Abstract.—The Atlantic spadefish *(Chaetodipterus faber)* is the only member of the family Ephippidae in the western Atlantic Ocean and its life history is poorly understood. We redescribe Atlantic spadefish larvae, discuss their relationship to known larvae of other ephippid genera, and discuss the distribution, abundance, and seasonal occurrence of Atlantic spadefish in the northern Gulf of Mexico. Larval Atlantic spadefish are characterized by a small, peak-like, median supraoccipital crest with a single, dorsally directed spine; large preopercle spines, numerous serrate ridges, and other spines on the head; a deep, robust body which becomes laterally compressed; heavy body pigmentation; and early development of specialized spinous scales or "prescales" (at about 5.5-mm standard length [SL]). Transition to juvenile stage begins about 8.0–8.5 mm SL. Developmental morphology and head spination of Atlantic spadefish is similar to that of Pacific spadefish, *Chaetodipterus zonatus*. Sequence of fin completion is pelvics — dorsal and anal soft rays — dorsal spines–pectorals. Overall, ≥85% of Atlantic spadefish larvae were found in waters ≥28.0°C and between 26.7 and 31.3 ppt. Larvae occur primarily in coastal waters, except near the Mississippi River delta, an area with a narrow shelf and rapidly increasing water depths. Delta waters may offer additional habitat suitable to Atlantic spadefish larvae because of lower salinities. Larvae are primarily collected between June and August and in the north-central Gulf of Mexico. Larval Atlantic spadefish are apparently rare in the eastern Gulf off Florida. Catch rates near the Mississippi River delta during August were higher than elsewhere in the north-central Gulf and suggest a possible association with riverine frontal areas which requires further study.

A re-description of Atlantic spadefish larvae, *Chaetodipterus faber* (family: Ephippidae), and their distribution, abundance, and seasonal occurrence in the northern Gulf of Mexico

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The percoid family Ephippidae is usually considered to comprise five genera and 17 species (Nelson, 1984). The Atlantic spadefish *(Chaetodipterus faber)* is the only member of this family in the western Atlantic Ocean. Rare north of Chesapeake Bay, Atlantic spadefish inhabit coastal waters which extend southward to Brazil (Johnson, 1978). Historically, Atlantic spadefish represented a relatively minor portion of recreational fisheries. Nevertheless, fishing tournaments are currently being used to stimulate interest in their fisheries (Schmied and Burgess, 1987). Ryder (1887) described eggs and yolk-sac larvae of Atlantic spadefish, but Johnson (1978) questioned the identity of these specimens. Larvae ≥2.5 mm standard length (SL) are described and illustrated by Hildebrand and Cable (1938), but this study is insufficient to examine important developmental details and is based on the static rather than dynamic approach to larval description (Berry and Richards, 1973). Finucane et al.[1] illustrated 5.1- and 6.4-mm SL Atlantic spadefish. Johnson (1984) commented on cranial morphology and provided insight on the value of larval characters in resolving the relations among ephippids and their relation to other families. Aspects of juvenile and adult life history are discussed for Atlantic spadefish from South Carolina waters (Hayse, 1990), but the distribution, abundance, and seasonal occurrence of Atlantic spadefish larvae are poorly understood. Our objectives are to redescribe the development of Atlantic spadefish larvae, discuss their relation to known larvae of other ephippid genera, and to describe the distribution, abundance, and seasonal occurrence of Atlantic spadefish larvae in the northern Gulf of Mexico (Gulf).

Materials and methods

The distribution, abundance, and seasonal occurrence of larval Atlan-

[1] Finucane, J. H., L. A. Collins, L. E. Barger, and J. D. McEachran. 1979. Ichthyoplankton/mackerel eggs and larvae. Environmental studies of the south Texas outer continental shelf, 1977. Final Rep. to Bur. Land Manage., Wash., DC, Southeast Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Galveston, TX 77550, 504 p.

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tic spadefish were determined from collections taken primarily during Southeast Area Monitoring and Assessment Program (SEAMAP) ichthyoplankton surveys of the Gulf between 1982 and 1986 (SEAMAP[2]). These years represent the first time interval for which a complete set of data were currently available. Latitude 24°30' N was the southern boundary of our study area in the eastern Gulf, a cutoff which approximates the continental shelf break off the southern tip of Florida. Latitude 26°00' N was the southern boundary of the central and western Gulf. These coordinates approximate the U.S. Exclusive Economic Zone (EEZ)/Fishery Conservation Zone (FCZ).

Standard ichthyoplankton survey techniques as outlined by Smith and Richardson (1977) were employed in data collection. Stations sampled by National Marine Fisheries Service (NMFS) vessels were arranged in a systematic grid of about 55–km intervals. NMFS vessels primarily sampled waters >10 m deep. Each cooperating state had its own sampling grid and primarily sampled their coastal waters. Hauls were continuous and made with a 60–cm bongo net (0.333–mm mesh) towed obliquely from within 5 m of the bottom or from a maximum depth of 200 m. A flowmeter was mounted in the mouth of each net to estimate volume of water filtered. Ship speed was about 0.75 m/sec; net retrieval was 20 m/min. At stations <95 m deep, tow retrieval was modified to extend a minimum of 10 minutes in clear water or 5 minutes in turbid water. Tows were made during both day and night depending on when the ship occupied the station. Overall, 1,823 bongo net tows were made between 1982 and 1986. The SEAMAP effort between 1982 and 1984 also involved the collection and processing of 814 neuston samples taken with an unmetered 1×2 m net (0.947–mm mesh) towed at the surface for 10 minutes at each station. SEAMAP sampling during April and May was conducted primarily off the continental shelf; sampling during March, and from June through December, was conducted primarily over the shelf at stations <180 m deep. Additional information on the spatial and temporal coverage of SEAMAP plankton surveys is found in Stuntz et al. (1985), Thompson and Bane (1986, a and b), Thompson et al. (1988), and Sanders et al. (1990). Atlantic spadefish larvae were also obtained from surface-towed 1×2 m neuston net collections (0.947–mm mesh, 71 samples) made by the National Marine Fisheries Service (NMFS, Panama City, Florida) during August 1988. These NMFS collections were associated with riverine/oceanic frontal zones off the Mississippi River delta. Frontal zones near the delta were not sampled during either June or July.

