

Abstract—Larval and juvenile development of finescale menhaden (*Brevoortia gunteri*) is described for the first time by using wild-caught individuals from Nueces Bay, Texas, and is compared with larval and juvenile development of co-occurring gulf menhaden (*B. patronus*). Meristics, morphometrics, and pigmentation patterns were examined as development proceeded. An illustrated series of finescale menhaden is presented to show changes that occurred during development. For finescale menhaden, transformation to the juvenile stage was completed by 17–19 mm standard length (SL). By contrast, transformation to the juvenile stage for gulf menhaden was not complete until 23–25 mm SL. Characteristics useful for separating larval and juvenile finescale menhaden from gulf menhaden included 1) the presence or absence of pigment at the base of the insertion of the pelvic fins; 2) the standard length at which medial predorsal pigment occurs; 3) differences in the number of dorsal fin ray elements; and, 4) the number of vertebrae.

Descriptions of larval, prejuvenile, and juvenile finescale menhaden (*Brevoortia gunteri*) (family Clupeidae), and comparisons to gulf menhaden (*B. patronus*)

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Finescale menhaden (*Brevoortia gunteri* Hildebrand), one of three recognized species of menhaden (Reintjes, 1969; Hettler, 1984) found in the Gulf of Mexico, occurs in the northern and western Gulf of Mexico, from Chandeleur Bay, Louisiana, to Campeche Bay, west of Punto Morros (McEachran and Fehhelm, 1998). Despite their common occurrence in coastal and estuarine waters along the Texas and Mexico coasts (Simmons, 1957; Hellier, 1962; Hoese, 1965; Whitehead, 1985; Castillo-Rivera and Kobelkowsky, 2000), their early development has not been described. Early development of gulf menhaden (*B. patronus* Goode), on the other hand, has been well described (Suttkus, 1956; Hettler, 1984; Ahrenholz, 1991).

In coastal waters of the western Gulf of Mexico, finescale menhaden are spatially and temporally sympatric with gulf menhaden (Castillo-Rivera et al., 1996). Gulf menhaden are found throughout the northern gulf from Florida Bay to Campeche Bay. Yellowfin menhaden (*B. smithi* Hildebrand) are found in the eastern gulf from the Mississippi River Delta to Cape Lookout, North Carolina, and co-occur with finescale menhaden only in its extreme western range (Dahlberg, 1970; Hoese and Moore, 1977). A large amount of hybrid introgression occurs between gulf and yellowfin menhaden, although finescale

hybrids (either finescale × gulf menhaden or finescale × yellowfin menhaden) have not been reported (Ahrenholz, 1991).

Both finescale and gulf menhaden are estuarine-dependent species inhabiting shallow nursery areas for their early development (Gunter, 1945; Shaw et al., 1985; Castillo-Rivera and Kobelkowsky, 2000). Gulf menhaden are intermittent or multiple spawners (Christmas and Waller, 1975; Lewis and Roithmayr, 1981), and adults move offshore in late summer and early fall. Spawning off the coast of Texas is protracted, and the spawning season begins at the end of August and continues through April (Shaw et al., 1985). Estuarine immigration of gulf menhaden ranging in size from 10 to 32 mm TL has been observed from late October through April (Copeland, 1965; Gallaway and Strawn, 1974; Allshouse, 1983). In Nueces Bay, the greatest densities of gulf menhaden larvae are seen from late February to early May, and the peak immigration of 19–26 mm TL individuals occurs from late April and early May (Newstead, 2003). Finescale menhaden spawn in estuarine or nearshore areas (Gunter, 1945; Simmons, 1957) and their spawning season has been reported from November to March (Ahrenholz, 1991). Hellier (1962) reported 25-mm-TL specimens taken from the Upper Laguna Madre

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on the lower Texas coast during February, and Gunter (1945), Simmons (1957), and Hoese (1965) have reported postlarval finescale menhaden from the middle and lower Texas coasts from January to May. Gulf menhaden have received considerable attention in fishery science because of their large population sizes and resulting ecological and economic importance in the northern Gulf of Mexico (Nelson and Ahrenholz, 1981; Smith, 1991), whereas finescale menhaden are less numerous and not directly sought by any recognized fishery (Ahrenholz, 1991). Our study describes for the first time the development of postflexion (late larval), prejuvenile, and juvenile finescale menhaden.

