

OCURRENCE OF PLANKTONIC LANCELETS FROM  
LOUISIANA'S CONTINENTAL SHELF, WITH A  
REVIEW OF PELAGIC *BRANCHIOSTOMA*  
(ORDER AMPHIOXI)

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ABSTRACT

Three forms of lancelets of the genus *Branchiostoma* (Family Branchiostomatidae) were collected on the continental shelf of western Louisiana. They were identified as larval and adult *Branchiostoma longirostrum* and adult *Branchiostoma* species. These findings represent the first collection of pelagic adults and larvae of *B. longirostrum*, the first large-scale collection of pelagic adults of the genus *Branchiostoma* in the Western Atlantic, and the first records of sexually immature adult specimens of a *Branchiostoma* species which is not unequivocally a described species. A total of 453 larval and metamorphosed (but sexually immature) adults were collected on five cruises during December 1981 to April 1982. The 24 larval specimens collected ranged from 6.2-8.0 mm TL. These larvae were "giant" in that they exceeded 5 mm TL. Neighboring *B. floridae* undergo metamorphosis at about 2-5 mm TL. Collectively lancelet density peaked in January with a mean density of 4.6 specimens/100 m<sup>3</sup>. Adult specimens were collected only at night while the larvae were taken equally during night or day. The *Branchiostoma* adults appeared to undergo diel vertical migration. We review literature and discuss research results on pelagic lancelets, a protracted spawning season, a prolonged larval stage, and diel vertical migration relative to various morphometric and ecological factors, and aspects of life history.

Numerous papers have been written discussing the ancestry of lancelets and their role in the evolution of vertebrates and other chordates. Lancelets may or may not be in the ancestry of higher chordates; nevertheless, a study of their systematics and ecology is of interest as an indication of the way in which animals at this grade of organization lived and behaved under the changing conditions which eventually led to selection of higher forms.

The general biology, ecology and distribution of lancelets from the western North Atlantic has been described (Boschung and Gunter, 1962; Pierce, 1965; Cory and Pierce, 1967; Frankenberg, 1968; Nelson, 1968; Harima, 1973). At one time lancelets were thought to be so rare in the Gulf of Mexico that the encounter of any specimen was worthy of note. The first to report lancelets in the Gulf was Garman (1885) but he gave no specific locality. Lancelet specimens were then reported from the west coast of Florida (Adams and Kendall, 1891; Wright, 1890; Wells, 1926; Fowler, 1945). Soon after, the first lancelets were collected off Texas (Baughman, 1950; Gunter and Knapp, 1951; Hoese, 1955), Louisiana and Mississippi (Hefley and Shoemaker, 1952; Dawson, 1961), Alabama (Boschung and Mallory, 1956) and as far south as Veracruz, Mexico (Chavez, 1965). Only in relatively recent years have we collected lancelets from the Gulf of Mexico in large enough numbers for statistical analyses of populations, resulting in the study of variation within a species (Boschung and Gunter, 1962; Howell, 1964; Harima, 1973) and the description of new species (Boschung and Gunter, 1966; Boschung, 1983).

It is of great interest that the larval and adult lancelets reported herein are planktonic, having been collected in surface tows from continental shelf waters

as deep as 115 m. Heretofore, almost all records of Western Atlantic lancelets were of adult benthic specimens. A larval lancelet is one that has not undergone metamorphosis and is characterized by a single row of gill openings numbering 27 or less, no cirri, no metapleural fold, and an asymmetrical mouth. Lancelet larvae exist in two described forms: "amphioxides" larvae of *Amphioxides* (Goldschmidt, 1905) in the family Amphioxidae, and "amphioxus" larvae, identified with the family Branchiostomatidae (Bigelow and Farfante, 1948). The essential differences are that the amphioxides have a longer planktonic life, grow to a larger size (> 5 mm), often reach a total length (TL) of about 10 mm, and may have a single row of rudimentary gonads on the right side. The latter character possibly is evidence relating them to the family Epigonichthyidae. Acraniates have been hypothesized to develop different larval forms according to circumstances (Bone, 1957). Wickstead (1964a) suggested that amphioxus larvae will develop into *Branchiostoma* adults, while amphioxides larvae will metamorphose into *Asymmetron* adults of the family Epigonichthyidae. Later, however, Wickstead (1964b) concluded that two distinct forms did not exist, the amphioxides larva being an extrapolation of the amphioxus type. We accept the latter opinion and associate the giant larvae (defined here as larvae whose metamorphosis has been delayed and are usually > 5 mm TL) collected off Louisiana with the genus *Branchiostoma*. Further evidence to support this opinion comes from Lubny-Tertsky (1962) who found emerging cirri in pelagic specimens from the Pacific Ocean; however, he failed to connect this character with *Branchiostoma* and associated his specimens with *Amphioxides pelagicus* (Günther, 1889).