A detailed examination of Atlantic spadefish larvae was made to describe developmental morphology. Body measurements were made on 21 Atlantic spadefish larvae between 1.9 and 12.5 mm (Table 1) and follow Hubbs and Lagler (1958) and Richardson and Laroche (1979). Measurements were made to the nearest 0.1 mm with an ocular micrometer in a dissecting microscope. We follow Leis and Trnski's (1989) criteria for defining length of preopercular spines, body depth, head length, eye diameter, and the eye diameter/head length ratio. We consider notochord length in preflexion and flexion larvae synonymous with SL in postflexion larvae and report all lengths as SL unless otherwise noted. Specimens were field-fixed in 10% formalin and later transferred to 70% ethyl alcohol. Terminology for

[2] SEAMAP. 1983–1987. (plankton). ASCII characters. Data for 1982–1986. Fisheries-independent survey data/National Marine Fisheries Service, Southeast Fisheries Center: Gulf States Marine Fisheries Commission, Ocean Springs, MS (producer).

Table 1

Morphometrics of larval Atlantic spadefish (*Chaetodipterus faber*) from the northern Gulf of Mexico. Measurements are expressed as % standard length (SL) and rounded to the nearest whole number

SL	*N*	Preanal length	Head length	Snout length	Orbit diameter	Body depth pectoral	Prepelvic distance
1.8–2.9	3	42–55	21–31	3–8	13–15	34–44	—
3.0–4.9	3	54–65	35–43	5–7	15–17	50–60	30–36
5.0–6.9	4	60–61	30–42	5–6	15–18	56–63	30–35
7.0–8.9	4	61–64	35–39	7–9	14	55–64	27–37
9.0–10.9	4	59–61	34–35	6–8	13–14	60–65	27–34
11.0–11.9	2	54–56	34–35	7–9	14	60–65	27
12.5	1	60	36	8	14	68	36

location of head spines followed Gregory (1933). One larva was cleared with trypsin then stained with alizarin in each millimeter (mm) length interval to examine small serrate ridges around the orbit (i.e. circumorbital bones), and spines and ridges on the head. We examined spines on the occipital and frontal bones with a scanning electron microscope (SEM), and specialized spinous scales with a compound microscope. Fin rays were counted when first segmented and spines when present. Representative specimens were illustrated with the aid of a camera lucida.

Estimates of larval density (number of larvae/100m^3 of water) and catch (number of larvae/10 tow) were calculated by month. Months were combined across years because not all months were sampled every year (Appendix Table). Densities for stations where larvae were collected (i.e. positive catch stations) were calculated by dividing sum of larvae collected in bongo net tows by total positive catch station volume of water filtered (VWF) and multiplying the result by 100. In addition, an overall (i.e. grand) density estimate was calculated by dividing sum of larvae by total VWF for all stations sampled that month and multiplying the result by 100. Overall density more closely reflects the density of larvae throughout the area by including the total volume of water filtered in calculations. Estimates of larval catch in neuston nets were calculated by dividing sum of larvae by number of positive catch neuston stations or by total number of neuston stations sampled and multiplying the result by 10. Estimates of larval density and catch included stations at long. ≥88°00' W because only one Atlantic spadefish larva was collected east of Mobile Bay, Alabama. Similarly, estimates were calculated only for June through August because May and September had but one positive catch station each.

Temperature and salinity data were gathered from the sea surface. Positive catch station hydrographic data were multiplied by total number of larvae collected at each station to obtain a monthly median and mean. Hydrographic data were also combined across months to obtain an overall (i.e. grand) median and mean. This method gives weight to distribution of larvae rather than to distribution of stations. We used a percent cumulative frequency of ≥85% for defining the relation between distribution of Atlantic spadefish larvae and water temperature, salinity, and station depth. Percent frequency indicates the range of hydrographic conditions most often associated with occurrences of larvae. Proc Univariate was used to calculate median, mean, and percent cumulative frequency statistics (SAS Institute, 1985).

Results

Morphometrics and pigmentation

Early larvae were rotund and deep-bodied; body depth was >50% SL by 3.5 mm and ≥60% by 9 mm (Table 1). Atlantic spadefish became increasingly deep-bodied and laterally compressed after notochord flexion. There were 24 myomeres but these became obscured by pigment in postflexion larvae. The head was large and averaged about 35% SL in larvae >3.0 mm. Head profile became steep and increasingly deeper than long. The mouth was terminal and the upper jaw reached to about mid-eye. Eyes were round and large, ranging from 36 to 43% of head length in larvae >3.5 mm (i.e. about 14–15% SL). The gut was tightly coiled in a single loop and the anus was slightly beyond mid-body (usually 55–60% SL).

Pigment was largely restricted to the anterior-half of the body in early preflexion larvae of Atlantic spadefish. On the head of a 1.8-mm larva, external pigment was scattered over the mid- and hindbrain, nape, opercle, branchiostegal membrane, and along the isthmus and quadrate. Internally, pigment was present along and above the anterior portion of the notochord, and a single median patch was observed on the roof of the mouth. On the abdomen, there was a patch of pigment on the visceral mass immediately anterior to and below the pectoral-fin base. In addition, melanophores were scattered over the pectoral fin base and its finfold and were distributed laterally over the visceral mass and hindgut. A row of about 20–25 small, closely spaced melanophores were visible along the ventral midline of the tail in early larvae. Number of melanophores along the ventral midline of the tail decreased as larvae grew. Melanophores on the nape, opercle, pectoral-fin base, and visceral mass formed a "swath" of pigment over the anterior 55–60% of the body by 2.5–3.0 mm (Fig. 1). By 3.0–3.5 mm, internal melanophores were visible anteriorly on the forebrain and laterally on the midbrain above the eye. Melanophores were also scattered both internally and externally over the hindbrain both anterior to and posterior to the base of the supraoccipital crest. By early postflexion (i.e. 5.0 mm), the head and abdomen were densely pigmented but the posterior portion of the body was sparsely pigmented. Pigmentation increased on the posterior-half of the body as larvae grew, and by 10.0 mm the entire body was pigmented (Fig. 1). Consolidation of pigment into bands began on the head of Atlantic spadefish larvae with one band visible above the eye by 10.0–11.0 mm. This band of pigment was enclosed by indefinite, pale crossbars. The

anterior pale crossbar was situated above the middle of the eye and the posterior crossbar was behind the eye, extending mid-way down the preopercle. Larvae <12.5 mm had only one band of pigment (Fig. 1).

The pelvics were the first fins to have pigment. Pelvic fin buds were pigmented by 4.0 mm; the pelvics were densely pigmented thereafter. Pigment appeared on the pectoral fin along the proximal portion of the rays at about 4.0–4.5 mm. Melanophores were lightly scattered over the pectoral fin in the largest specimen examined (Fig. 1). Melanophores were scattered over the membrane covering the anterior-most dorsal spines by about 6.0 mm and the anal spines by about 8.0 mm. Melanophores were added along the dorsal and anal fins as larvae developed, covering the proximal-third of each soft ray in the largest specimen examined. Pigment was present along the proximal portion of the central rays of the caudal fin by 11.0 mm (Fig. 1).