Materials and methods

A total of 170 wild-caught finescale menhaden larvae and juveniles were used to describe early development. All specimens came from ichthyoplankton collections in Nueces Bay, Texas (27.87°N, 97.51°W), during May and June 2003. Individuals were collected in the tidal channels of Nueces Delta with a side-mounted push net (60-cm ring net, 0.505-mm mesh). For comparison, 357 wild-caught gulf menhaden larvae and juveniles collected during May and June of 1999, 2000, and 2002 from two nearby stations outside the delta (less than 1.5 km away), in addition to the tidal channel collections of 2003, were also studied. All individuals were initially fixed in either 10% formalin or 95% ethanol and transferred to fresh 95% ethanol after 48 hours.

Pigment patterns were recorded and specimens of finescale menhaden were illustrated. Gulf menhaden were not illustrated because the figures in Hettler (1984) are adequate.

Morphometrics

Body measurements were made to the nearest 0.1 mm with an ocular micrometer fitted to a dissecting microscope. All individuals collected were postflexion, prejuvenile, or juvenile stage as defined in Leis and Rennis (1983), and standard length (SL) was measured as the distance from the tip of the snout along the midline to a vertical line through the posterior edge of the hypural plate. All lengths are SL unless otherwise noted. Definitions and other terms are as follows:

- BD = body depth; vertical depth at the pectoral symphysis.
- CP = caudal peduncle; horizontal distance from the posterior edge of the dorsal fin base to the posterior edge of the hypural plate.
- EYE = eye diameter; horizontal distance between the anterior and posterior edges of the fleshy orbit.
- PAL = preanal length; distance from the tip of the snout to the origin of the anal fin, measured along the midline.

Ratios of these four body proportion measurements in relation to SL were fitted by means of nonlinear least

squares regression techniques (SigmaPlot, version 5.0, SPSS Inc., Chicago, IL) in order to graphically illustrate any development differences between the two species. Increasing ratios (BD/SL, CP/SL, and EYE/SL) were described with an exponential rise-to-maximum equation:

$$y = a(1 - e^{-bx}),$$

whereas, the decreasing ratio of PAL/SL measurements were described with an exponential decay equation:

$$y = ae^{-bx}.$$

In both equations, y = body proportion ratio; x = SL; a = intercept; and b = SL specific exponential rate of change.

Meristics

Each specimen was examined to determine whether scale formation had been initiated, and a total count of ventral scutes for specimens in which they were sufficiently developed was obtained. A total of 37 finescale and 48 gulf menhaden from the 2003 collections were cleared and stained according to Potthoff (1984) and used for fin-ray and vertebrae counts. Because of the difficulty in accurately counting myomeres in transforming clupeids (Hettler, 1984; Ditty et al., 1994), we chose to count total vertebrae and use the number of postdorsal and preanal vertebrae instead of postdorsal and preanal myomeres as a potential diagnostic character. Fin-ray counts included dorsal, anal, and caudal fins (both principal and procurent rays).

Results

Morphological development

Finescale menhaden larvae were first collected at 9.7 mm and ranged to 22.5 mm as transforming juveniles (Fig. 1). Transformation from the larval to the juvenile form began around 14 mm and was completed by around 20 mm (Fig 2). Ratios of body depth, caudal peduncle, and eye diameter all increased in relation to standard length as larvae grew, whereas snout-to-anal length decreased (Table 1). The decrease in snout-to-anal length reflected the transformation from the elongate fusiform shape of the larvae to the laterally compressed deep-bodied shape of the juvenile. Scales began to form at around 15 mm on the caudal peduncle region and progressed forward along the ventral and lateral surfaces towards the dorsal surface. None of the individuals examined had the enlarged and fringed median scales preceding the dorsal fin, which are an adult characteristic of the genus *Brevoortia*. Ventral scutes also began forming around 15 mm, and the full complement of 27–31 scutes (McEachran and Fechhelm, 1998) was found by 19 mm.

Gulf menhaden ranged from 11.7 mm as larvae to 40.4 mm juveniles. For gulf menhaden, body depth,

Table 1

Proportional measurements in relation to standard length (SL) used to describe finescale menhaden (*Brevoortia gunteri*) larval development.

