Proceedings of the National Shellfisheries Association
Volume 60 — June 1970

LARVAL DEVELOPMENT OF THE HOOKED MUSSEL, *BRACHIDONTES RECURVUS* RAFINESQUE (BIVALVIA: MYTILIDAE) INCLUDING A LITERATURE REVIEW OF LARVAL CHARACTERISTICS OF THE MYTILIDAE [1]

Paul Chanley [2]
VIRGINIA INSTITUTE OF MARINE SCIENCE
GLOUCESTER POINT, VIRGINIA

ABSTRACT

Brachidontes recurvus *larvae were reared from eggs in the laboratory. Larval length increased from 90-220 μ during shelled stages with straight-hinge stage from 90-165 μ, umbo stage from 135-220 μ, and pediveliger stage from 165-220 μ. Height was 23 ± 10 μ less than length. Depth was 54 ± 15 μ less than length. The hinge line increased with growth and ranged from 68-84 μ. Hinge structure consisted of small taxodont hinge teeth over the entire hinge line with teeth becoming larger at both ends. Larvae are typical D-shaped mytilid larvae during straight-hinge stages but develop a conspicuous, broadly rounded umbo and steeply sloping shoulders. Ends are blunt and the ventral margin flattened. The eyespot appears at a length of about 165 μ.*

Larvae are more likely to be confused with larvae of Modiolus demissus *than those of other bivalves.*

INTRODUCTION

Brachidontes recurvus, the hooked mussel, reportedly occurs from Cape Cod to the West Indies (Abbott, 1954). Truly indigenous populations are likely to have a much more limited distribution. Hooked mussels north of New Jersey probably were imported with commercial shipments of oysters and do not represent permanent populations.

B. recurvus is the most common subtidal mussel in the brackish waters of Chesapeake Bay, sometimes so abundant it becomes a serious fouling problem on oyster beds. Because of this, the hooked mussel has been the subject of more studies than most bivalves that are not commercially harvested (Chanley, 1958; Allen, 1960; Nagabhushanam, 1965).

In upper Chesapeake Bay *B. recurvus* spawns from June until November with peaks of spawning activity in June, late July and in November (Allen, 1962). Larvae taken in plankton samples by Allen were classified as "pre-hinge" and "post-hinge." No more detailed description of larval *B. recurvus* has been found in the literature.

The purpose of this report is to describe the larval development of the hooked mussel and to compare its larvae to those of other mytilids by means of a comprehensive literature review of larval development in the Mytilidae.

MATERIALS AND METHODS

Mussels from Horsehead Shoals in the James River were kept in the laboratory in heated, running sea water at 23-25°C from mid-March until 2 May at a salinity of about 20 ppt. Several mussels spawned in less than an hour when placed in Pyrex baking dishes containing filtered sea water fluctuating between 20 and 32°C. Previous attempts to spawn *B. recurvus* by rapidly fluctuating water temperature, adding stripped gametes to the water and stretching or injuring adductor muscles were unsuccessful though the mussels were apparently sexually mature.

Fertilized eggs were first poured through a stainless steel screen to remove debris, and

---

[1] Contribution No. 336, Virginia Institute of Marine Science.

[2] Present address — O/SD Sea Farms, Inc., 502 Colony Street, Melbourne Beach, Florida.