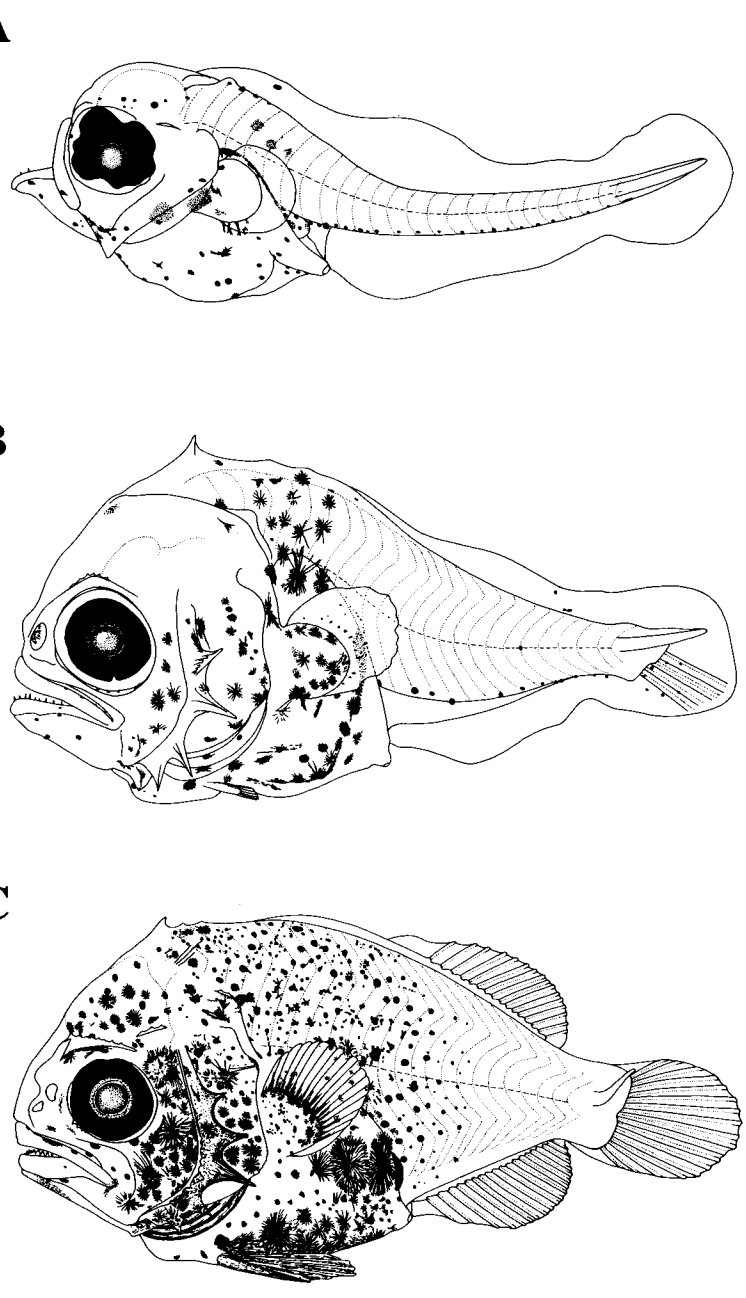

Figure 1

Larval development of Atlantic spadefish, *Chaetodipterus faber,* from the northern Gulf of Mexico. (**A**)1.8 mm; (**B**) 3.5 mm; (**C**) 5.0 mm; (**D**) 7.0 mm; (**E**) 11.6 mm. All measurements are standard length (SL).

Head and body spination

Atlantic spadefish larvae develop two series of preopercular spines, one along the posterior margin of the outer shelf and the other along the inner shelf. Both the outer and inner shelf have dorsal and ventral limbs. Three preopercular spines were present along the outer shelf of a 1.8-mm larva, the largest of which was present at its preopercular angle (Fig. 1). A fourth and a fifth spine were added by 3.5 mm, one dorsal and one ventral to the angle of the preopercle. A sixth preopercular spine, smaller than the others and often difficult to locate, was present by 5.0 mm. This sixth spine was the anterior-most spine along the ventral limb of the exterior shelf and was resorbed by 11.0–12.0 mm in some specimens. One larva we examined had seven preopercular spines along the outer shelf but most had two spines along the dorsal limb, one at the angle, and three along the ventral limb (Fig. 2). Spines along the outer shelf were simple. Two to three spines were also present along the inner shelf of the preopercle by 3.5 mm. Number of spines along the inner shelf increased as larvae grew, resulting in a serrate margin (Fig. 2). A small, poorly developed opercle

spine was forming by 5.0 mm and was difficult to locate on larvae not cleared and stained. A spine also was present along the posterior margin of the interopercle near its junction with the subopercle by 6.0 mm (Fig. 2). The interopercular spine often was hidden by the large spine at the preopercular angle but was more easily located as the preopercular angle spine regressed.

Atlantic spadefish larvae have numerous spines and ridges scattered over the head. A thickened ridge was visible dorsally along the supraoccipital of 2.0-mm larvae. This thickened ridge became a small, peak-like, median supraoccipital crest with a single, dorsally directed spine by 2.5 mm. The supraoccipital spine began to regress by 5.0 mm and was resorbed by 10.0–10.5 mm. A supraorbital ridge was present by 3.5 mm. This ridge became serrate by 4.0 mm. Small serrate ridges were visible along the dorsal margin of both the lacrimal and jugal bones (i.e. first and second suborbitals; Gregory, 1933) and third suborbital bone by 5.0 mm. Spines or spinous ridges were also visible along the fourth and fifth suborbitals, dermosphenotic (i.e. sixth suborbital), posttemporal, pterotic, tabular, and supracleithral bones by 6.0 mm. The ventral margin of the jugal bone near the posterior margin of the maxillary had a single, ventrally directed spine by 7.0 mm (Fig. 2). Individual spines were also scattered over the frontal and occipital bones of young Atlantic spadefish. The bases of these spines were covered by integument so that only a portion of each spine was visible (Fig. 3). All head spines and spinous ridges were present in the largest specimen examined (12.5 mm) but were difficult to locate on larvae not cleared and stained because of heavy body pigment.