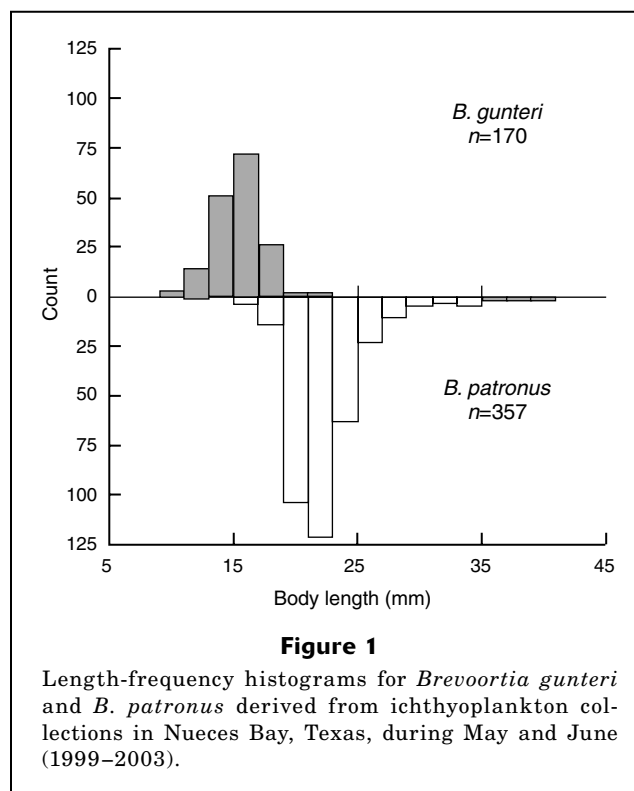
Length class (mm, SL)	Number of specimens	Body depth: SL	Preanal length: SL	Caudal peduncle: SL	Eye diameter: SL
<11.0	1	0.100	0.804	0.256	0.054
11.1–12.0	2	0.108	0.798	0.259	0.059
12.1–13.0	5	0.119	0.778	0.251	0.059
13.1–14.0	15	0.139	0.764	0.263	0.064
14.1–15.0	28	0.136	0.756	0.269	0.062
15.1–16.0	25	0.168	0.735	0.281	0.074
16.1–17.0	23	0.208	0.711	0.302	0.082
17.1–18.0	17	0.220	0.705	0.311	0.085
18.1–19.0	3	0.239	0.700	0.327	0.080
19.1–20.0	2	0.219	0.700	0.304	0.078
>20.1	1	0.318	0.690	0.304	0.093

caudal peduncle, and eye diameter ratios all similarly increased in relation to standard length as larvae grew, whereas snout-to-anal length decreased (Table 2). Scale initiation in gulf menhaden was not seen until 19 mm, and ventral scutes did not begin forming until around 18 mm. The full complement of scutes (28–32 scutes; McEachran and Fechhelm, 1998) was seen by around 25 mm. No enlarged median dorsal scales were noted from the gulf menhaden individuals examined.

With little overlap in the 15–20 mm size range (see Fig. 1) and a limited number of juvenile-size finescale menhaden (SL>20 mm), it was not possible to effectively separate finescale and gulf menhaden morphometrically on the basis of BD:SL, PAL:SL, CP:SL, and EYE:SL ratios (Fig 3). By 25 mm, proportional body measurements had become nearly constant for gulf menhaden whereas body measurements were still changing for finescale menhaden even though they appeared to be fully transformed. For a fish of given size, finescale menhaden typically had a greater body depth, a shorter preanal length, and a greater caudal peduncle length than gulf menhaden.

