# DESCRIPTION OF EGGS AND LARVAE OF YELLOWFIN MENHADEN. BREVOORTIA SMITHI

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#### ABSTRACT

Development of yellowfin menhaden, Brevoortia smithi, is described from eggs and larvae reared in the laboratory. Eggs were collected during November 1972 in Biscayne Bay, Florida. Eight embryos and 66 larvae and juveniles ranging from 3.7 to 36.2 mm standard length were used to describe development. Mean egg diameter was 1.27 mm, mean oil globule diameter was 0.15 mm, and mean yolk diameter was 1.07 mm. The perivitelline space averaged 16% of the egg diameter. Length at hatching was about 3.0 mm standard length. Larvae were fed on zooplankton and grew about 0.45 mm per day from the 4th until the 20th day after hatching at 26°C. Morphology, meristics, osteology, and pigmentation are described. Transformation from larvae to juveniles apparently was completed at 20 to 23 mm standard length. During transformation full complements of fin rays were developed, the dorsal fin moved forward, the gut shortened, and the anal fin moved forward. Yellowfin menhaden larvae have some characteristics that serve to distinguish them from larvae of other clupeid genera occupying the same geographic range, and also have some characters that may be helpful to distinguish them from other species in the genus Brevoortia.

The yellowfin menhaden, Brevoortia smithi Hidelbrand, is one of four species of Brevoortia that occur along the Atlantic and Gulf of Mexico coasts of the United States. The biology and systematics of yellowfin menhaden were discussed in detail by Hildebrand (1963) and most recently by Dahlberg (1970). Dahlberg reported that B. smithi occurs from North Carolina to Louisiana. Atlantic and Gulf of Mexico populations exist, which apparently are distinct, and the species is uncommon south of West Palm Beach on the Florida Atlantic coast and north of Tampa Bay on the Florida west coast. Although common in parts of its range, yellowfin menhaden are not abundant enough to contribute substantially to commercial menhaden catches (Dahlberg 1970). Reproducing populations apparently are confined to coastal areas of the United States, but Levi (1973) reported some juveniles from the Bahamas. Hybrids of B. smithi  $\times$  B. tyrannus on the Atlantic coast and B. smithi  $\times$  B. patronus on the Gulf coast commonly occur (Turner 1969; Dahlberg 1970).

Reintjes (1962) artificially fertilized eggs of vellowfin menhaden from Indian River, Fla. He presented a series of photographs and described developing embryos and yolk-sac larvae. Hybrid embryos and yolk-sac larvae of yellowfin menhaden and Gulf menhaden, B. patronus, were produced artificially (Hettler 1968), and photographs of these embryos and larvae were published. More recently, Hettler (1970a) reared some vellowfin menhaden larvae from artificially fertilized eggs to 14.9 mm. He illustrated larvae of 7.6 and 11.9 mm total length (TL). Despite the literature on yellowfin menhaden development, no complete series from egg through transformation of larvae to the juvenile stage is available, nor have detailed illustrations been published that would be helpful to distinguish yellowfin menhaden from other similar clupeid larvae. We have reared yellowfin menhaden from naturally spawned planktonic eggs to advanced juveniles and we describe development of these stages in this paper.

Eggs and larvae of other Brevoortia species have been described, but only those of the Atlantic menhaden, Brevoortia tyrannus, are well known. Mansueti and Hardy (1967) have reviewed published information on Atlantic menhaden development. Suttkus (1956) described larvae of Gulf menhaden 18.9 mm and longer, but smaller specimens are undescribed. The eggs and larvae of finescale menhaden, Brevoortia gunteri, have not

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been described. DeCiechomski (1968) has discussed occurrence and photographed eggs and yolk-sac larvae of *Brevoortia aurea* from Argentina.

Using our rearing techniques (Houde 1973b), it was relatively simple to rear yellowfin menhaden from eggs to advanced juveniles. Presumably the other species, including Atlantic and Gulf menhaden, can be reared by similar methods if their eggs can be obtained. It should now be possible to conduct experiments under laboratory conditions, testing environmental factors on development of eggs and larvae of these important commercial species.

# **METHODS**

# **Collecting Eggs**

Naturally fertilized eggs from Biscayne Bay, Miami. Fla. were collected in 1-m diameter. 505- $\mu$ m mesh plankton nets suspended from the dock of the Rosenstiel School of Marine and Atmospheric Science on 3 November and 26 November 1972. Surface temperatures were 25.4° and 22.7°C on the respective collecting days and salinity was 32-33%. Yellowfin menhaden eggs were sorted by pipette from the other plankton organisms. The eggs that were sorted were known to be vellowfin menhaden because some of the same type had been hatched and the larvae reared during rearing trials in 1971. A total of 90 eggs on 3 November and 170 eggs on 26 November were placed in rectangular tanks of 38-liter capacity for rearing.

# **Rearing and Preserving Methods**

Rearing techniques were similar to those described by Houde (1973b) and Houde and Palko (1970). For the first 20 days of culture, temperature was controlled at  $26^{\circ} \pm 1.0^{\circ}$ C. Salinities ranged from 33.5 to  $37.0^{\circ}/_{\infty}$  and light was provided by fluorescent fixtures at an intensity of 2,500 lx. Zooplankton, consisting mostly of copepod nauplii and copepodites, collected in a 35- $\mu$ m mesh plankton net, was fed to larvae for the first 12 days; subsequently *Artemia salina* nauplii were fed in addition to zooplankton. A total of 8 embryos and 66 surviving larvae were preserved in 5% buffered Formalin<sup>4</sup> during the culture period to provide the series used to describe development. Specimens from 3.7 mm to 36.2 mm SL (standard length) were included in the developmental series (Table 1), but many juveniles continued to survive and were reared to lengths of 50-60 mm before experiments were terminated.

### **Meristics and Morphometrics**

Methods for counting and measuring are identical to those used by Houde et al. (1974) for *Harengula jaguana* Poey larvae.