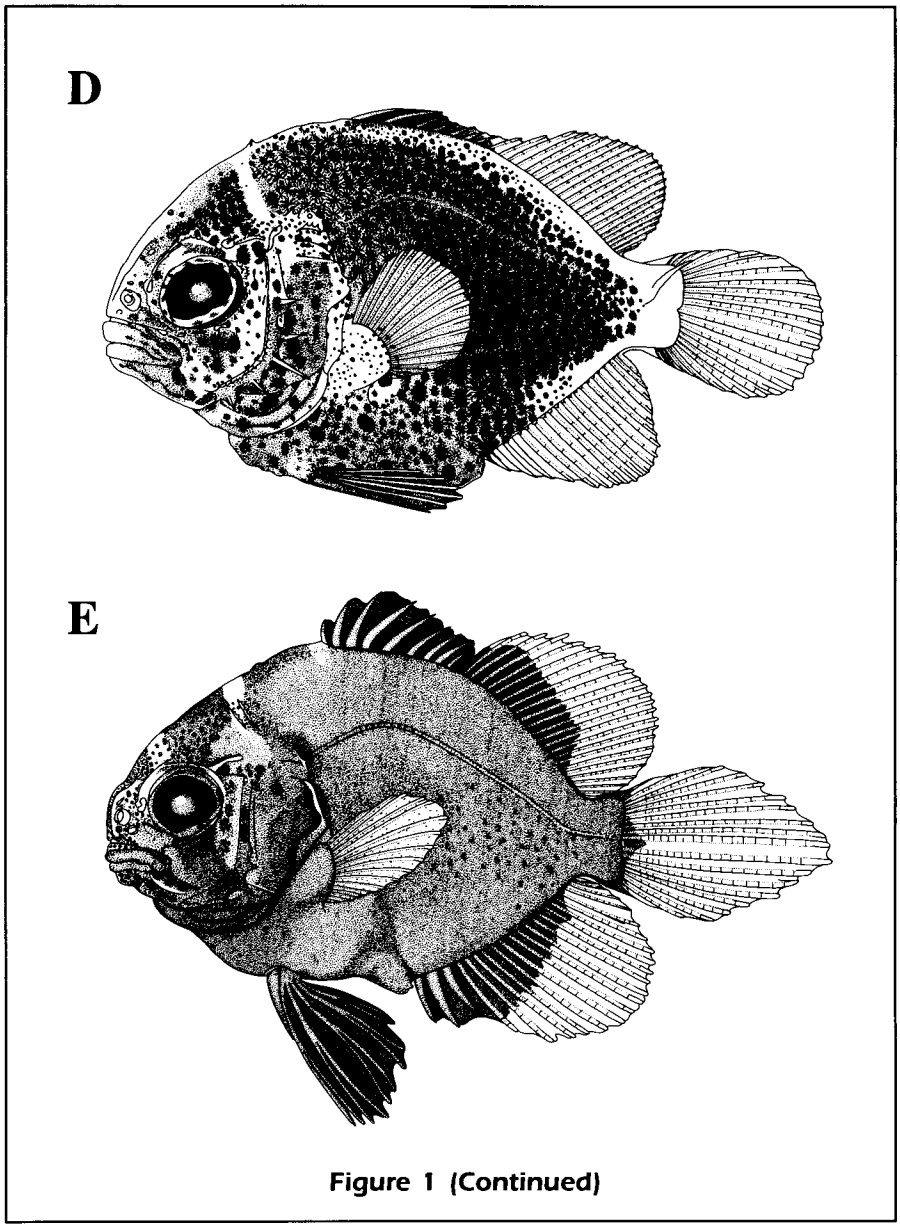

Figure 1 (Continued)

Teeth in Atlantic spadefish were placed in an inner and outer band. Teeth first appeared in a single band on the premaxillary and anteriorly on the dentary at about 2.5 mm. Teeth were pointed and closely spaced. A second band of teeth formed along the upper and lower jaws by 4.0 mm; the outer band was slightly larger than the inner band. Teeth were added along the upper and lower jaws as larvae developed (Figs. 1 and 2).

Specialized spinous scales or "pre-scales" began to develop at about 5.5 mm. Pre-scales were characterized by a single, elevated, posteriorly directed spine that was positioned near the center of the scale. Pre-scales developed first on the head and later appeared anteriorly along the lateral midline. Pre-scales were added outward toward the dorsal and ventral midlines and proceeded in a posterior direction, covering the body by 10.0 mm.

The first bones to ossify were the preopercular spines, supraoccipital crest, premaxillary, dentary, and cleithrum. Three predorsal bones (i.e. supra-

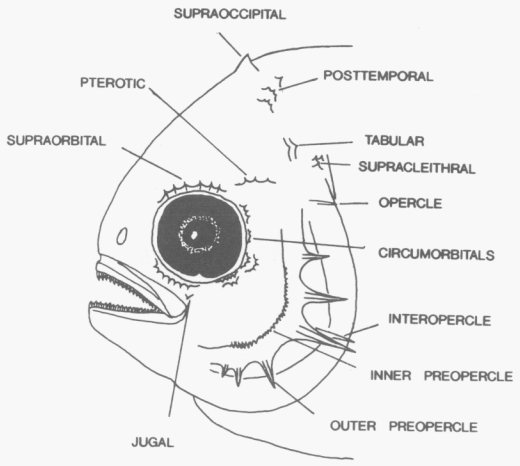

Figure 2

Location of head spines on a 7.0-mm SL larva of Atlantic spadefish, *Chaetodipterus faber*, from the northern Gulf of Mexico.

neurals) were ossifying by 6.0 mm. The anteriormost precaudal vertebrae and dorsal- and anal-fin pterygiophores ossified first; ossification proceeded posteriorly. All caudal bones were ossifying by 8.0 mm. Six branchiostegal rays and 10+14 vertebrae were present in all cleared and stained specimens.

Fin development

A continuous median finfold extended around the body from the nape to the anus of early larvae. Fin ray anlagen began forming obliquely downward in the caudal finfold during flexion (usually 3.5–4.5 mm). Caudal-fin ray development proceeded outward from mid-base as the hypural complex shifted to a terminal position, with the adult complement of 9+8 principal rays attained at about 6.0 mm (Table 2). Development of the dorsal- and anal-fin bases coincided with notochord flexion. Both fin bases and their ray anlagen began to differentiate near mid-fin; development proceeded outward from mid-fin. All dorsal and anal soft rays were present by about 7.0 mm. Soft dorsal and anal fin ray complements were present before their spines (Table 2); dorsal and anal spines developed in an anterior