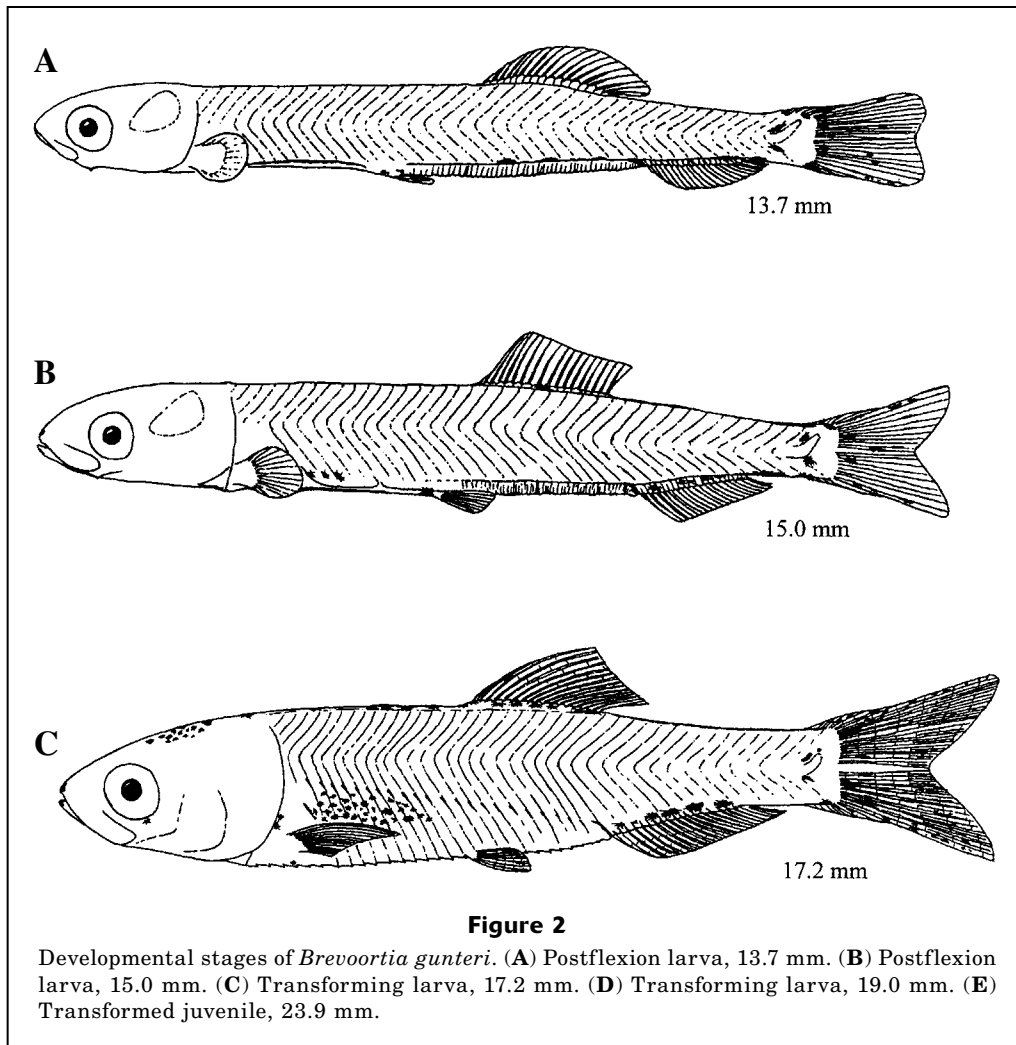
Meristic features

No recently hatched or preflexion finescale menhaden were examined and all postflexion individuals followed the fin development sequence identified for other clupeids (Houde et al., 1974; Hettler, 1984; Ditty et al., 1994). The caudal and dorsal fins are first to develop, followed by the pelvic fins, whereas the pectoral fins are the last to fully develop even though the pectorals are the first fins to form as nonrayed buds. Only vertebrae and dorsal-fin ray counts were useful in separating finescale and gulf menhaden, because most other meristics overlapped (Table 3). Finescale menhaden had fewer total vertebrae (=43 vs. 46) and fewer dorsal-fin rays (median

**Figure 1**

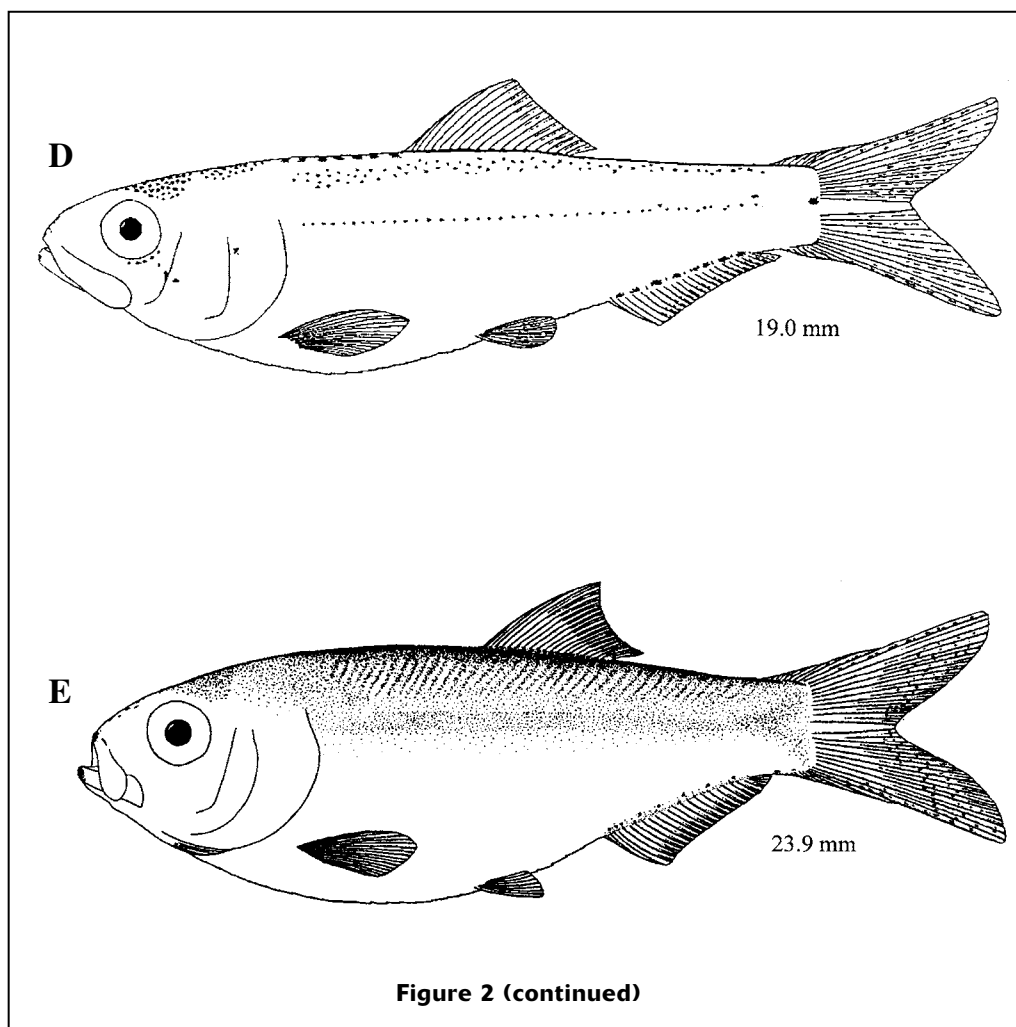
Length-frequency histograms for *Brevoortia gunteri* and *B. patronus* derived from ichthyoplankton collections in Nueces Bay, Texas, during May and June (1999–2003).