Fin rays were counted in each of the developing fins of unstained larvae (Table 2). Myomeres were counted (Table 3) and examined in relation to the dorsal fin and anus. The following myomere counts were made:

- Total myomeres: all myomeres; does not include the triangular area preceding the first myoseptum.
- Preanus myomeres: number anterior to the anus.
- Postanus myomeres: number posterior to the anus.
- Predorsal myomeres: number anterior to the dorsal fin origin.
- Postdorsal-preanus myomeres: number between the posterior insertion of the dorsal fin and the anus.

The following measurements were made (Table 1): total length, standard length, preanus length, predorsal length, prepelvic length, head length, snout length, eye diameter, and body depth. All references to lengths of larvae in text are to standard length unless otherwise noted.

# Osteology

Sequence of ossification was determined from 10 specimens ranging from 5.2 to 25.3 mm SL. They were cleared with trypsin and stained with alizarin, using the method of Taylor (1967).

# DESCRIPTION

# Embryos

Eight fertilized eggs from the plankton collections were preserved. The embryos were approximately at the midstage of development at the time of collection. Eggs were spherical, the

<sup>&#</sup>x27;Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

 TABLE 1.—Specimens of laboratory-reared Brevoortia smithi used to describe development. Measurements in millimeters.

Total length	Standard length	Preanus length	Predorsal length	Prepelvic length	Head length	Snout length	Eye diameter	Body depth
4.0	3.7	3.1	_	_	0.46	0.08	0.22	
4.2	4.0	3.4	_		0.60	0.11	0.22	0.38
4.2	4.1	3.3			0.56	0.09	0.20	0.39
4.3	4.1	3.4			0.52	0.10	0.24	-
4.3 4.4	4.2 4.2	3.4 3.4			0.52	0.09	0.24	0.40
4.4	4.2	3.4		_	0.56 0.54	0.10 0.06	0.19 0.20	0.40 0.37
4.4	4.2	3.5			0.60	0.08	0.26	0.57
4.4	4.2	3.6	_		0.54	0.08	0.26	
4.5	4.3	3.5		_	0.56	0.07	0.22	0,39
4.6	4.4	3.5			0.55	0.08	0.22	0.34
4.6	4.4	3.6			0.56	0.08	0.20	0.40
4.6	4.4	3.6	-		0.57	0.08	0.23	0.34
4.6	4.4	3.6		_	0.60	0.08	0.22	0.38
4.6	4.4	3.6	_		0.61	0.10	0.21	0.42
4.7	4.5	3.7	—	—	0.56	0.06	0.24	
4.7 4.7	4.5 4.5	3.8	_	_	0.62	0.09	0.24	0.34
4.7 4.8	4.5 4.6	3.7 3.8			0.56	0.07	0.24	0.40 0.36
4.8	4.6	3.8			0.56 0.55	0.08 0.08	0.24 0.22	0.36
4.8	4.6	3.7	_	_	0.56	0.00	0.22	0.36
4.9	4.7	3.7	_		0.60	0,09	0.24	0.30
5.4	5.2	4.3		_	0.69	0.03	0.25	0.43
5.5	5.2	4.2			0.74	0.16	0.24	0.43
5.9	5.7	4.8		-	0.72	0.10	0.26	0.43
6.3	6.1	5.0		_	0.86	0.16	0.26	0.48
6.7	6.4	5.5	_		0.84	0.18	0.27	0.47
7.3	7.0	5.9	—		0.93	0.18	0.28	0.50
7.5	7.3	6.1	5.0		0.88	0.16	0.34	0.58
7.5	7.2	6.0	4.9	—	0.82	0.12	0.26	0.50
7.7	7.4	6.1	5.0	_	1.04	0.26	0.32	0.56
7.7	7.5	6.2	5.1		1.08	* 0.18	0.36	0.65
7.8 8.8	7.4 8.6	6.3 7.2	4.8 5.7	_	1.14 1.28	0.20 0.22	0.26 0.36	0.64 0.72
8.8	8.6	7.1	5.5		1.20	0.22	0.42	0.72
8.9	8.6	7.1	5.8		1.04	0.30	0.42	0.60
8.9	8.6	7.2	5.0	_	1.16	0.28	0.32	0.56
9.3	8.8	7.6	5.8		1.42	0.32	0.40	0.74
9.6	9.2	7.8	6.1		1.20	0.34	0.38	0.72
10.0	9.5	8.0	6.2	_	1.36	0.22	0.42	0.73
10.2	9.6	8.1	6.3	_	1.56	0.36	0.42	0.72
10.6	10.2	8.6	6.9		1.48	0.32	0.42	0.84
10.7	9.9	8.4	6.4		1.68	0.30	0.46	0.80
10.8	10.0	8.4	6.5		1.64	0.30	0.44	0.80
11.0	10.1	8.5	6.4	_	1.72	0.34	0.48	0.86
11.1	10.3	8.7	6.8		1.80	0.38	0.48 0.48	0.92
11.2 11.3	10.5 10.3	8.9 8.7	6.7 6.6		1.64 1.80	0.34 0.34	0.48	0.80 0.88
11.8	10.3	9.3	6.8	_	2.04	0.34	0.59	0.88
12.3	11.2	9.5	7.0	_	2.24	0.52	0.64	1.04
12.8	11.3	9.3	6.8	5.5	2.14	0.47	0.60	1.00
13.6	12.1	10.3	7.9		2.32	0.47	0.60	1.12
13.7	12.3	10.6	7.7	5.8	2.32	0.48	0.76	1.18
14.2	12.6	10.3	7.7	6.1	2.76	0.56	0.84	1.42
15.2	13.5	10.9	8.4	6.6	3.00	0.66	0.80	1.48
15.6	13.8	11.4	8.4	6.2	2.68	0.52	0.82	1.54
18.0	15.5	12.5	9.2	7.9	4.00	0.83	1.32	2.60
18.0	15.9	13.0	9.2	6.9	3.12	0.68	0.90	1,80
19.1	16.2	12.6	9.2	7.9	4.12 4.83	0.86	1.24	2.66
19.5	16.9	13.0	9.3	8.8 9.1	4.83 5.25	1.00	1.50	3.42
21.1	17.8	13.3	9.4	9.1 9.1	5.25	1.20	1.56	3.92
21.2 27.1	18.0 22.7	14.2 16.8	9.5 11.7	9.1 11,8	7.46	1.25 1.67	1.62 2.50	4.25 6.58
30.1	22.7	18.3	12.5	13.2	7.92	1.90	2.50	6.58 7.50
41.2	33.3	23.9	12.5	17.4	11.10	2.31	3.42	10.60
43.9	36.2	26.7	18.0	20.0	12.05	2.74	3.42	11.96

chorion was thin and unsculptured, and they had a single yellowish oil globule. Egg diameters ranged from 1.21 to 1.34 mm (mean = 1.27 mm), and oil globule diameters ranged from 0.12 to 0.17 mm