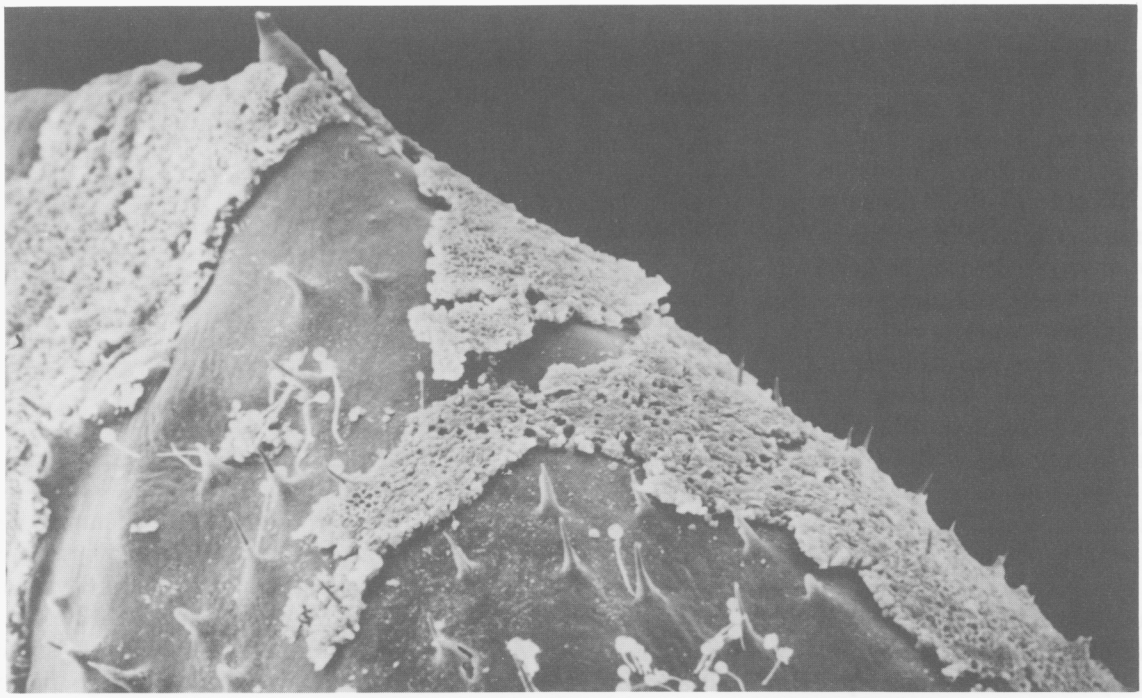

Figure 3

Scanning electromicrograph of the frontal and occipital spines of a 7.0-mm SL Atlantic spadefish, *Chaetodipterus faber*. Epithelium was partially digested with trypsin to enhance visibility of frontal and occipital spines. Magnification: 140×.

to posterior direction. Pelvic fins were precocious and heavily pigmented. Pelvic buds were visible by 4.0 mm; pelvics had a full complement of elements (I, 5) by 6.0 mm. Pectoral rays began to develop by 5.0 mm and a full complement (17) was present by 8.0 mm. Sequence of fin completion was pelvics – soft dorsal and anal rays – dorsal spines – pectorals. A full complement of elements in all fins by 8.0–8.5 mm marked the beginning of transition to the juvenile stage (Table 2).

Table 2

Fin-ray counts of larval Atlantic spadefish *(Chaetodipterus faber)* from the northern Gulf of Mexico.

Length (mm SL)[1]	Dorsal	Anal	Pectoral	Pelvic	Caudal
4.3	III, Anlagen	8	Anlagen	Anlagen	0–7+7–0
5.0	III, 14	11	7	4	0–6+6–0
6.1	VII, 24	II, 17	13	I, 5	3–9+8–3
7.0	VII, 23	II, 18	16	I, 5	4–9+8–5
8.3	IX, 21	III, 17	17	I, 5	4–9+8–4
9.3	IX, 21	III, 18	17	I, 5	5–9+8–4
10.0	VIII, 23	III, 18	17	I, 5	5–9+8–5

[1] One larva of each length.

Temporal and spatial distribution

Alantic spadefish larvae were collected from May through September primarily in the north-central Gulf. Larvae were usually collected between June and August, density being highest during June and catch highest during August (Table 3). Larval Atlantic spadefish were especially abundant near the Mississippi River delta during August 1988, when 19 of 72 neuston tows (26%) associated with riverine frontal zones collected larvae. During August 1984, however, <5% of neuston tows (n=162) from other areas of the north-central and western Gulf not associated with the delta captured larvae. Only one Atlantic spadefish larva was collected east of Mobile Bay, Alabama (long. 88°00' W). This 4.0-mm specimen was found off Apalachicola Bay (Florida) during August 1984 at a station 13 m deep (Fig. 4). Salinity at this station (34.2 ppt) was the highest recorded with a positive catch during the study. The largest specimen collected in surface-towed nets was 12.5 mm; this observation may indicate that larvae move out of surface waters by this size.

Table 3

Density (number of larvae/100 m^3) and catch (number of larvae/10 neuston tows) of Atlantic spadefish larvae (*Chaetodipterus faber*) from the northern Gulf of Mexico. Months are combined across years (1982–1986, and August 1988). Not all months were sampled each year. Numbers in parentheses are positive catch stations over total stations sampled by month. Monthly density estimates were calculated by dividing sum of larvae by either sum of volume water filtered (VWF) overall, or sum of positive station VWF. Monthly catch estimates were calculated by dividing sum of larvae by number of stations sampled overall or by number of positive catch stations.

Gear	June	July	August
Bongo			
Overall density	0.3[1]	<0.1[2, 3]	<0.1[4, 5]
Positive density	6.2 (19/341)	1.3 (4/134)	1.5 (4/221)
Neuston			
Overall catch	4.0	0.4	17.0
Positive catch	42.6 (19/201)	13.3 (3/92)	131.6 (32/248)

[1] Total VWF – 43,730 m^3, positive catch station VWF – 1,799 m^3, number of larvae collected was 111.
[2] 0.02/100 m^3.
[3] Total VWF – 22,207 m^3, positive catch station VWF – 381 m^3, number of larvae collected was 5.
[4] 0.03/100 m^3.
[5] Total VWF – 35,174 m^3, positive catch station VWF – 796 m^3, number of larvae collected was 12.