value=18 vs. 21) than gulf menhaden. Postdorsal and preanal vertebrae also showed a high degree of overlap between the two species (Table 3). The forward movement of the anal fin in relation to the dorsal fin was most evident in fully transformed gulf menhaden, and the number of postdorsal-preanal vertebrae decreased from 4 to –3. The relative placement of the anal fin also

**Table 2**

Proportional measurements relative to standard length (SL) used to describe gulf menhaden (*Brevoortia patronus*) larval development.

Length class (mm, SL)	Number of specimens	Body depth: SL	Preal anal length: SL	Caudal peduncle: SL	Eye diameter: SL
<14.0	1	0.086	0.829	0.229	0.061
14.1–15.0	1	0.119	0.786	0.238	0.061
15.1–16.0	3	0.136	0.764	0.261	0.063
16.1–17.0	4	0.136	0.764	0.261	0.063
17.1–18.0	5	0.144	0.749	0.257	0.065
18.1–19.0	13	0.169	0.733	0.265	0.067
19.1–20.0	26	0.183	0.725	0.274	0.074
20.1–21.0	22	0.176	0.735	0.271	0.068
21.1–22.0	17	0.236	0.719	0.282	0.084
22.1–24.0	9	0.286	0.709	0.298	0.095
24.1–26.0	2	0.337	0.730	0.313	0.103
26.1–29.0	11	0.352	0.730	0.299	0.098
29.1–32.0	4	0.356	0.740	0.308	0.100
>32.1	3	0.380	0.736	0.294	0.097