*Branchiostoma* larvae are a known component of the plankton of the world and in certain seas they occur in high numbers and constitute a major part of the zooplankton. *Branchiostoma senegalense* larvae occur by the millions of tons off northwest Africa (Flood et al., 1982), and comprise the larger part of the zooplankton by both weight and numbers (Gosselck and Kuehner, 1973). The abundance of larval/juvenile *Branchiostoma* (species unidentified but probably *B. virginia* or possibly *B. longirostrum*) on the northeast Florida shelf often exceeds 1,000/m<sup>3</sup> in and below the thermocline (Paffenhöfer, 1983). Such dense populations of lancelet larvae are exceptional and have been linked with upwellings off the northeast Florida and northwest Africa coasts.

Larval *B. belcheri* have been taken in nocturnal collections from surface waters of Singapore (Bedford, 1900) and 2–3 mm specimens have been taken in the plankton off Amoy, China (Chin, 1941). It is here that lancelets support a fishery, the adults being harvested from the sediments by the tons. "Giant larvae," 6.5–10.3 mm, have been reported from plankton tows of the upper 164 m over depths as great as 2,080 m in Japanese waters (Nishikawa, 1981). The first definite account of pelagic larvae from the western North Atlantic was by Wilson (1900) who collected specimens off Beaufort, North Carolina. There are other accounts of both amphioxus and amphioxides larvae from various parts of the world and these are discussed later in the paper.

Unlike the larvae, the occurrences of pelagic adult *Branchiostoma* are uncommon. In addition to the specimens of *B. longirostrum* and *Branchiostoma* sp. reported herein from off western Louisiana, Bedford (1900) reported metamorphosed pelagic forms of *B. belcheri* from Singapore, and Bles' (1892) "young amphioxus" from Plymouth, England may have been adults. Planktonic "young" (as well as benthic adults) of *Branchiostoma* have also been reported from Fort Wool, Virginia (Rice, 1880). The only records of pelagic adult lancelets from the Gulf of Mexico known to us consist of a single, 19-mm specimen (Dawson, 1961), two other specimens of *B. bennetti* 22.6 and 25.4 mm long (Boschung and Gunter,

1966), and four specimens (11–15 mm, probably *B. floridae*) reported by Gunter and Knapp (1951). These reported pelagic adults were relatively small and sexually immature. To our knowledge, sexually mature *Branchiostoma* have not been identified with the planktonic fauna anywhere in the world; they apparently are benthic creatures.

The purpose of this paper is to document the first large-scale collection of pelagic adult *Branchiostoma* in the western Atlantic, to report the first pelagic collection of positively-identified adult and larval *B. longirostrum*, to present evidence for the diel vertical migration of adult *Branchiostoma*, and to review and discuss their ecology relative to the world literature on pelagic lancelets.

## MATERIALS AND METHODS

A sample grid consisting of 37 stations spaced on five transects, was established off the coast of western Louisiana (Fig. 1). Lines A and E, approximately 90 km apart, extended to the continental shelf break 200 km offshore. Lines B, C, and D extended to the 18m isobath, 65 km offshore. Samples were collected on each of five cruises from December 1981 to April 1982. Because of adverse weather conditions, the December cruise sampled only line A and the outer portion of line E was not sampled in January and February.

All plankton collections were made with an opening and closing 60-cm bongo-type plankton sampler. Most collections consisted of 10-min stepped-oblique tows from near-bottom to the surface. Each tow had five steps with a retrieval rate between steps of 20m/min. Towing speed was about 1 m/sec. A flow meter was secured in each net.

