. Nat. Resour., Mar. Res. Lab., Leafl. Ser. Vol. IV, Pt. 1, No. 23, 14 p.

HOUDE, E. D., AND L. J. SWANSON, JR.
1975. Description of eggs and larvae of yellowfin menhaden, *Brevoortia smithi*. Fish. Bull., U.S. 73:660-673.

JONES, P. W., F. D. MARTIN, AND J. D. HARDY, JR.
1978. Development of fishes of the Mid-Atlantic Bight. Vol. 1, Acipenseridae through Ictaluridae. U.S. Fish Wildl. Serv., Biol. Serv. Program FWS/OBS-78/12, 314 p.

LEWIS, R. M., E. P. H. WILKENS, AND H. R. GORDY.
1972. A description of young Atlantic menhaden, *Brevoortia tyrannus*, in the White Oak River estuary, North Carolina. Fish. Bull., U.S. 70:115-118.

POWLES, H.
1977. Description of larval *Jenkinsia lamprotaenia* (Clupeidae, Dussumieriinae) and their distribution off Barbados, West Indies. Bull. Mar. Sci. 27:788-801.

RICHARDS, W. J., R. V. MILLER, AND E. D. HOUDE.
1974. Egg and larval development of the Atlantic thread herring, *Opisthonema oglinum*. Fish. Bull., U.S. 72:1123-1136.

SUTTKUS, R. D.
1956. Early life history of the largescale menhaden, *Brevoortia patronis*, in Louisiana. Trans. North Am. Wildl. Conf. 21:390-407.

TURNER, W. R.
1969. Life history of menhadens in the eastern Gulf of Mexico. Trans. Am. Fish. Soc. 98:216-224.

U.S. NATIONAL MARINE FISHERIES SERVICE.
1982. Fisheries of the United States, 1981. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Curr. Fish. Stat. 8200, 131 p.