**Table 3**

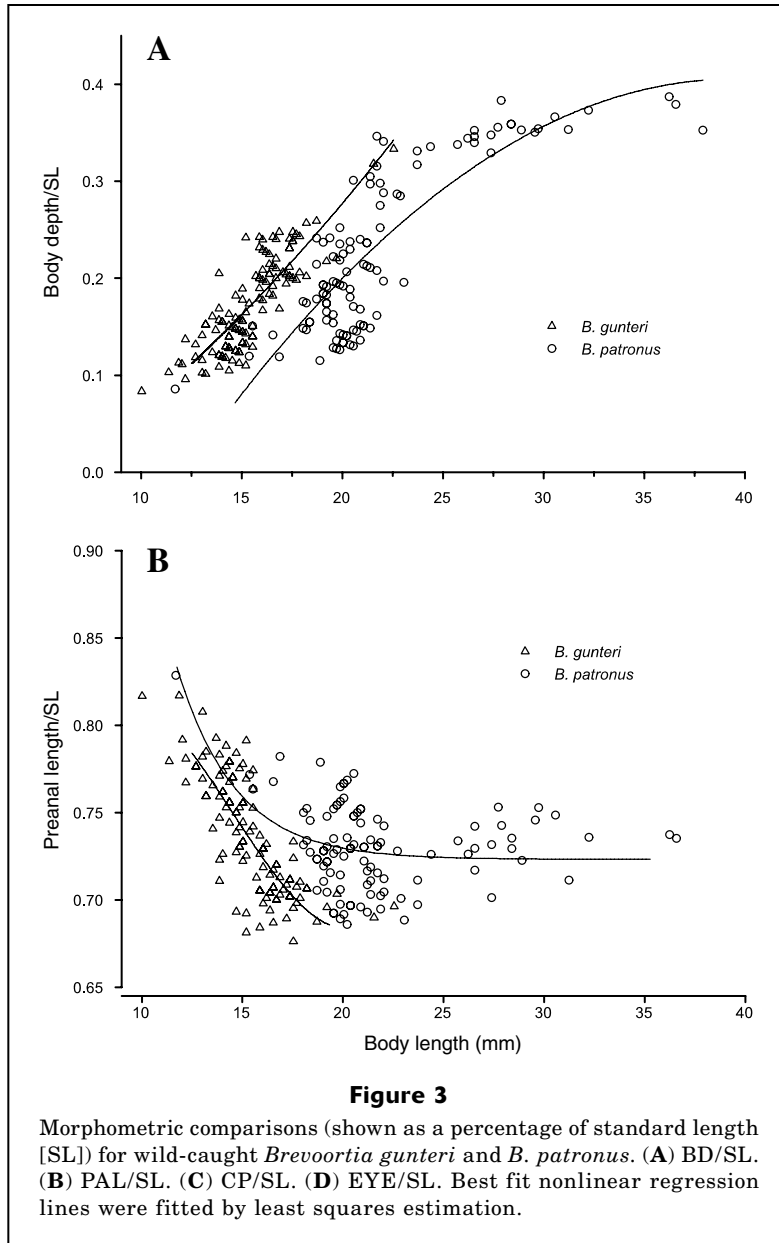
Meristics in finescale menhaden, *Brevoortia gunteri*, (37 specimens) and in gulf menhaden, *B. patronus*, (48 specimens). Median values are given in parentheses.

Meristic	<i>B. gunteri</i>	<i>B. patronus</i>	Number in full complement	
			<i>B. gunteri</i>	<i>B. patronus</i>
Caudal-fin rays				
Principal (dorsal)	10	10		10–11
(ventral)	9	9		9–10
Procurrent (dorsal)	7–9 (8)	8–9 (8)		8–9
(ventral)	7–8 (7)	5 ¹ –8 (7)		7–8
Dorsal-fin rays	17–20 (18)	16 ¹ –23 (21)	17–20	21–23
Anal-fin rays	18–24 (22)	20–23 (21)	20–25	18–22
Vertebrae	43–44 (43)	40 ¹ –46 (46)	42–44	45–46
Postdorsal and preanal vertebrae	0–3 (2)	–3 ² –4 (1)		2–4 ³

¹ *B. patronus* larva SL=11.7 mm.

² *B. patronus* fully transformed individual SL=40.4 mm.

³ Postdorsal and preanal myomere counts in larvae 10–15 mm SL (Ditty et al., 1994)



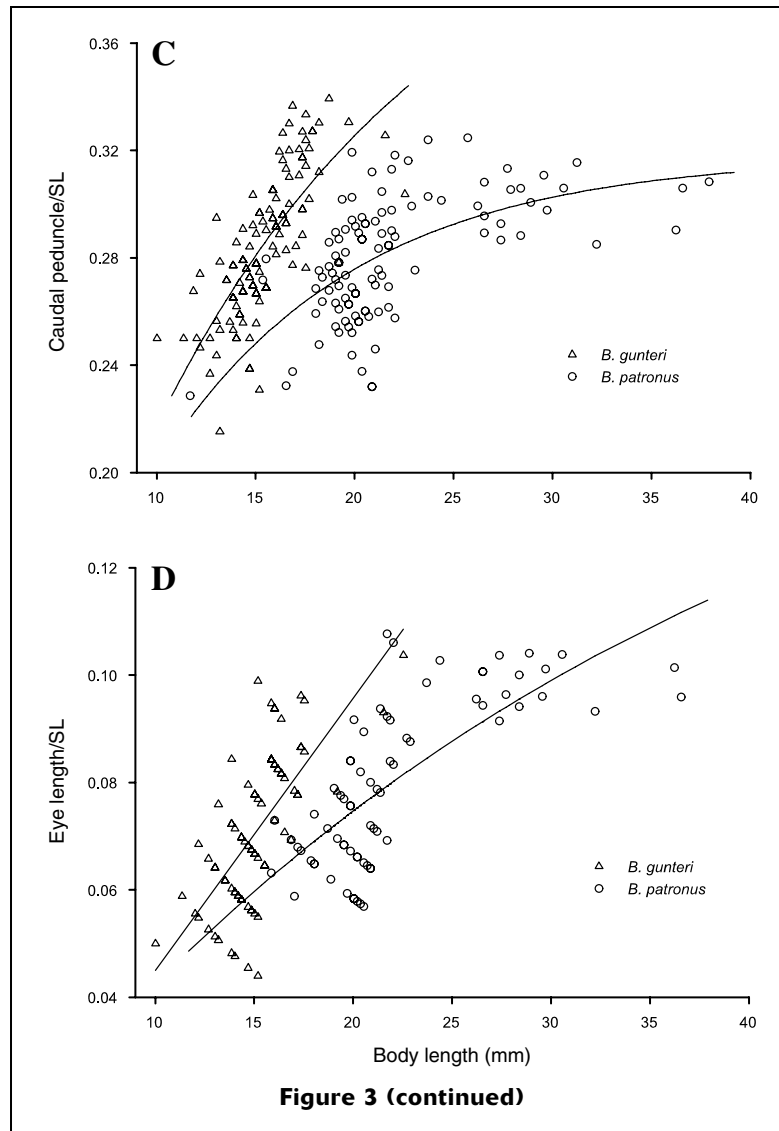
changed in finescale menhaden, although the number of postdorsal-preanal vertebrae only decreased from three to zero.