In order to delineate possible vertical stratification of plankton, 10-min simultaneous surface and near-bottom horizontal tows were taken during each cruise at the following stations: A-1, A-8, B-2, B-6, C-1, C-5, D-2, D-7, E-1, and E-8. Samples analyzed were taken with a 0.335-mm mesh net, preserved in 10% buffered formalin, and later transferred into 4% buffered formalin in the lab. Temperature, salinity and dissolved oxygen data were taken with a CSTD (Guildline 8770) with oxygen probe. The dissolved oxygen readings were calibrated with Winkler titrations. A more detailed description of the materials and methods can be found in Shaw et al. (1985).

## RESULTS

A total of 453 sexually immature adult and larval *Branchiostoma* were collected between 15 December 1981 and 19 April 1982. The specimens were identifiable as three forms:

(1) Adult *Branchiostoma longirostrum*. We collected the smallest known specimens of this species at six stations (ten net collections), all at or beyond the 18 m isobath. There were 25 specimens, ranging from 6.3 to 17.8 mm TL (Table 1).

(2) Adult *Branchiostoma* species. These are clearly *Branchiostoma* but not unequivocally a described species. In some characters they are close to *B. bennetti* Boschung and Gunter (1966), whereas in other characters they agree with *B. floridae* (Hubbs, 1922; Boschung and Gunter, 1962; Howell, 1964; Harima, 1973). Because we lack sexually mature specimens we prefer not to name and describe the species at this time; herein, they will be referred to as *Branchiostoma* sp. The majority of the planktonic lancelets collected during this study were of this form. Specimens were taken at 10 stations (17 collections) between the 10 and 26 m isobaths. The 404 specimens, ranging from 9.1 to 32.2 mm TL, were all sexually immature (Table 2).

(3) Larval *Branchiostoma longirostrum*. Twenty-four larval specimens, taken at nine stations (15 collections) were collected concurrently with adult *B. longirostrum* at several stations and always at or beyond the 18 m isobath. They were "giant" larvae that ranged from 6.2 to about 8.0 mm TL with mean length of 6.9 mm (Table 3). By comparison, *B. floridae* from neighboring Mississippi Sound usually undergo metamorphosis at about 2 to 5 mm (Harima, 1973). Characters