(mean = 0.15 mm). Yolk diameters ranged from 0.80 to 1.19 mm (mean = 1.07 mm) and were large relative to egg diameter. Our egg diameters and oil globule diameters are much like those reported

Standard length	Days after	Principal		urrent al rays	Dorsal	Anal	Pectoral	Pelvic
(mm)	hatching	caudal rays	Dorsal	Ventral	rays	rays	rays	rays
3.7-7.2	0-5		No eleme	nts present	on 29 specim	ens in this	size range.	
7.3	5		_	_	6	—	—	
7.4	7		_	_	7		—	—
7.4	5	—			4			_
7.5	9	2	—		7	_		
8.6	6	2	_	_	6			
8.6	5	2	_	_	6		—	
8.6	7	4	—	_	8			
8.6	15	3	—		12		—	
8.8	9	18			14	7	-	
9.2	7	3	_	—	9			
9.5	8	17	_	_	11		-	—
9.6	9	19			13	?		
9.9	11	19		_	15	10	—	_
10.0	10	19	—		14	—		_
10.1	16	19		<u> </u>	17	7		—
10.2	7	17	—	—	13		—	
10.3	13	19		_	16	12	_	_
10.3	11	19	_	-	14	8		-
10.5	11	19			15	9	—	
10.9	18	19			16	16	—	—
11.2	18	19	3	2	18	14	_	
11.3	15	19	2	1	18	18		
12.1	15	19	3	2	17	14		_
12.3	20	19	3	2	19	18		
12.6	29	19	4	3	18	20	—	6
13.5	24	19	5	3	18	19	—	6
13.8	24	19	4	3	19	19		6
15.5	43	19	7	6	20	21	13	7
15.9	-18	19	6	5	17	18	5	4
16.2	28	19	8	6	19	20	13	7
16.9	43	19	7	6	19	20	14	7
17.8	31	19	8	7	20	21	15	7
18.0	38	19	9	8	20	20	14	7
22.7	60	19	8	6	21	21	14	7
25.3	50	19	8	7	20	21	14	7
33.3	176	19	8	7	20	21	16	7
36.2	102	19	8	7	20	20	15	7

TABLE 2.-Some meristic characters of laboratory-reared specimens of Brevoortia smithi.

TABLE 3.-Distribution of myomeres relative to other body parts for Brevoortia smithi larvae.

Length	Preanus myomeres		Postanus myomeres		Predorsal myomeres			Postdorsal-preanus myomeres				
class (mm, SL)	Number of specimens	Range	Mean	Number of specimens	Range	Mean	Number of specimens	Range	Mean	Number of specimens	Range	Mean
3.7- 6.0	24	36-39	37.58	24	7-9	7.96						
6.1-8.0	8	36-38	37.25	8	7-9	8.12	4	27-29	28.00	4	5-6	5.25
8.1-10.0	10	35-37	36.20	10	8-11	9,70	10	24-28	26,20	10	4-5	4.60
10.1-12.0	8	33-37	35.38	8	10-13	10.75	8	22-25	24.00	8	3-5	4.00
12,1-14.0	5	33-35	33.40	5	11-13	12.20	5	21-22	21.40	5	3-4	3.40
14.1-16.0	2	30-33	31.50	2	13-15	14.00	2	19-21	20.00	2	2-4	3.00
16.1-18.0	4	29-31	29.75	4	15-16	15.50	4	18-22	19,50	4	2	2.00
>22.7	4	28-29	28.50	4	16-18	17.00	4	15-17	15.75	4	2-3	2.25

by Reintjes (1962) for yellowfin menhaden, but yolk diameters differ greatly. In his specimens the perivitelline space averaged more than 30% of the egg diameter, but in our specimens it averaged only 16%. The difference might be partly accounted for by the incubation salinities. Salinities at Indian River where Reintjes did his study were relatively low, ranging from 20.5 to  $27.2^{\circ}/\infty$ , while those in Biscayne Bay during our study exceeded  $32^{\circ}/\infty$  Hettler (1968) also reported narrow perivitelline spaces in hybrid eggs from B. smithi  $\times$  B. patronus that he artificially fertilized at the collection site where salinities were  $33-34^{\circ/\circ\circ}$ . Previtelline spaces in his embryos ranged from 7 to 17% of the egg diameters, and he attributed the narrow spaces to possible effects of high salinity. Yellowfin menhaden eggs have been collected by us from Biscayne Bay on many occasions in 1971 to 1973, and they always are characterized by a relatively narrow perivitelline space, which is unusual for clupeid species that spawn in South Florida marine waters.

Developing embryos resembled those described and photographically illustrated by Reintjes (1962). On our preserved specimens, tiny melanophores were present only on the dorsal surface of the developing embryo. The yolk mass was segmented, but this was observed with difficulty in preserved material. No pigment was observed on the yolk sac or oil globule of our preserved eggs.

Spawning by yellowfin menhaden in Biscayne Bay occurred at least between November and February. Spawning by this species has not been reported previously in Biscayne Bay, but eggs were common during 1971-73. We do not know the time of day at which spawning took place or the total incubation time at 22° to 26°C. Hettler (1970b) collected planktonic eggs of yellowfin menhaden in the Indian River and observed that they spawned at dusk. Reintjes (1962) reported hatching in 46 h at 19°C. Since we have collected embryos only in a single stage of development when temperatures were above 22°C, incubation time might be 24 h or less at these temperatures. Eggs were collected between 0900 and 1400 h; hatching in our aquaria was complete before 2400 h.