Pigmentation

Early pigmentation patterns in finescale menhaden (Fig. 2) were similar, but not identical, to the pigmentation described for gulf menhaden (Suttkus, 1956; Hettler, 1984). Both dorsal and ventral notochord tip pigment, which are diagnostic for the genus *Brevoortia* (Fig. 2), were found in all individuals examined. In specimens <14 mm, pigmentation was sparse and found primarily along the ventral margin of the caudal peduncle, the base of the anal fin, at the end of the gut near the vent,

and ventrally as two lines beginning at the pectoral fin bases below the foregut. Along the dorsal margin of the hindgut, 3–6 fine melanophores were usually present. At the base of the pelvic fins, 1–2 small, paired stellate melanophores were present. Additionally, all individuals had a medial melanophore along the isthmus (ventral midline anterior to the cleithrum) and most had an internal melanophore at the nape. Other pigment present in the smallest finescale larvae included a series of paired melanophores anterior to the dorsal fin base (seen in 26% of the larvae examined). This predorsal mid-line pigment series increased both in size and number as the larvae grew. The head was unpigmented.

By 16 mm, pigment increased along the dorsal surface of the hindgut, the base of the dorsal fin, and the



base of the anal fin (Fig. 2). The predorsal midline melanophores series was more prominent (51% of the individuals displayed this pigment pattern). Additional pigmentation included paired lateral melanophores near the dorsal region of the brain cavity, internal pigment above the notochord from the posterior margin of the base of the dorsal fin to the caudal fin, and internal pigment over the gas bladder. A large melanophore was also present above the base of the pectoral fin.

By 18 mm, the dorsal surface of the head became highly pigmented with up to 25 small melanophores. The snout, lower jaw, and pelvic fins were also pigmented by this size. The dorsal and ventral surfaces of the caudal peduncle, as well as the medial predorsal region became more densely pigmented. Outstanding features at this size included 2–9 ventrolateral melanophores in a series along the digestive tract level with the pectoral fins, and isthmus pigment was separated into two spots

in many individuals. By 20 mm, the head region was heavily pigmented and the mid-line predorsal pigment progressed fully to the head. Ventrolaterally, 10–30 melanophores forming a triangular pattern covered much of the digestive tract. New pigmentation features at this size included 1–3 small melanophores at the base of the eye and an internal series below the notochord from the base of the dorsal fin to the caudal fin. Pigmentation at the pelvic fin insertion was lost in some specimens, although it was still visible internally in all but one of the cleared and stained specimens. Isthmus pigmentation was also lost at this size.

Living juveniles (>20 mm) are silvery in color over most of the body. The head, back, and dorsal and caudal fins are all pigmented. In preservation, two dark, slash-like pigments spots were present on the posterior lateral body above and below the urostyle. In nearly all other aspects, juvenile finescape menhaden closely

resembled adults by this size. No humeral spots were noted in the two individuals examined.