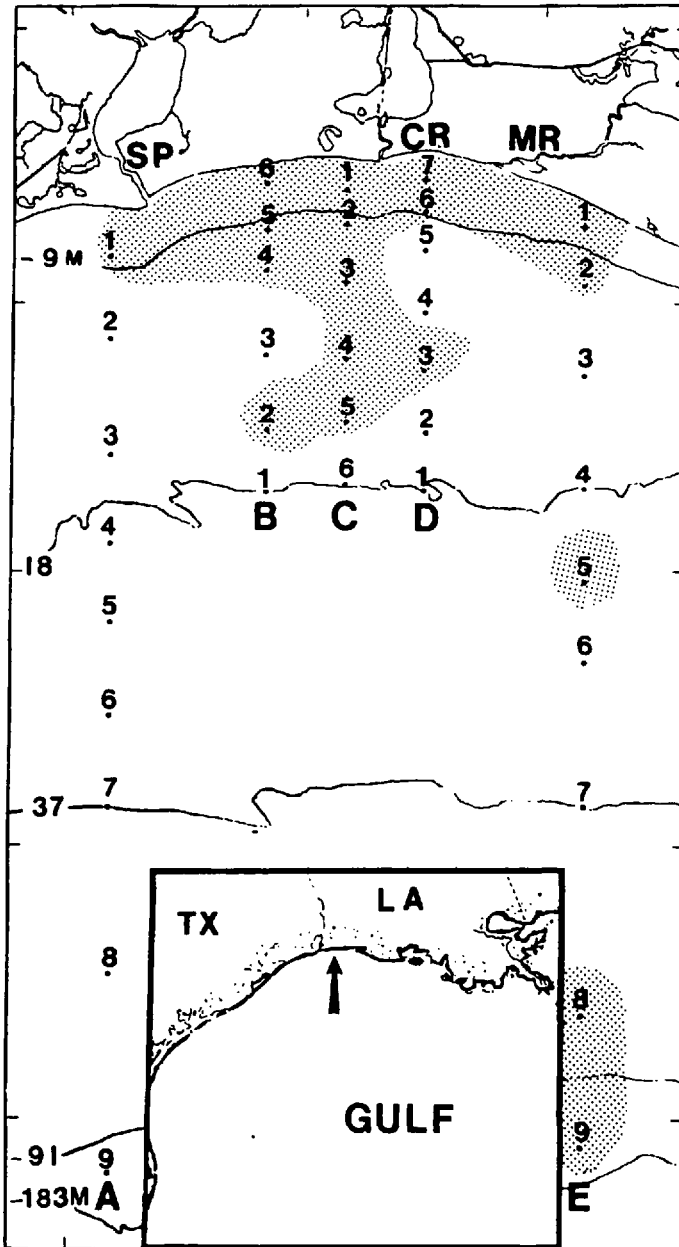


Figure 1. Cruise transects (A-E) and station locations off Sabine Pass (SP), Texas (TX) and the Calcasieu and Mermentau Rivers (CR and MR), Louisiana (LA). Depth contours (in meters) are labeled on left margin. Shaded area represents stations where lancelets were not collected.

that are established early in ontogeny, such as myotome formula and number of dorsal fin-ray chambers, agree with *B. longirostrum*.

Collectively lancelet density peaked in January with a mean of 4.6 specimens/100 m<sup>3</sup>. Mean monthly densities from December, February, March and April were 0.5, 1.2, 0.2 and 0.2 specimens/100 m<sup>3</sup>, respectively. *Branchiostoma* were

Table 1. Summary of data regarding *Branchiostoma longirostrum* adults. Tow type: 0 = stepped-oblique plankton tow, HS = horizontal surface tow, and HB = horizontal near-bottom tow. Of the two day collections (d), one was at dawn, the other at dusk. Sample or tow depth measured as meters off the bottom

Station, tow type	Date	Time	Sample depth (m off bottom)	Station depth (m)	Number, size (mm TL)	Density (No./100 m <sup>3</sup> )
A-4, 0	02/11/82	2143	3-17	18	1, 8.6	0.7
A-5, 0	12/15/81	1856	6-23	24	1, 17.8	0.4
	01/19/82	0415	2-23	24	4, 7.6-11.9	1.9
A-7, 0	12/15/81	2236	11-36	37	5, 6.3-7.0	2.4
	03/08/82	0205	13-35	36	1, 7.2	0.4
	04/17/82	0616(d)	9-33	34	1, 6.4	0.7
A-8, 0	12/16/81	0153	13-61	62	1, 6.7	0.6
A-9, HS	01/19/82	1720(d)	114	115	2, 8.5	0.8
B-1, HB	01/20/82	0401	8	18	1, 8.4	0.3
HB	02/12/81	2148	4	18	8, 8.5-13.2	5.2
Total ranges			2-114	18-115	25, 6.3-17.8	0.3-5.2

taken in waters with a wide range of environmental characters: temperatures ranged from 10.5 to 22.7°C; salinities from 27.05 to 36.25‰; and dissolved oxygen from 5.04 to 9.28 mg/per liter (Table 4). Lancelets were captured at station depths ranging from 10 to 115 m.

All specimens of adult *Branchiostoma* sp. were collected only at night (Table 2). All but three specimens of *B. longirostrum* adults were also collected at night; the exceptions were taken during dawn and dusk (Table 1). *B. longirostrum* larvae, however, were taken equally during night and day tows. The eight nocturnal collections had a mean density of 0.9 larvae/100 m<sup>3</sup>, while the 7-day collections had a mean density of 1.1. There was no difference between the length frequencies

Table 2. Summary of data regarding adult *Branchiostoma* species. Tow type code as in Table 1. Upper range in sample depths given in meters off the bottom is definitely known only for horizontal tows