### Description of Larvae

#### Body Shape and Growth

Larvae were about 3.0 mm SL at hatching. They averaged 4.2 mm SL at 20 h after hatching (Figure 2A) when the body axis had straightened. During the first 2 days after hatching they were similar to yellowfin menhaden larvae described by Reintjes (1962). Larvae resemble those of other clupeid fishes. They are elongate, rod-shaped larvae after the yolk has been absorbed. At transformation they become deeper bodied and more laterally compressed. Proportional measurements of larvae in relation to standard length are summarized in Table 4.

Most larvae did not grow in length from the 1st until the 4th day after hatching at 26°C. Growth was rapid from the 4th until the 10th day (Figure 1), averaging about 0.80 mm/day. Growth was slower and more variable on subsequent days, but averaged about 0.45 mm/day from the 4th until the 20th day after hatching. Our 36.2-mm specimen was preserved 102 days after hatching,



FIGURE 1.-Growth of laboratory-reared larvae of Brevoortia smithi.

but growth rate of juveniles was almost certainly lower than might be expected under better feeding conditions because we did not maintain a careful feeding schedule after larvae transformed to the juvenile stage. Several juveniles from 50 to 60 mm were preserved when the experiments were terminated at 235 days after hatching. At 20°C, Hettler (1970a) reported growth rates of about 0.27 mm/day for yellowfin menhaden larvae that he reared for 27 days. The four smallest larvae that we preserved on the 4th and 5th days after hatching were smaller than larvae preserved on previous days (Figure 1). It is probable that those larvae had not begun to feed and that they were starving at the time of preservation.

#### Yolk Absorption and Gut Differentiation

The yolk sac is broadly ellipsoid in newly hatched larvae with the oil globule located ventrally and just posterior to the middle of the yolk mass (Figure 2A; see also Reintjes 1962). The yolk was nearly absorbed in specimens preserved 1 day after hatching (Figure 2B). All visible yolk remains, including the oil globule, had disappeared by 60 h after hatching at 26°C. Many larvae were observed to begin feeding before all of the yolk had been absorbed. At that time the gut was a straight tube, but within 24 h (at about 5.0 to 5.5 mm SL) it had developed into distinct fore and hind sections, the latter characterized by the bands of muscle common to all clupeid larvae.

#### **Preanus Length**

Preanus length averaged 82 to 84% SL from hatching until larvae were 15.0 mm SL (Table 4).

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TABLE 4Summary of the measurements of various body parts of Brevoortia smithi larvae and juveniles in
relation to standard length. Tabulated measurements are means for measurements from 1-mm length classes.

Length class (mm, SL)	Number of specimens	Preanus length:SL	Predorsal length:SL	Prepelvic length:SL	Body depth:SL	Head length:SL	Snout length:SL	Eye diam- eter:SL
3.1- 4.0	2	0.84			0.09	0.14	0.02	0.06
4.1- 5.0	20	0.82		_	0.09	0.13	0.02	0.05
5.1- 6.0	3	0.82	—		0.08	0.13	0.02	0.05
6.1-7.0	3	0.84	_		0.08	0.14	0.03	0.04
7.1- 8.0	5	0.84	0.67		0.08	0.13	0.03	0.04
8.1- 9.0	5	0.84	0.66	_	0.08	0.15	0.03	0.04
9.1-10.0	5	0.84	0.65		0.08	0.15	0.03	0.04
10.1-11.0	6	0.84	0.64	~	0.08	0.17	0.03	0.05
11.1-12.0	2	0.84	0.62	0.49	0.09	0.20	0.04	0.06
12.1-13.0	3	0.84	0.63	0.47	0.10	0.20	0.04	0.06
13.1-14.0	2	0.82	0.62	0.47	0.11	0.21	0.04	0.06
15.1-16.0	2	0.81	0.59	0.47	0.14	0.23	0,05	0.07
16.1-17.0	2	0.77	0.56	0.50	0.18	0.27	0.06	0.08
17.1-18.0	2	0.77	0.53	0.51	0.23	0.29	0.07	0.09
22.7	1	0.74	0.52	0.52	0.29	0.33	0.07	0.11
25.3	1	0.72	0.49	0.52	0.30	0.31	0.08	0.10
33,3	1	0.72	0.47	0.52	0.32	0.33	0.07	0.10
36.2	1	0.73	0.49	0.55	0.33	0.33	0.08	0.09



FIGURE 2.-4.2-mm SL (20 h posthatching) and 4.6-mm SL (41 h posthatching) larvae of Brevoortia smithi.

As the gut shortened during transformation, preanus length was reduced to 77% SL at 16.0 to 18.0 mm and averaged 72 to 74% for juveniles 22.7 mm and longer.

#### Head Length

Head length averaged 13 to 14% SL for larvae from 3.0 to 8.0 mm (Table 4). It then increased gradually to 29% at 18.0 mm and stabilized at 31 to 33% SL for juvenile specimens. Hildebrand (1963) and Dahlberg (1970) recorded head lengths ranging from 29 to 32.5% SL for large juvenile and adult yellowfin menhaden.

#### Eye Diameter

Eye diameter averaged 6% SL on newly hatched larvae but gradually decreased to 4% SL at about 6.0 mm and was stable until larvae grew to 10.0 mm (Table 4). Eye diameter then increased to 9% SL at 18.0 mm and averaged 9 to 11% SL for juveniles 22.7 to 36.2 mm. A relative decrease in eye diameter must occur in older juveniles because Hildebrand (1963) reported eye diameters ranging from 6.1 to 7.5% SL for specimens 91 mm and longer.

# Snout Length

Snout length increased gradually throughout development. It averaged 2% SL at hatching and increased to 7 to 8% SL in our juveniles (Table 4). Snout lengths of large juvenile and adult yellowfin menhaden range from 6.8 to 8.0% SL (Hildebrand 1963).