Discussion

Finescale menhaden larvae resemble the larvae of other clupeids (Houde and Fore, 1973; Jones et al., 1978; McGowan and Berry, 1983; Hettler, 1984; Ditty et al., 1994) in having elongate, slender bodies, light pigmentation, and a small head lacking spines. They have a long, straight gut, often with striations along the hind-gut, posteriorly placed dorsal and anal fins, and the vent is always posterior to the dorsal fin base (Jones et al., 1978). Hettler (1984) discussed the separation of individual species of *Brevoortia*, and Ditty et al. (1994) presented a synopsis of characters to separate clupeid larvae (<15 mm) based on meristic, morphometrics, and pigmentation. Finescale menhaden have 43–44 vertebrae, whereas gulf menhaden have 44–46. Yellowfin menhaden are reported to have 45–47 vertebrae (Houde and Swanson, 1975). The number of vertebrae, which should approximate the number of myomeres in larvae much smaller than those collected in this study, in conjunction with pigment differences have been shown to be useful in separating clupeid species complexes (Ditty et al., 1994). In the western gulf, counts of 43–44 vertebrae (=myomeres) would separate finescale menhaden from other clupeid larvae such as *Sardinella aurita* (45–47 vertebrae; Ditty et al., 1994), *Etrumeus teres* (48–50 vertebrae; Fahay, 1983), and *Opisthonema oglinum* (45–46 vertebrae; Richards et al., 1974). Species from the western gulf with similar vertebral counts (*Harengula jaguana*, 39–42; Houde et al., 1974; and *Jenkinsia lamprotaenia*, 39–42; Powles, 1977) can be distinguished from finescale menhaden by their larger PAL:SL ratio (>85% at 15 mm for *Harengula* vs. <85% for finescale menhaden, Table 1) and fewer anal rays (13–14 for *Jenkinsia* vs. 18–24 for finescale menhaden, Table 3). Although vertebral counts were used successfully in distinguishing finescale menhaden from gulf menhaden, the time necessary to clear and stain larvae makes this method impractical for distinguishing between large numbers of menhaden.

In larval and prejuvenile stages, finescale and gulf menhaden are morphologically very similar. Proportional body measurements overlapped too greatly to reliably distinguish the two species. Only the presence of medial predorsal pigment prior to transformation, stellate melanophores at the pelvic fin base, and the size at transformation were useful characters in distinguishing the two species. Hettler (1984) noted that gulf menhaden lack paired melanophores in the predorsal region until initiation of transformation. Pigment at the pelvic fin base appears to be a diagnostic character for the small-scale menhadens because Houde and Swanson (1975) also reported a similar feature in yellowfin menhaden as small as 12.3 mm. Although the presence of this pigment at the pelvic fin base is proposed to be diagnostic for the small-scale menhadens (present

study), Hettler's (1984) illustration of a 16.5-mm gulf menhaden shows this pigment. Pigmentation descriptions for developing gulf menhaden have not specifically addressed melanophores at the pelvic fin insertion (Hettler, 1984). Finescale menhaden transform at a smaller size (17–19 mm) than any of the other Gulf of Mexico menhadens. Gulf menhaden did not complete transformation until around 25 mm, which is in agreement with the reported lengths of 25–28 mm for both laboratory reared and wild-caught individuals (Suttkus, 1956; Hettler, 1984). Yellowfin menhaden reach transformation at an intermediate size (20–23 mm; Houde and Swanson, 1975).

Even as adults, finescale menhaden very closely resemble gulf menhaden (Hoese and Moore, 1977) and few reliable characters effectively separate them. Only the absence of striations on the margin of the operculum, a single humeral spot (with no hint of trailing spots along the lateral margins), and more scale rows (60–77 in finescale vs. 36–50 in gulf menhaden; Hoese and Moore, 1977; McEachran and Fechhelm, 1998) distinguish finescale from gulf menhaden. All other meristics overlap greatly; i.e., counts of dorsal-fin rays, anal-fin rays, pectoral-fin rays, pelvic-fin rays, gill-raker counts, and ventral scutes. Although externally similar, significant differences in internal structure between finescale and gulf menhaden have been documented. Finescale menhaden have fewer branchiospinules and shorter intermediate gill rakers than gulf menhaden and, as such, filter mainly zooplankton from the water column; gulf menhaden, in contrast, feed primarily on phytoplankton and detritus (Castillo-Rivera et al., 1996).

Based on length-frequency differences seen between the two species (Fig. 1), the reported spawning season for finescale menhaden along the middle Texas coast could be extended to late May. We still do not know of characters that would distinguish finescale menhaden eggs, and yolksac, preflexion, and flexion larvae from other species in the genus *Brevoortia*. In order to fully describe the development of finescale menhaden, laboratory spawning and rearing experiments are needed to fully describe these early-life stages. Houde (1973) presented relatively simple rearing techniques that allow descriptions of the developmental stages of larval fish (from egg through transformation of larvae to the juvenile stage). These methods have been used successfully for Atlantic, gulf, and yellowfin menhaden, and presumably, finescale menhaden could be reared with these same techniques if their eggs could be obtained. The rearing of finescale menhaden would also allow the effectiveness of the proposed pigment characters used to separate finescale menhaden from gulf menhaden to be tested.

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