Station, tow type	Date	Time	Sample depth (m off bottom)	Station depth (m)	Number, size (mm TL)	Density (No./100 m <sup>3</sup> )
A-2, 0	01/18/82	2012	1-9	10	1, 22.7	0.6
A-3, HS	01/18/82	2249	13	14	58, 15.7-25.0	48.3
HB	01/18/82	2249	3	14	265, 12.0-26.6	110.8
HS	02/11/82	1954	14	15	6, 12.8-18.7	3.8
HB	02/11/82	1954	3	15	28, 14.2-26.1	28.2
HB	04/16/82	2138	5	16	3, 19.5-23.7	2.7
A-4, 0	01/19/82	0146	4-17	18	1, 12.3	1.5
	02/11/82	2143	3-17	18	5, 10.3-18.4	4.5
	04/16/82	2341	4-19	20	3, 10.3-11.4	3.8
A-5, 0	01/19/82	0415	2-23	24	2, 14.7-16.6	1.0
A-6, HB	04/17/82	0348	1	26	2, 9.1	2.2
B-1, HB	02/12/82	2148	4	18	2, 17.7-24.2	1.3
B-3, 0	02/13/82	1919	2-11	12	7, 22.5-26.6	5.1
D-4, 0	01/21/82	0509	2-10	11	3, 15.3-16.6	3.3
D-5, 0	04/19/82	0140	5-9	10	1, 19.5	0.5
E-3, HS	02/14/82	2100	14	15	2, 11.5-21.9	1.0
HB	02/14/82	2100	8	15	15, 16.8-32.2	7.4
Total ranges			1-14	10-26	404, 9.1-32.2	0.5-110.8

for night (size range = 6.2–8.0 mm TL, N = 11) and day collections (size range = 6.4–7.8 mm TL, N = 13).

Lancelets were not collected at 18 stations and were absent from a group of stations inside or around the 11-m contour, two deep stations, and a number of stations on the mid-shelf (Fig. 1).

#### DISCUSSION

Arguments, which go beyond the scope of this paper, have persisted for many years regarding the systematics of larval lancelets (Bone, 1957; Cooper, 1903; Fuller, 1958; Gibson, 1910; Gill, 1895; Goldschmidt, 1905; 1906; 1909; 1933; Tattersall, 1903; Wickstead, 1964a; 1964b; Willey, 1906). Suffice it to say, we are dealing with three forms of *Branchiostoma*. One of which is a "giant" larval form that by definition is the "amphioxides" type, which we consider to be the larva of *B. longirostrum*. Our conclusion is based on myotome and dorsal fin-ray counts. These characters are established early in ontogeny, as early as 4 mm in *B. senegalense* (Gosselck and Kuehner, 1973), and their numbers are invariable with body length as shown by several authors, including Boschung and Gunter (1962). Since these are the only known *B. longirostrum* larvae, we cannot be sure that the amphioxides state is not typical of the species. Others have associated amphioxides larvae with the family Branchiostomatidae (Fuller, 1958; Wickstead and Bone, 1959).

There may be two larval forms within a species: one metamorphosing in loco and remaining in the benthic community; and the other leaving the benthos for a prolonged pelagic life, metamorphosing much later (Goldschmidt, 1933). A prolonged larval stage provides for a wider species distribution and may benefit lancelets relative to susceptibility to environmental changes and predation. On this latter point, if we assume that planktonic larvae and immature adults are more dispersed than semisessile benthic forms, then, the predators' perception of these lancelets would be primarily visual. In contrast, bottom dwelling predators would have the advantage of both visual and tactile cues in detecting benthic lancelets, be they larvae or adult. Adult benthic lancelets are preyed on by such demersal fish as Atlantic sturgeon, *Acipenser oxyrinchus* (Boschung and Mallory, 1956), hardhead catfish, *Arius felis* (Dawson, 1965; Harima, 1973), and leopard searobin, *Prionotus scitulus* (Ross, 1978). *Branchiostoma belcheri* larvae feed at the bottom during the day and rise to the pelagic layers at night and it has been suggested that in doing so, they protect themselves from bottom-oriented nocturnal predators, particularly penaeid shrimp (Wickstead and Bone, 1959). *Branchiostoma* larvae, however, serve as food for a number of pelagic fishes such as *Scomber colias* (Wiktor, 1970; Gosselck and Kuehner, 1973) and *Trachurus trachurus* (Gosselck and Kuehner, 1973).