Overall, ≥85% of Atlantic spadefish larvae were collected in surface waters ≥28.0°C (median: 28.1°C, mean: 28.7°C, range: 25.0°–32.2°C), at salinities between 26.7 and 31.3 ppt (median: 28.8 ppt, mean: 28.4 ppt, range: 11.8–34.2 ppt), and at station depths <238 m (median: 83 m, mean: 139 m, range: 9–470 m) (Fig. 5). However, distribution of larvae versus station depth was strongly influenced by two very large neuston-net collections of 192 and 64 larvae during August 1985 which represented 40% of all larval Atlantic spadefish taken. These two stations were located in waters near the shelf edge, 50 and 75 km east of the Mississippi River delta (28.1°C, 30.1 ppt, 235 m deep; 27.9°C, 28.1 ppt, 238 m deep, respectively). Other stations had 27 or fewer larvae. Distribution of larvae versus station depth without the two large collections shifted median station depth

shoreward from 83 to 26 m; larvae may, therefore, primarily inhabit coastal waters. This shoreward shift in median station depth was reinforced by distribution of larvae in bongo net tows and by distribution of larvae during June and July (Fig. 4, Table 4). About 86% of all Atlantic spadefish larvae collected in bongo net tows (n=128) were from waters ≤25 m deep. In addition, distribution of larvae during June and July was shoreward of that during August. Similarly, 51% of all stations where larvae were collected (i.e. 41 of 81) were inside 25 m; 64% were inside 50 m. Only 14% of positive catch stations were located beyond the 100 m isobath; most of these stations were near the Mississippi River delta, an area with a narrow shelf and rapidly increasing water depths.

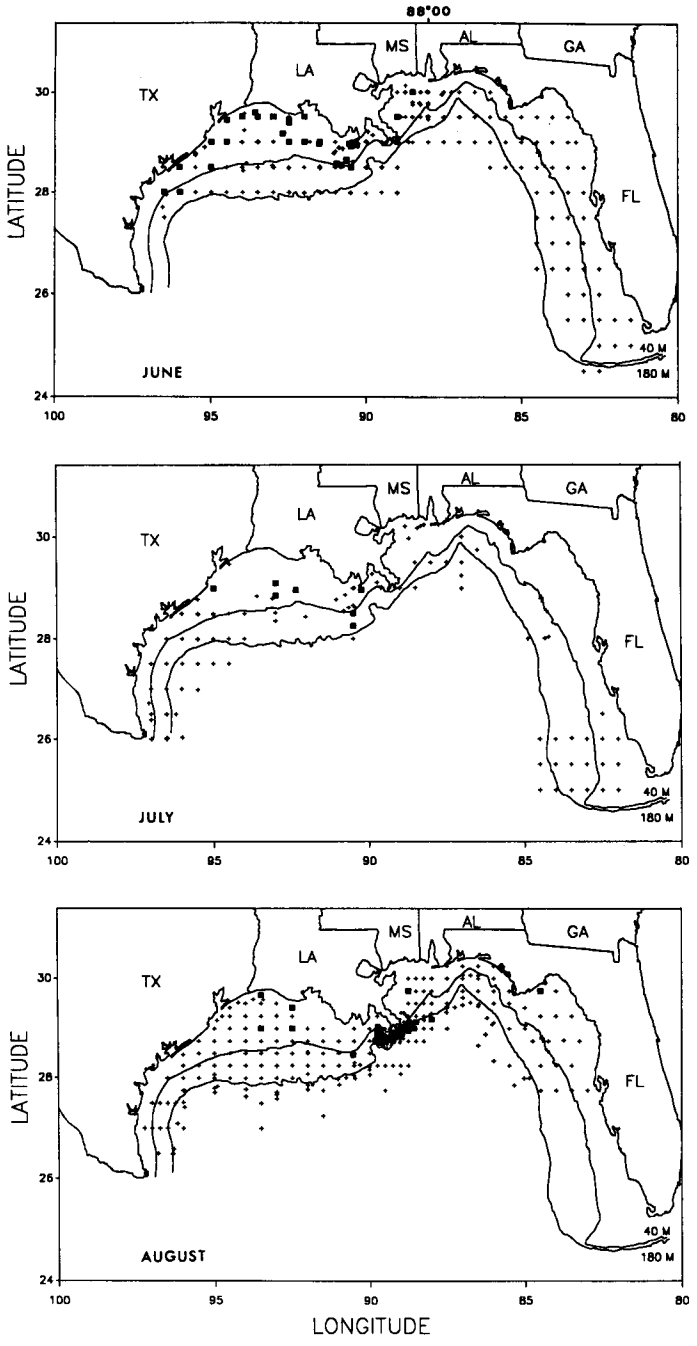

Figure 4

Distribution of Atlantic spadefish larvae (*Chaetodipterus faber*) in the northern Gulf of Mexico by month. Months are combined across years (1982–1986, and August 1988). Not all months sampled each year. Plus (+) signs are total stations sampled and squares are positive catch stations. Distribution of stations are for both bongo and neuston net tows.

Discussion

Our observations on the morphological development of Atlantic spadefish larvae generally agree with Hildebrand and Cable (1938). These authors, however, do not discuss pigment on the roof of the mouth. The presence of a single, median patch of pigment on the roof of the mouth is helpful in identifying early Atlantic spadefish larvae before the supraoccipital crest is clearly visible. Hildebrand and Cable (1938) do not discuss small spines or ridges along the circumorbital bones (i.e. supraorbital, suborbitals, and dermosphenotic) or tabular bone (Fig. 2) but do illustrate serrate ridges above the eye and in the pterotic region (Hildebrand and Cable, 1938, their Figs. 26 and 27). Spination on the circumorbital bones has generally been found only in those larval percoids with cranial ornamentation (Johnson, 1984). Most of these larval percoids also have other specializations, such as spinous scales and an elongate spine at the angle of the preopercle, among other characters (Johnson, 1984). Neither Hildebrand and Cable (1938) nor Johnson (1984) mention the supracleithral spines we found on Atlantic spadefish larvae (Fig. 2) and in larvae of Pacific spadefish, *Chaetodipterus zonatus* (Martinez-Pecero et al., 1990). The "short, hair-like spines on the upper surface of the head" noted by Hildebrand and Cable (1938) on 9.0-mm Atlantic spadefish larvae may be the same spines we found scattered over the frontal and occipital bones (Fig. 3). These frontal and occipital spines are difficult to see under a dissecting microscope because