### Body Depth

Body depth, measured at the pectoral symphysis, averaged 8 to 9% SL from hatching until larvae were 12.0 mm (Table 4). A rapid increase in body depth then occurred; it was 23% SL at 18.0 mm and apparently was still increasing in juvenile specimens 22.7 mm and longer. Our 36.2-mm specimen had a body depth of 33% SL. Hildebrand (1963) did not measure body depth by the same method that we used, but he noted that yellowfin menhaden juveniles are deep bodied, more so than adults of this species.

#### Predorsal Length

Predorsal lengths were measured on larvae that had dorsal fin rays developing. No dorsal fin development was observed on any specimens less than 7.3 mm. Predorsal length decreased gradually from 67 to 62% SL for larvae from 7.3 to 14.0 mm and then decreased more rapidly for larger specimens (Table 4). It was 52% SL for our 22.7mm specimen and ranged from 47 to 49% SL for larger individuals. The decrease in predorsal length from 67 to 62% for 7.3- to 14.0-mm larvae may be partly due to measuring predorsal length on specimens with incompletely developed dorsal fins. The marked decrease in predorsal length on larger larvae resulted from forward movement of the dorsal fin as larvae began to transform to the juvenile stage.

### Prepelvic Length

Prepelvic lengths were measured on larvae that had pelvic fin buds or fins. From 11.1 to 16.0 mm, prepelvic lengths ranged from 47 to 49% SL (Table 4). In larger specimens, prepelvic lengths increased to 51% SL at 18.0 mm and to about 52% SL for 22.7- to 33.3-mm individuals. Our 36.2-mm specimen had a prepelvic length of 55% SL. Pelvic fins moved posteriorly during growth of yellowfin menhaden larvae, causing the observed increase in prepelvic length.

# Meristics

### Myomeres

The number of myomeres in fishes corresponds approximately to the number of vertebrae. Dahlberg (1970) reported 43 to 46 vertebrae (mean = 45) for juvenile and adult *B. smithi*. Myomeres can be counted on larvae before development of vertebrae and are a valuable meristic character. Total numbers of myomeres in our specimens ranged from 45 to 47 on the 63 individuals for which accurate counts were obtained. There was no correlation between the number of myomeres and standard length, indicating that the full complement was present at hatching. The frequencies of occurrence were as follows:

Number of myomeres	45	46	47
Frequency	26	32	5

The mean number of myomeres was 45.67 ( $S_{\overline{x}} = 0.1109$ ).

The distribution of myomeres in relation to other body parts can be useful for identifying clupeid larvae (Ahlstrom 1968). We examined the distribution of myomeres for yellowfin menhaden larvae relative to the dorsal fin and anus (Table 3). Preanus myomeres decreased from a mean number of 37.6 in newly hatched larvae to 28.5 in juveniles that were 22.7 mm and longer. Postanus myomeres increased accordingly, from 8.0 in newly hatched larvae to 17.0 for juveniles. Shortening of the gut during development caused the change in distribution of preanus and postanus myomeres. Predorsal myomeres decreased in numbers as larvae developed, because the dorsal fin moved forward. Larvae of 6.1 to 8.0 mm had a mean number of 28.0 predorsal myomeres, but juveniles had only 15.8. Numbers of predorsal myomeres were variable for specimens within any given size class (Table 3). The number of postdorsal-preanus myomeres decreased as larvae grew. Larvae 6.1 to 8.0 mm had a mean number of 5.3 postdorsal-preanus myomeres, but advanced larvae and juveniles always had 4 or fewer (usually 2 or 3). Larvae of *Opisthonema oglinum* and *Harengula jaguana* always had 5 or more postdorsal-preanus myomeres during all developmental stages (Richards et al. 1974; Houde et al. 1974).

#### Fin Development

A finfold surrounded the trunk and caudal area of newly hatched yellowfin menhaden larvae. Some parts of it remained along the ventral body margin until larvae were approximately 16.0 mm. Pectoral fin buds were already present when larvae hatched (Figure 2A), but the pelvic and median fins were not formed. Rays first appeared in fins in the following sequence: dorsal, caudal, anal, pelvics, and pectorals. Because rays first develop as cartilaginous structures, the size at which full complements were present was not necessarily the size at which all rays were ossified (Tables 2, 5). Although the beginning and completion of fin ray development were best correlated with length of larvae, age was also a factor, especially for anal fin development (Table 2).

Median fins had full complements of rays when larvae were 17.0 mm (Table 5). Dorsal rays first appeared at 7.3 mm, although an opaque area was present in the dorsal finfold, near the future dorsal fin, in some larvae as small as 6.4 mm. Full complements of 20 or 21 dorsal rays usually were attained when larvae were 15.5 to 17.0 mm. Principal caudal rays first appeared at 7.5 to 8.6 mm and the full complement of 19 principal rays was present when larvae were 9.6 to 10.3 mm. The notochord began to flex while principal caudal rays and other caudal fin structures were developing. Procurrent caudal rays began to develop at 11.2 mm, and full complements of 8 or 9 dorsal and 6 or 7 ventral rays were present at 16.2 to 17.8 mm. Anal rays first developed at 8.8 to 10.3 mm. A full complement of 20 or 21 rays was present on all larvae 16.2 mm or longer, although one specimen

only 12.6 mm had 20 anal rays. Hildebrand (1963) and Miller and Jorgenson (1973) reported from 21 to 24 anal rays in yellowfin menhaden specimens longer than 72 mm that they examined. We examined six juveniles from our rearing experiment that were 40-50 mm in length. Two of these specimens had 22 anal rays, two had 21 rays, and two had 20 rays.

Rays in paired fins began to develop later than in median fins. Pectoral fins without rays were present soon after hatching, but no rays developed until larvae had attained approximately 15.5 mm. A full complement of 14 to 16 pectoral rays was present on larvae 16.9 mm and longer. Pelvic fins appeared as tiny buds when larvae were 10.9 to 11.3 mm, but rays did not develop until larvae were about 13.0 mm. A full complement of 7 pelvic rays was attained at 15.5 to 16.2 mm.

### Scales and Scutes

Scales and ventral scutes were observed in specimens 17.8 mm and longer. Scales first developed anterior to the dorsal fin and in the region of the caudal peduncle. Specimens 22.7 mm or longer were fully scaled. Ventral scutes first developed anterior to the pelvic fins when larvae were 16.9 mm. Full complements of 30 to 32 (18 to 20 anterior to the pelvic fins and 11 to 13 posterior to the pelvic fins) were present on specimens 22.7 mm and longer. These counts are the same as those given for adult *B. smithi* by Dahlberg (1970).