Several authors contend that the habitat of lancelet larvae seems to be chiefly the sea bottom (van Wijhe, 1925, 1927; Wickstead and Bone, 1959). Lancelets of the genus *Branchiostoma* appear to be benthic spawners and the free-swimming neurulae stage (very small larvae which have a ciliated body and an adhesive substance on the anterior of the body) has been observed in dishes to leave the bottom 15 to 18 h after fertilization, but by the 40th h they returned to the bottom (Bone, 1958). It seems to us that the neurula, depending on long cilia for locomotion, would remain free of the bottom sediments until it developed muscular locomotion. However, after muscular locomotion is achieved, the larva is free to migrate in the water column. Larval *B. nigeriense* beyond the 6-gill-pouch stage

Table 3. Summary of data regarding *Branchiostoma longirostrum* larvae (notes as in Table 1 and 2 legends)

Station, tow type	Date	Time	Sample depth (m off bottom)	Station depth (m)	Number, size (mm TL)	Density (No./100 m <sup>3</sup> )
A-4, 0	03/07/82	1918	2-19	20	4, 6.2-6.9	2.3
A-5, 0	03/07/82	2012	1-23	24	1, 6.4	0.5
	04/17/82	0230	1-23	24	1, 6.9	0.9
A-8, 0	03/08/82	0502	15-59	60	1, 6.4	1.1
C-6, HS	02/13/82	1548(d)	17	18	1, 6.8	0.6
HB	02/13/82	1548(d)	6	18	2, 6.6-6.8	1.5
D-1, HS	02/14/82	0828(d)	17	18	1, 7.0	0.7
HB	02/14/82	0828(d)	4	18	2, 7.0	1.0
D-2, 0	04/18/82	2143	10-16	17	1, 6.6	0.7
E-4, 0	01/21/82	1926	2-19	20	1, 7.2	0.7
E-6, HB	02/14/82	1301(d)	4	25	1, 6.6	0.8
HB	03/10/82	0840(d)	17	25	3, 6.8-7.8	1.4
0	04/19/82	1813	6-25	26	1, 6.8	0.6
E-7, 0	03/10/82	1108(d)	6-35	36	3, 6.4-7.3	1.9
	04/19/82	2043	6-34	35	1, ca 8.0	0.6
Total ranges			1-17	17-60	24, 6.2-8.0	0.5-2.3

(20 days old) are collected only in the plankton at Logos Harbor, Nigeria; it was assumed that prior to this stage they were bottom-living (Webb 1958). Paffenhöfer (1983) found that larvae generally increase in number with increasing depth. This may be generally true during the day but the pattern is more or less reversed at night (Wickstead and Bone, 1959). Chin (1941) hypothesizes that lancelet larvae are photonegative, thus descending in the water during the day. Flood et al. (1982) report a slight tendency for diel vertical migration.

Some authors contend that there is no evidence suggesting larvae make diel vertical migrations (John et al., 1981; Gosselch and Kuehner, 1973); however, the latter authors emphasize the role upwelling plays in the vertical and horizontal drift of plankton. Webb (1969) says that *B. lanceolatum* larvae occur at different depths as a result of their alternating upward swimming and sinking behavior (van Wijhe, 1927; Webb and Hill, 1958).

Larvae and adults from the Louisiana shelf were found in all parts of the water column (Tables 1, 2 and 3). Even at one of our deepest stations, 115 m, two *B. longirostrum* adults had evidently migrated to the surface (Table 1). As mentioned previously adult *Branchiostoma* were collected only at night. Such an observed distribution could support two hypotheses: diel vertical migration or daytime net avoidance. The absence of adult specimens from 67 daytime oblique tows and 20 daytime near-bottom horizontal tows (vs. 53 oblique and 14 surface and near-bottom nocturnal tows) strongly supports the diel vertical migration hypothesis. *Branchiostoma longirostrum* larvae, however, were collected equally during day (7 collections; density = 1.1 larvae/100 m<sup>3</sup>) and night (8 collections; density = 0.9). Although the sample size was small (N = 24), the frequency of occurrence, density and length data (daytime range = 6.4-7.8 mm TL vs. night = 6.2-8.0 mm) suggest that for larvae at least, daytime net avoidance does not appear to be a significant factor.