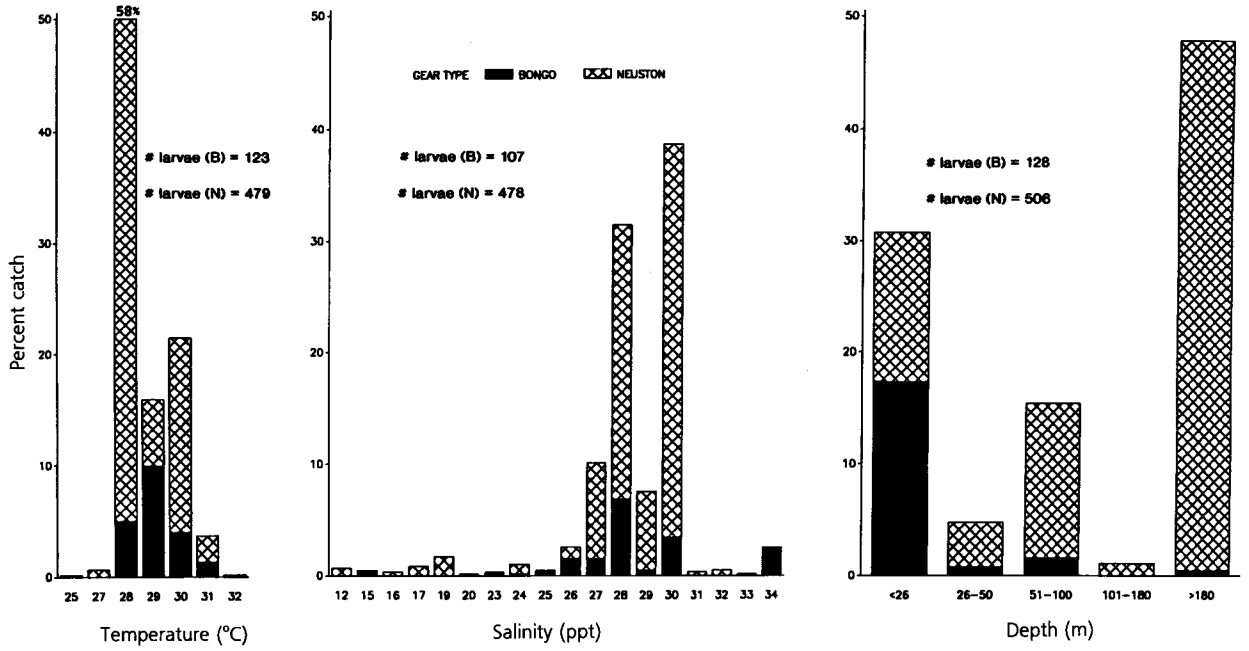

Figure 5

Summary of positive catch station hydrographic data for larval Atlantic spadefish (*Chaetodipterus faber*) from the northern Gulf of Mexico. Percent catch is sum of larvae by interval and gear divided by total number of Atlantic spadefish larvae collected overall. Discrepancies in number of larvae by month among parameters are the result of missing hydrographic data.

Table 4

Summary of hydrographic data by month for Atlantic spadefish (*Chaetodipterus faber*) larvae from the northern Gulf of Mexico. Data are from the surface and for positive catch bongo and neuston net stations only. Station hydrographic data are multiplied by total number of larvae collected at each station to obtain monthly mean and median values.[1] '*N*' is the number of larvae used to obtain mean and median values. Discrepancies in '*N*' by month among parameters resulted from missing hydrographic data.

	Water temperature (°C)				Salinity (ppt)				Station depth (m)			
	N	Mean	Median	Range	*N*	Mean	Median	Range	*N*	Mean	Median	Range
June	160	29.0	29.3	25.0–30.5	143	27.6	27.6	12.1–33.9	192	17.3	16	9–90
July	9	29.4	29.8	29.3–30.5	9	27.6	27.6	25.4–28.6	9	27.3	21	16–70
August	433	28.1	28.6	27.6–32.2	433	28.8	29.4	11.8–34.2	433	194	235	11–470

[1] This method gives weight to distribution of larvae rather than distribution of stations.

they are largely covered by integument. The supraoccipital crest was resorbed by about 10.0–10.5 mm in Gulf larvae but still present on a 11.5-mm specimen from the U. S. Atlantic coast (Hildebrand and Cable, 1938).

The identity of Ryder's (1887) yolk-sac Atlantic spadefish larvae is uncertain (Johnson, 1978). Ryder's 3.5-mm and 4.0-mm larvae lack a supraoccipital crest and preopercular spines, both of which Hildebrand and Cable (1938) and we found by 2.5 mm in Atlantic spadefish larvae. Ryder's 4.0-mm larva also has an oil globule in the yolk sac and the gut does not have the single, tightly coiled loop we found in preflexion Atlantic spadefish. Neither Hildebrand and Cable (1938) nor we found an oil globule in Atlantic spadefish larvae of 2.0 mm or

2.5 mm, respectively. Differences between Ryder's and our study do not support identification of Ryder's larvae <4.0 mm as Atlantic spadefish even if we allow for specimen shrinkage (also noted by Johnson, 1978) and for slower development times due to cooler waters of Chesapeake Bay during the summer when Atlantic spadefish spawn.

Johnson (1984) characterized the sequence of fin completion in larval Atlantic spadefish as pattern A: dorsal and anal soft rays – spinous dorsal – pelvics – pectorals. We cleared and stained seven larvae and found the sequence of fin completion more closely resembles Johnson's (1984) pattern F with all elements of the pelvic fin present before dorsal and anal soft rays. This difference in fin completion pattern, however, may be due to differences in how we and Johnson interpreted spine formation and fin completion. We counted rays when first segmented and spines when present; Johnson may have counted pterygiophores. Pattern F is found in *Hapalogenys*, Monodactylidae, and Pempheridídae (Johnson, 1984).

Larvae of Atlantic spadefish are characterized by early development of specialized spinous scales or "prescales" (at about 5.5 mm, this study) that eventually transform into adult ctenoid scales. Spinous larval scales are present to about 15.0 mm (Johnson, 1984). Ctenoid scales are well developed by 18.0 mm (Hildebrand and Cable, 1938).

Developmental morphology and head spination of Atlantic spadefish is generally similar to that of Pacific spadefish (Martinez-Pecero et al., 1990). Both species are deep-bodied (usually 55–60% SL) and preanal length is about 60% SL. Pigmentation and standard length at which fins develop also are similar; a full complement of rays is present in all fins by 8.0–9.0 mm in both species (Hildebrand and Cable, 1938; Martinez-Pecero et al., 1990; this study). However, consolidation of pigment into lateral bands, resorption of the supraoccipital crest, and the beginning of transition to the juvenile stage occur earlier in Pacific spadefish than in Atlantic spadefish. Larvae of ephippids from the Indo-Pacific region differ from *Chaetodipterus* from the western Atlantic and Pacific Oceans in extent of head spination (Leis and Trnski, 1989; Martinez-Pecero et al., 1990; this study). Larvae of *Platax* from the Indo-Pacific have a median supraoccipital crest with a serrate leading edge (Leis and Trnski, 1989) but do not have the circumorbital series of spinous ridges, nor spines on the jugal, tabular, pterotic, or supracleithral bones found in *Chaetodipterus* (Martinez-Pecero et al., 1990; this study). Head spination in *Ephippus* larvae from the Indo-Pacific is similar to that of *Chaetodipterus* and these two genera are probably more closely related than either is to *Platax*. Other species-specific head spination found in *Chaetodipterus* larvae from the western Atlantic and Pacific Oceans, and in *Ephippus orbis*, *Platax batavianus*, and three *Platax* species from the Indo-Pacific region include a posttemporal spine which may be reduced to a ridge in some species, a supraorbital ridge that varies in size among species, and one or two subopercular spines (Leis and Trnski, 1989; Martinez-Pecero et al., 1990; this study).