# Osteology

Ten specimens of yellowfin menhaden were cleared and stained to determine sequence of development of skeletal structures. Ossification was similar to that described for larvae of Atlantic thread herring (Richards et al. 1974) and of scaled sardine (Houde et al. 1974). Consequently,

TABLE 5Summary of fin develo	opment sequence in	n larvae of .	Brevoortia smithi
TABLE 0Dummary of his develo	spinene sequence n	II IAL VAC UL .	DICCOULCIU SHEELICE.

		Standa			
Fin	Buds first appear	Rays first appear	Full complement of rays	Number of rays in fully developed fin	
Dorsal Caudal:		7.3	15.5 to~17.0	19 to 21	
Principal		7.5 to 8.6	9.6 to 10.3	19	
Procurrent	—	11.2	16.2 to 17.8	8 or 9 dorsal 6 or 7 ventral	
Anal		8.8 to 10.3	12.6 to 16.2	20 or 21	
Pelvic	10.9 to 11.3	~12.6	15.5 to 16.2	7	
Pectoral	<4.0	∼15.5 mm	16.9	14 to 16	

Rays were present at the tabulated lengths, but not necessarily ossified at those sizes.

osteology of yellowfin menhaden larvae is treated rather briefly in this paper. Ossification of most structures occurred at a smaller size in yellowfin menhaden than in either Atlantic thread herring or scaled sardines, but the sequence of development was similar in all of the species.

No bones were ossified in our 5.2-mm specimen, but the cleithra were lightly stained in 6.1- and 7.2-mm specimens. Cleithra were well stained in a 7.4-mm specimen, but no other bones were ossified. Slight ossification of the maxillaries and dentaries, in addition to the cleithra, was observed in our 8.6-mm larva. At 10.5 mm, the caudal fin complex began to ossify, cranial bones were lightly stained, and 8 maxillary and 3 dentary teeth were present. Vertebral centra were beginning to stain at 12.3 mm; neural and hemal arches were developing, but were unstained. Dorsal fin rays were ossifying at 12.3 mm. Also, cranial bones were ossifying, the hyoid apparatus was stained, 11 teeth were present on the maxillaries, and 4 were present on the dentaries. At 16.2 mm, most of the major skeletal structures were at least partly ossified. Rays in median and paired fins were stained as were neural and hemal spines along the vertebral column. Premaxillaries and posterior supramaxillaries were ossified in this specimen. At 18.0 mm, the degree of stain uptake increased in most bones. Also, ribs were stained, anterior supramaxillaries were stained, and 16 maxillary teeth were present, but the dentary bore no teeth. Ossification was complete in our 25.3-mm specimen. A total of 25 maxillary teeth but no dentary teeth were present. Dentary teeth are a transient larval character in B. smithi. One large, erect tooth was present on the basihval of our 18.0-mm specimen, and two were present on the 25.3-mm specimen. Basihyal teeth also were reported from Atlantic thread herring and scaled sardine larvae (Richards et al. 1974; Houde et al. 1974).

The caudal fin complex of yellowfin menhaden developed much like that of scaled sardine, and we give a brief description here, using the terminology of Houde et al. (1974) in their description of scaled sardine. Some cartilaginous, principal caudal rays developed in specimens as small as 7.5 mm. Flexure of the notochord and appearance of cartilaginous hypural plate elements occurred at about 8.5 to 9.0 mm. Our 10.5-mm specimen had stain uptake in the proximal parts of the 19 principal caudal rays, and the first uroneural was slightly stained. Hypural elements were present

but unstained. At 12.3 mm, the 19 principal caudal rays were fully stained, the second ural vertebra was stained as were the first and second uroneurals, and the parhypural was lightly stained. The hypurals were present but unstained as were two epural bones. Ossification was progressing in our 16.2-mm specimen. Both the first and second ural vertebrae were stained, the six hypurals were stained, the parhypural was well stained, and all three uroneurals were now stained. In addition to the 19 principal caudal rays, 8 dorsal procurrent caudal rays and 6 ventral procurrent caudal rays were stained. Two epurals were present on this specimen but were unstained. At 18.0 mm, all of the bones in the caudal fin area were at least partly ossified. The two epurals were now slightly stained, and 9 dorsal plus 8 ventral procurrent caudal rays were present and stained. The 25.3-mm specimen had all caudal fin bones ossified. The two epurals were well stained on this specimen, these bones being the last to ossify in the caudal fin complex.

# Pigmentation

Melanophore distribution on yellowfin menhaden larvae is similar to other clupeid larvae, but there are some distinctive characteristics which may serve to distinguish them from other clupeid larvae with which they can occur. Melanophores were contracted on some specimens and expanded on others, accounting for some of the apparent variability among individuals. Our illustrated specimens (Figures 2-5) have pigment that is typical of most specimens of those lengths.

# Head Region

Newly hatched yellowfin menhaden larvae have several tiny melanophores on the snout and a few over the brain. Within 1 day after hatching those melanophores have migrated or disappeared, because no pigment is present on the heads until larvae attain about 9.0 mm. The eyes became pigmented at about 4.5 mm, at 1 day after hatching. Typical pigmentation on the pectoral symphysis and over the heart developed at 4.5 to 6.0 mm. One or two melanophores appeared on the pectoral symphysis after yolk absorption when larvae were 4.5 to 5.0 mm. Those melanophores developed into two distinct pairs by 7.0 mm. Either one or two melanophores developed over the heart at about 6.0 mm. A single melanophore occurred at the



FIGURE 3.-7.0-mm SL (4 days posthatching) and 8.6-mm SL (6 days posthatching) larvae of Brevoortia smithi.



FIGURE 4.-12.1-mm SL (15 days posthatching), 15.9-mm SL (18 days posthatching), and 17.8-mm SL (31 days posthatching) larvae of Brevoortia smithi.