Wickstead and Bone (1959) estimated that 3.6-5.2 mm lancelet larvae can move vertically 6.5 mm/sec (23.4 m/h). Based on the calculations of Webb and Hill (1958) for *B. nigeriense*, 2.5 mm larvae passively sink 1 cm in 20 seconds

(1.8 m/h), 3.5 mm larvae sink at a rate of 3.6 m/h, and larvae 5–6 mm sink 9 m/h. The Louisiana larvae are larger than these, but assuming an upward migration rate of 23.4 m/h as minimum, they would require 5 h to swim to the surface from 115 m (10 h for an active round trip) and a conservative estimate of about 13 h to passively sink to the bottom. This is clearly ample time for vertical migration, even in the deepest water sampled. Sinking passively conserves energy, and the larger the lancelet the faster it sinks; therefore, the amphioxides type larvae could afford to occupy deeper water, having the time to make longer vertical migrations.

On the Louisiana shelf spawning appears to be protracted, since pelagic larval lancelets appear in January through April (last month of sampling) with no significant difference in size from one month to the next (Table 3). Neighboring *B. floridae* apparently spawns in July and August, while *B. virginiae* spawns from April to August off Georgia based on gonadal development (Frankenberg, 1968, 1971). *B. nigeriense* spawns between August and November and is thought to live for only 1 year, growing to a length of 30 mm (Webb, 1958). *B. belcheri*, however, spawns twice from May to July and again in December, lives for 3 or 4 years, and grows to a large size, having a growth rate similar to *B. nigeriense* (Chin, 1941). *B. lanceolatum* reportedly spawns between May and September at Faro near Messina (Willey, 1891), in late May to early June at Naples (Bone, 1958), in June at Helgoland (Webb, 1969), and in July–August and also from December to February in the inshore waters of Madros, India (Azariah, 1965). The consensus regarding the time of day of spawning is just after sunset (Willey, 1891; Bone, 1958; Webb, 1958; and others).

The planktonic larval stage is believed to be greater than 55 days (Bone, 1958) after which contact with the bottom sediments may trigger metamorphosis (Wickstead, 1964b). The larval stage duration of *B. nigeriense* is usually about 75 days but can be as long as 140 days (Webb, 1958). If this is approximately true for the Louisiana lancelets, spawning took place as late as mid-October, but possibly earlier since amphioxides larvae have extended metamorphoses. In the brackish lagoons of Nigeria, lancelets are in the plankton for a 9-month period from mid-September to mid-June, when the local salinity is high enough for their survival (Webb, 1958).

Salinities on the west Louisiana shelf are hardly expected to be a limiting factor for lancelets (Table 4). Although salinity fluctuates somewhat throughout the year, it is not known to become critically low. However, in Mississippi Sound a sudden drop in salinity due to a rain storm caused mass mortality in *B. floridae* (Dawson, 1965). Lancelet mortality due to fresh water in Mississippi Sound is not a predictable annual event as is the intrusion of fresh water into Nigerian lagoons. *Branchiostoma floridae* from Mississippi Sound have been collected in salinities ranging from 15.5 to 33.1‰ (Boschung and Gunter, 1962). Lethal maximum and minimum salinities for *Branchiostoma* vary with species, stage of development, and duration of exposure. Under hyposmotic conditions emaciation or death is probably caused by cessation of solenocytes and gill cilia. Adult *B. belcheri* appear to be comparatively stenohaline, their salt tolerance being between 19 and 29‰ (Chin, 1941). *Branchiostoma nigeriense* appear to be even more tolerant, with a lower threshold for larvae and adults near 13‰, while adults in evaporating sea water survived until about 60‰ (Webb and Hill, 1958). They also showed experimentally that adults can withstand diurnal fluctuations of salinity ranging from 14.5 to 31‰. The lower threshold salinity for *B. lanceolatum* is about 18‰ (Binyon, 1981).



Table 4. Summary of environmental data from all stations where lancelets were collected from 15 December 1981 to 19 April 1982. Tow type as in Tables 1-3. The range in values for temperature, salinity and dissolved oxygen (DO) are presented from throughout the water column for stations where oblique plankton tows were taken and from the appropriate depth for stations where horizontal tows were taken. (B) = DO value available only from bottom level; (S) = DO value available only from surface