Early larvae of Atlantic spadefish could be confused with priacanthids, lobotids, some carangids and stromateoids, the wreckfish—*Polyprion americanus,* and *Menticirrhus* spp. because of similarities in head spination or in body pigmentation. Priacanthids have an elongate, serrate, median supraoccipital crest that extends posteriorly over the mid- and hindbrain; serrations along the lower jaw and frontal bone; and the angle preopercular spine is elongate and serrate as is the pelvic spine. Tripletail, *Lobotes surinamensis*, have a vaulted, serrate supraoccipital crest in early larvae, the pelvics are inserted behind the pectoral fins, and have fewer anal fin elements than Atlantic spadefish (Atlantic spadefish: A. III, 17–18, tripletail: A. III, 11–12). In carangids, the two anteriormost anal spines are separated from the third by a distinct gap and most species have a low, median supraoccipital crest that has serrations along the dorsal edge; other carangids lack a supraoccipital crest entirely. Some carangids also have a precocious dorsal fin with anterior spines or rays elongate, or with serrations along the angle preopercular spine. Some stromateoids (e.g. *Ariommus* spp., *Nomeus gronovii*) resemble Atlantic spadefish in early body pigmentation, body shape, and by having precocious pelvics, but stromateoids lack a median supraoccipital crest, a large preopercular angle spine, and all but *Hyperoglyphe* have >30 myomeres. *Polyprion americanus* larvae have a small, peak-like median supraoccipital crest, but with serrations along the leading edge, and lack a serrate pterotic ridge and spines on the tabular bone (Johnson, 1984). Wreckfish also have 27 myomeres, fewer dorsal (22–24) and anal fin (11–13) elements, and the mouth is larger than in Atlantic spadefish. Larval Atlantic spadefish differ from early larvae of *Menticirrhus* spp. by lack of both preopercular spines and the median supraoccipital crest in the latter.

We recently examined specimens reported by Dawson (1971) as larval black driftfish, *Hyperoglyphe bythites*. These specimens had a supraoccipital crest, pterotic ridge, spine on the interopercle, other head spination, and a pigmentation pattern identical to Atlantic spadefish. Vertebral,

dorsal, and anal fin counts overlap between black driftfish and Atlantic spadefish, but teeth are found in a single band on the dentary in black driftfish (Ginsburg, 1954) and in two bands in Atlantic spadefish (Hildebrand and Cable, 1938; this study). Dawson's 5.7–7.9 mm specimens had teeth in two bands along the dentary. Because it is unlikely that black driftfish larvae have the same suite of characters as Atlantic spadefish, Dawson's specimens should be assigned to Atlantic spadefish.

Atlantic spadefish spawn from May through September based on seasonal abundance of Atlantic spadefish larvae in the northern Gulf; peak spawning occurs between June and August (Ditty et al., 1988; this study). Density estimates were highest during June in this study (Table 3), during July in a previous study of coastal waters off central Louisiana (Ditty, 1986), and during July and August off Mississippi Sound (Stuck and Perry, 1982). Neuston net collections were greatest during August (Table 3). Gonad maturity data off South Carolina support peak spawning of Atlantic spadefish during summer (Hayse, 1990).

Spatial distribution data indicate that Atlantic spadefish larvae are apparently rare in the eastern Gulf. Only one larva was collected east of Mobile Bay (Alabama) during this study, and one larva by Houde et al.[3] in a survey of Gulf waters off Florida. In addition, distribution of both larvae and station depths where larvae were collected indicates that Atlantic spadefish occur primarily in coastal waters (Ditty and Truesdale, 1984; this study), except near the Mississippi River delta where waters may offer additional habitat suitable to larvae because of lower salinities. The relatively high number of positive stations (26%) near the delta during August 1988 sampling of frontal zones suggests that frontal zones may concentrate larvae. Frontal zone waters may also provide a richer environment for feeding and growth of larvae because of higher phytoplankton and zooplankton biomass (Govoni et al., 1989; Grimes and Finucane, 1991). However, Powell et al. (1990) were unable to demonstrate consistently that larvae have a nutritional advantage when associated with the Mississippi River plume. A possible association of Atlantic spadefish larvae with riverine frontal areas requires further study.

In conclusion, understanding the biology, life history, and relations of Atlantic spadefish requires a knowledge of the morphology, distribution, and ecology of their larvae. Larval characters (e.g. degree of head spination) may also provide insight into the interrelationships among the Ephippidae and their relationship to other families. The potential use of larval characters in defining these relationships, however, cannot be clearly understood until larval development within the family is more fully documented (Watson and Walker, 1992).

[3] Houde, E. D., J. C. Leak, C. E. Dowd, S. A. Berkeley, and W. J. Richards. 1979. Ichthyoplankton abundance and diversity in the eastern Gulf of Mexico. Univ. Miami Report BLM Contract No. AA550-CT7-28, Miami, FL 33149, 546 p.

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Appendix Table

Summary of total number of bongo net/neuston net stations examined for Atlantic spadefish larvae (*Chaetodipterus faber*) in the Gulf of Mexico. Acronyms are as follows: SEAMAP - Southeast Area Monitoring and Assessment Program; NMFS - National Marine Fisheries Service, Panama City, Florida. NS means no samples.

	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
SEAMAP										
1982	77[1]/0[2]	69/68	71/73	102/100	26/24	NS	NS	3/8	29/3	NS
1983	15/13	27/27	84/84	55/45	44/42	NS	NS	39/26	NS	24/23
1984	23/0	44/0	46/0	55/54	20/26	155/162	NS	24/0	6/0	36/36
1985	29/0	NS	NS	85/0	39/0	69/0	20/0	4/0	2/0	24/0
1986	NS	24/0	90/0	57/0	10/0	NS	145/0	43/0	73/0	24/0
Total	144/13	164/95	291/157	354/199	139/92	224/162	165/0	113/34	110/3	108/59
NMFS[2]										
1988	55	71	36							

[1] 60-cm bongo net, 0.333-mm mesh, oblique-tow from depth.
[2] 1 × 2 m neuston net, 0.947-mm mesh, 10 min. surface-tow, unmetered.