FIGURE 5.-22.7-mm SL (60 days posthatching) juvenile of Brevoortia smithi.

pectoral fin base in some larvae as small as 4.5 mm and was present in all larvae at 7.0 mm. The pigment pattern associated with the pectoral symphysis, heart area, and pectoral fin base was retained until larvae were about 16.5 mm.

At 9.0 mm, from one to three stellate melanophores had developed internally and could be seen through the otic capsules. A single, stellate melanophore frequently was present over the hindbrain at 10.0 mm, and some specimens had a small melanophore just posterior to and dorsal to the eye at that length. At about 12.0 mm, the pigmentation on the head began to increase substantially. Melanophores appeared on both jaws, on the side of the head, and over both midbrain and hindbrain regions. The number of melanophores increased as larvae grew, and numerous stellate melanophores were present on the heads of the larvae at 16.5 mm. Melanophores were especially concentrated on the jaws and over the brain in larvae larger than 16.5 mm.

#### Gut and Trunk Region

Newly hatched yellowfin menhaden had a few tiny melanophores on the dorsal surface of the trunk along the forebody. Within 12 h of hatching, these melanophores apparently migrated ventrally because they disappeared on the dorsal surface, but a series of malanophores was developing along the gut region of larvae.

Paired series of melanophores along the gut margin, which are typical of clupeid larvae, were present on yellowfin menhaden larvae of 4.5 mm and longer. Distinct pairs, numbering from 8 to 16, developed along the dorsolateral margin of the foregut and less distinct pairs, numbering 9 to 14, occurred along the ventral margin of the hindgut. These series were clearly visible until larvae were about 17.0 mm; they were not present on specimens longer than 18.0 mm. From one to three stellate melanophores usually occurred near the anus along the dorsal surface of the gut on larvae longer than 4.5 mm. These were continuous with an internal series of melanophores that were visible over the hindgut on most specimens longer than 8.5 mm. The number in this series increased from 6 to about 17 at 10.5 mm. Three or four melanophores were associated with the developing swim bladder in 10.0- to 12.0-mm larvae. A second internal series of melanophores was associated with developing vertebrae, but these were too indistinct to count accurately.

Pigment developed along the sides of the trunk of some yellowfin menhaden as small as 5.2 mm. From 1 to 3 stellate melanophores were present on some larvae between 5.5 and 7.0 mm, and this number usually increased to as many as 10 for 7.0to 10.0-mm larvae. Some larvae up to 8.6 mm had no lateral pigment on the trunk, but most specimens, when examined closely, were observed to have these melanophores. The number of lateral melanophores increased greatly when larvae were between 10.0 and 12.0 mm; some specimens of those lengths had as many as 25 lateral melanophores. When larvae were 14.0 mm or longer, these melanophores became very numerous, and most were located above the lateral midline. A paired series of melanophores developed along the dorsal midline, both anterior and posterior to the dorsal fin, on specimens longer than 16.5 mm.

There are melanophores associated with the developing fins. From 1 to 3 stellate melanophores

were present at the dorsal fin base of 9.5- to 11.0mm larvae. They numbered from 3 to 8 at about 14.0 mm and then as many as 15 at 18.0 mm. Two or three stellate melanophores were present at the anal fin base on 11.0- to 12.0-mm larvae; these numbers increased rapidly to 11 or 12 at 18.0 mm. Numbers of melanophores at the dorsal and anal fin bases were variable among individuals of the same length. A single stellate melanophore developed at the pelvic fin base on specimens as small as 12.3 mm. Some tiny melanophores began to occur in the pectoral, dorsal, and anal fins at 16.2 mm.

# **Caudal Region**

Newly hatched larvae have melanophores on both the dorsal and ventral sides of the notochord tip. Numbers on the dorsal tip range from one to two, while those on the ventral tip range from one to three. In addition, one or two melanophores are located along the ventral midline posterior to the anus. Pigment along the ventral tip of the notochord began to migrate into the caudal finfold at 7.0 to 7.2 mm. This pigment was associated with developing caudal rays in larger larvae. Pigment in the caudal fin increased rapidly when larvae exceeded 10.0 mm. Internal melanophores were first present in the hypural plate region on larvae 10.3 mm and longer. Larvae longer than 16.5 mm invariably had many melanophores among the rays of the caudal fin.

# Transformation

Transformation of larvae to juveniles apparently was complete between 20 and 23 mm. Unfortunately, we preserved no specimens that were between 18.0 and 22.7 mm. However, our specimens of 17.8 and 18.0 mm were not completely transformed while the 22.7-mm specimen had acquired nearly all of the juvenile characteristics. Larvae began transforming at about 14.0 mm. At that time, proportional measurements relating preanal length, predorsal length, body depth, head length, snout length, and eye diameter to standard length (Table 4) began to change rapidly. Except for body depth, which continued to increase, the proportional measurements became nearly constant at 22.7 mm. The distribution of myomeres relative to other body parts became stable for specimens 22.7 to 36.2 mm (Table 3). Fin rays were completely ossified at 18.0 mm (Table 5), but the

epural bones of the caudal skeleton were still unossified at that size. Although some scales were present on our 17.8- and 18.0-mm specimens, the 22.7-mm specimen was the smallest that was fully scaled. The slender, rodlike shape of the larva was replaced by the deeper bodied, laterally compressed form of the juvenile between 17.8 and 22.7 mm. The silvery coloration of juveniles was present on our specimens from 22.7 to 36.2 mm. Transformation included the following features: forward movement of the dorsal fin: shortening of the gut; forward movement of the anal fin; and relative increases in head length, snout length, eye diameter, and body depth. The same features were noted for transforming larvae of Atlantic thread herring (Richards et al. 1974) and scaled sardine (Houde et al. 1974).