Station, tow type	Date	Temperature range (°C)	Salinity range (‰)	DO range (mg/l)
A-2, 0	01/18/82	10.5-10.7	30.16-30.82	—
A-3, HS	01/18/82	12.8	33.18	—
HB	01/18/82	12.3	33.16	9.28
HS	02/11/82	13.1	34.86	7.91
HB	02/11/82	13.1	34.85	8.01
HB	04/16/82	19.7	30.01	—
A-4, 0	01/19/82	13.5-14.0	34.12-35.19	8.12(B)
	02/11/82	14.3	35.83-35.84	7.58-7.65
	03/07/82	15.7-15.8	33.86-33.92	—
	04/16/82	20.0-20.6	33.30-34.26	—
A-5, 0	12/15/81	20.2-20.3	35.69	7.76
	01/19/82	14.2-14.4	35.23-35.35	8.03
	03/07/82	16.0-16.2	33.88-34.09	8.01(S)
	04/17/82	20.2-21.0	34.68-34.81	—
A-6, HB	04/17/82	20.0	35.44	—
A-7, 0	12/15/81	21.1-21.7	34.84-35.51	7.28-7.42
	03/08/82	17.6	36.15-36.17	—
	04/17/82	20.3-20.8	35.96-36.25	—
A-8, 0	12/15/81	22.2-22.6	35.58-35.85	7.28-7.40
	03/08/82	18.9-19.0	36.20-36.22	—
A-9, HS	01/19/82	21.0	36.19	—
B-1, HB	01/20/82	14.2	35.17	—
HB	02/12/82	13.7	34.98	7.93
B-3, 0	02/13/82	12.8	33.13-33.14	8.51(B)
C-6, HS	02/13/82	14.3	34.92	—
HB	02/13/82	14.3	34.91	7.79
D-1, HS	02/14/82	14.5	35.02	—
HB	02/14/82	14.5	35.02	7.64
D-2, 0	04/18/82	21.3	32.23-32.26	—
D-4, 0	01/21/82	13.0-13.1	32.81-33.25	—
D-5, 0	04/19/82	21.0-21.1	27.05-27.22	—
E-3, HS	02/14/82	12.3	28.65	—
HB	02/14/82	12.4	28.92	8.01
E-4, 0	01/21/82	15.2-16.3	35.06-35.41	—
E-6, HB	02/14/82	16.7	35.30	5.04
HB	03/10/82	17.7	35.61	7.55
0	04/19/82	21.1-22.3	35.89-36.02	6.97(B)
E-7, 0	03/10/82	17.8-18.0	36.20-36.22	7.50(B)
	04/19/82	20.7-22.7	36.16-36.23	7.01(B)
Total ranges		10.5-22.7	27.05-36.25	5.04-9.28

One explanation, however, for the observed absence of *Branchiostoma* from 18 of our plankton stations, may be bottom sediment type. The nature of the bottom sediments has been found to be the main distributional factor for the three species of lancelets in the Gulf of Thailand (Piyakarnchana and Vajropala, 1961). All available information on occurrences, abundances, and preferred surface-sediment type show that virtually all *Branchiostoma* species are restricted to coarse sand or sandy-shell bottom substrates (Webb and Hill, 1958; Frankenberg, 1968); and are generally absent from bottoms with high proportions of silt or fine

sand (Chin, 1941). *Branchiostoma bennetti*, however, appears to be the exception to this pattern, having soft bottom morphometric adaptations such as cirri studded with numerous and relatively long lateral projections which serve as a finer first filter (Boschung and Gunter, 1966).

On a macroscale, the continental shelf sediment type in our sampling area has been characterized as being coarse grained (i.e., sand or mixed sand) with the exception of two areas in the vicinity of our A-1, E-8 and E-9 stations, which are reported to have fine grained sediments composed of silt and clay (Darnell et al., 1983). On the microscale, Gaston and Weston (1983) reported on sediment analyses done on a small area encompassing our inner station category ( $\leq 11$  m depth) mentioned earlier. They found this area's sediments to be composed of silty clay, sand-silt-clay, and clayey silt. Sediment type would therefore appear to explain the absence of larval and adult *B. longirostrum*, at least from our inner shelf and deep station categories. Perhaps the mid-shelf absences would also be explained in this fashion if we had additional microscale sediment data from that area.

Life history reports regarding lancelets in general are contradictory, confusing, and incomplete. Confusion may arise from different species having different reproductive strategies, and from reports that within a species there may be two types of larvae, each with its own unique set of life history requirements.

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