# COMPARISONS

Eggs and larvae of the genus Brevoortia almost always can be distinguished from those of other clupeid genera that spawn in marine waters of the south Florida and Gulf of Mexico region. Members of the genera Alosa and Dorosoma have demersal eggs, unlike those of Brevoortia which are pelagic. Dorosoma spawns in fresh waters and Alosa in fresh or nearly fresh waters, so that occurrence of their larvae with those of Brevoortia is unlikely. Larvae of Alosa spp. have more total myomeres than any species of Brevoortia, and the genera can be easily distinguished. Dwarf herrings (Jenkinsia spp.) might occur with B. smithi at the southern extreme of their range in Florida. Neither spawning habits nor eggs and larvae of Jenkinsia have been described, but the total myomeres of Jenkinsia did not exceed 42 (Miller and Jorgenson 1973), making it unlikely that larvae could be confused with Brevoortia which have higher myomere numbers (Brevoortia, 44-48). Since B. smithi may occur with either B. tyrannus or B. patronus and because hybrids are known (Dahlberg 1970), the specific identification of menhaden eggs and larvae from plankton collections is still in doubt where the species' ranges overlap.

Eggs of *B. smithi* are smaller than those of *Harengula jaguana* which range from 1.55 to 1.78 mm in diameter (Houde et al. 1974), and they cannot be confused with those of *Etrumeus teres* because eggs of that species have no oil globule. Our *B. smithi* eggs were similar to those of *Opisthonema oglinum* (Richards et al. 1974) and to those of western Atlantic Sardinella sp. (Simpson and Gonzales 1967; Matsuura 1971; Houde and Fore 1973), but their average diameter was greater than for those species. Our B. smithi eggs ranged from 1.21 to 1.34 mm in diameter (mean = 1.27 mm) while those of O. oglinum are 1.10 to 1.28 mm (mean = 1.19 mm) (Richards et al. 1974) and those of western Atlantic Sardinella sp. are 1.00 to 1.32 mm (mean = 1.12-1.18 mm) (Simpson and Gonzales 1967: Matsuura 1971: Houde and Fore 1973). Reintjes (1962) reported B. smithi eggs ranging from 1.15 to 1.48 mm, including both planktonic and artificially fertilized eggs. The eggs of O. oglinum would not usually occur with those of B. smithi because Opisthonema spawns during spring and summer (Fuss et al 1969; Houde 1973a; Richards et al. 1974), while members of the genus Brevoortia are winter spawners (e.g., Turner 1969; Dahlberg 1970) in waters of south Florida and the Gulf of Mexico. Sardinella eggs could conceivably occur with those of B. smithi, but Sardinella probably spawns farther offshore than does B. smithi. Eggs of B. tyrannus apparently are larger than those of B. smithi, the reported diameters ranging from 1.30 to 1.95 mm (Mansueti and Hardy 1967). Brevoortia patronus eggs usually are slightly smaller than B. smithi eggs, the diameters ranging from 1.04 to 1.30 mm (Houde and Fore 1973). Hybrid embryos from artificial fertilization of B. smithi  $\times$  B. patronus ranged from 1.05 to 1.18 mm (Hettler 1968).

Larvae of *Brevoortia* spp. have some distinctive characters that serve to distinguish them from other clupeid larvae with which they may occur. Newly hatched larvae of *B. smithi* have been photographed by Reintjes (1962), but these photographs fail to show distinguishing characters of larvae in that size range. Hettler (1970a) presented illustrations of 7.6- and 11.9-mm TL larvae of *B. smithi*, but only the 11.9-mm specimen has some characteristics illustrated that help to identify it as a *Brevoortia* sp.

Myomere numbers ranged from 45 to 47 in B. smithi, thus separating it from H. jaguana (42 or fewer) (Houde et al. 1974) and E. teres (48 or more) (Houde and Fore 1973). Total myomere counts of B. smithi overlap those of O. oglinum (45 to 49), Sardinella sp. (45 to 47) (Houde and Fore 1973), and the other species of Brevoortia. Numbers of postdorsal-preanus myomeres always were fewer than 5 in B. smithi larvae longer than 10 mm and never exceeded 6 in smaller larvae (usually 4 or 5). The other identified clupeid genera from this region, excepting *Etrumeus*, have 5 or more (usually 6 to 9) postdorsal-preanus myomeres in all length classes, thus serving to distinguish them from *Brevoortia* larvae.

Pigmentation of newly hatched Brevoortia larvae apparently differs from that of other clupeid genera in its details. Recently hatched B. smithi larvae have pigment on both the dorsal and ventral sides of the notochord tip (Figures 2A-3B), distinguishing them from other co-occurring clupeid genera, except for some specimens of Harengula (see Houde et al. 1974). Brevoortia tyrannus has pigmentation similar to B. smithi at the notochord tip (Mansueti and Hardy 1967), and we suspect that B. patronus also has this pigment characteristic based on our observations of Brevoortia larvae that were collected in the northern Gulf of Mexico, where B. patronus is known to spawn. Recently hatched larvae of O. oglinum, Sardinella sp., and E. teres have pigment only on the ventral side of the notochord tip.

Lateral pigmentation is present on *B. smithi* larvae as small as 5.2 mm-which is smaller than other clupeids found in their geographical range. At 10 to 12 mm, most of our *B. smithi* larvae had more than 5 melanophores on their sides, and some had as many as 25. No larvae of *Harengula*, *Opisthonema*, *Sardinella*, or *Etrumeus* that we have observed have had pigment on the sides until they were at least 15 mm in length. We do not know if *B. tyrannus* or *B. patronus* develop lateral pigmentation at sizes as small as *B. smithi*, but illustrations of *B. tyrannus* larvae (Mansueti and Hardy 1967) from 8 to 23 mm do not show any such pigment, nor is it mentioned in their text.

Size at transformation varies among clupeid species. Brevoortia smithi had completed transformation at about the same size as H. jaguana (Houde et al. 1974) and O. oglinum (Richards et al. 1974), at lengths from 20 to 24 mm. However, other species of Brevoortia apparently do not transform until they are of larger size. Brevoortia tyrannus exceeds 30 mm before having a typical juvenile form (Mansueti and Hardy 1967), and the observations and morphological data of Suttkus (1956) suggest that B. patronus does not transform until 28 mm or longer. It is possible that our tank-reared B. smithi transformed at smaller sizes than in nature, but the seemingly good growth rate and the selection of normal appearing larvae to describe development lead us to believe that B. smithi is transformed at approximately 22 mm.

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