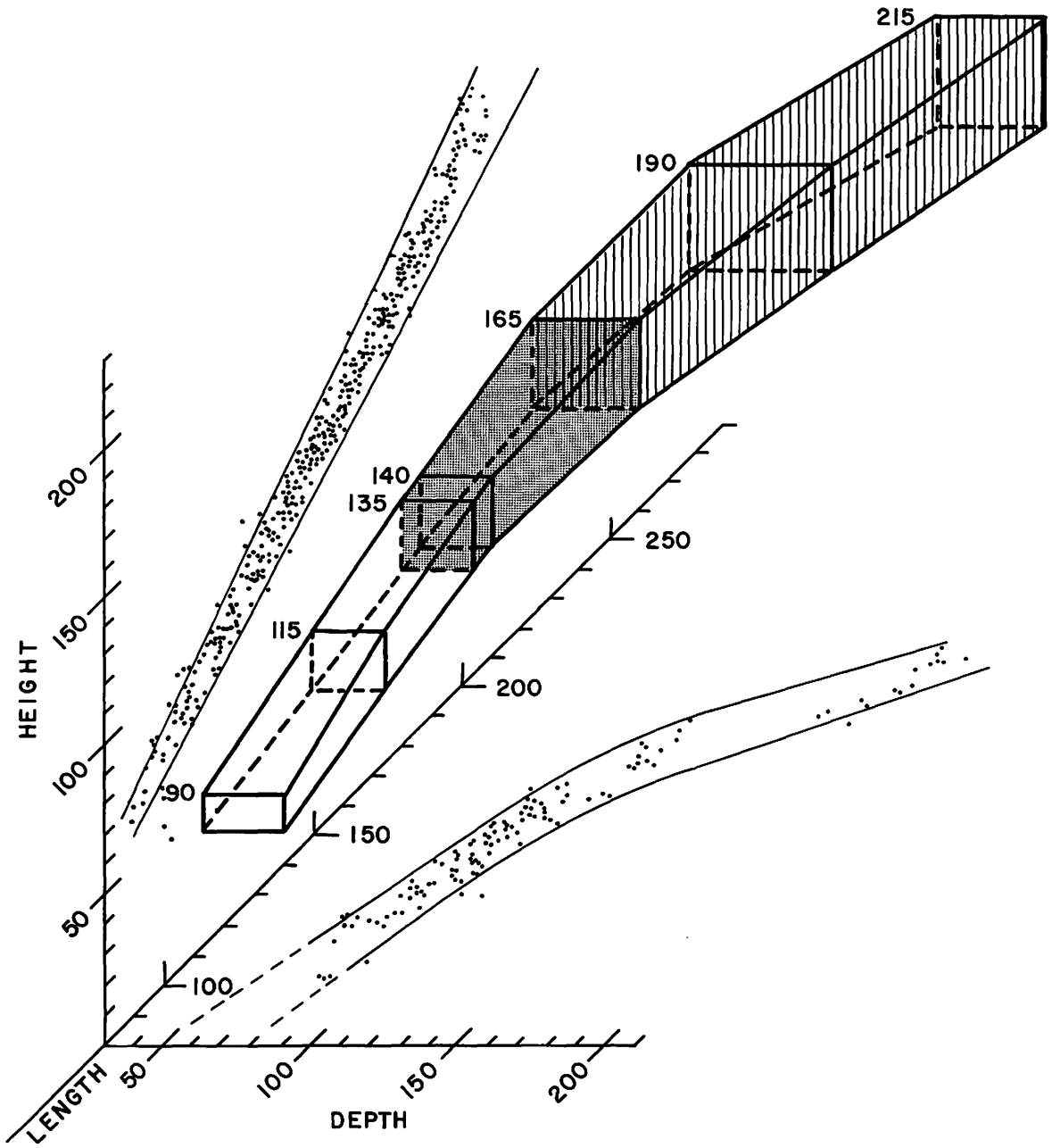

FIG. 1. *Larval dimensions of* Brachidontes recurvus. *Height and depth coordinates run parallel to the length axis. Dots represent observed length-height, or length-depth measurements. Lines enclosing the dots were fitted by eye and represent probable maximum and minimum dimensions. The 3-dimensional figure encompasses all possible length-depth-height combinations of* B. recurvus *larvae (Chanley and Van Engel, 1969). The clear area represents straight hinge stages, the lined area, umbo stages and the darkest area, intermediate stages.*

then cultured at concentrations of about 30/cc in polyethylene garbage pails containing filtered sea water. Larval concentrations were adjusted to 15/cc after two days. Three times a week water was changed by siphoning it through a stainless steel screen of appropriate mesh size to collect the larvae. Larvae were maintained at about 25°C in water of 18-22 ppt and were fed daily at the rate of one liter of a unialgal culture of *Mocochrysis lutheri* for each 70 liters of larval culture. Periodically larvae were examined microscopically and preserved in Carriker's (1950) fixative. A minimum of 10 were measured at each 5 μ length interval. Measurements, using a filar micrometer, were made of hinge-line length, total length, height and depth.

In this report dimensions are given in microns: L = length, the maximum anterior-posterior dimension; H = height, the maximum dorsal-ventral dimension, and D = depth, the maximum left-right dimension. Descriptive terminology is that used by Chanley and Andrews (in press).

RESULTS

Spawned eggs of *B. recurvus* were greenish tan to brown. They ranged from 62-68 μ and averaged 65 μ in diameter.

Larval dimensions (Fig. 1)

Straight-hinge stage: L = 90-165 μ; H = 60-150 μ; D = 67-115 μ, generally increasing more slowly

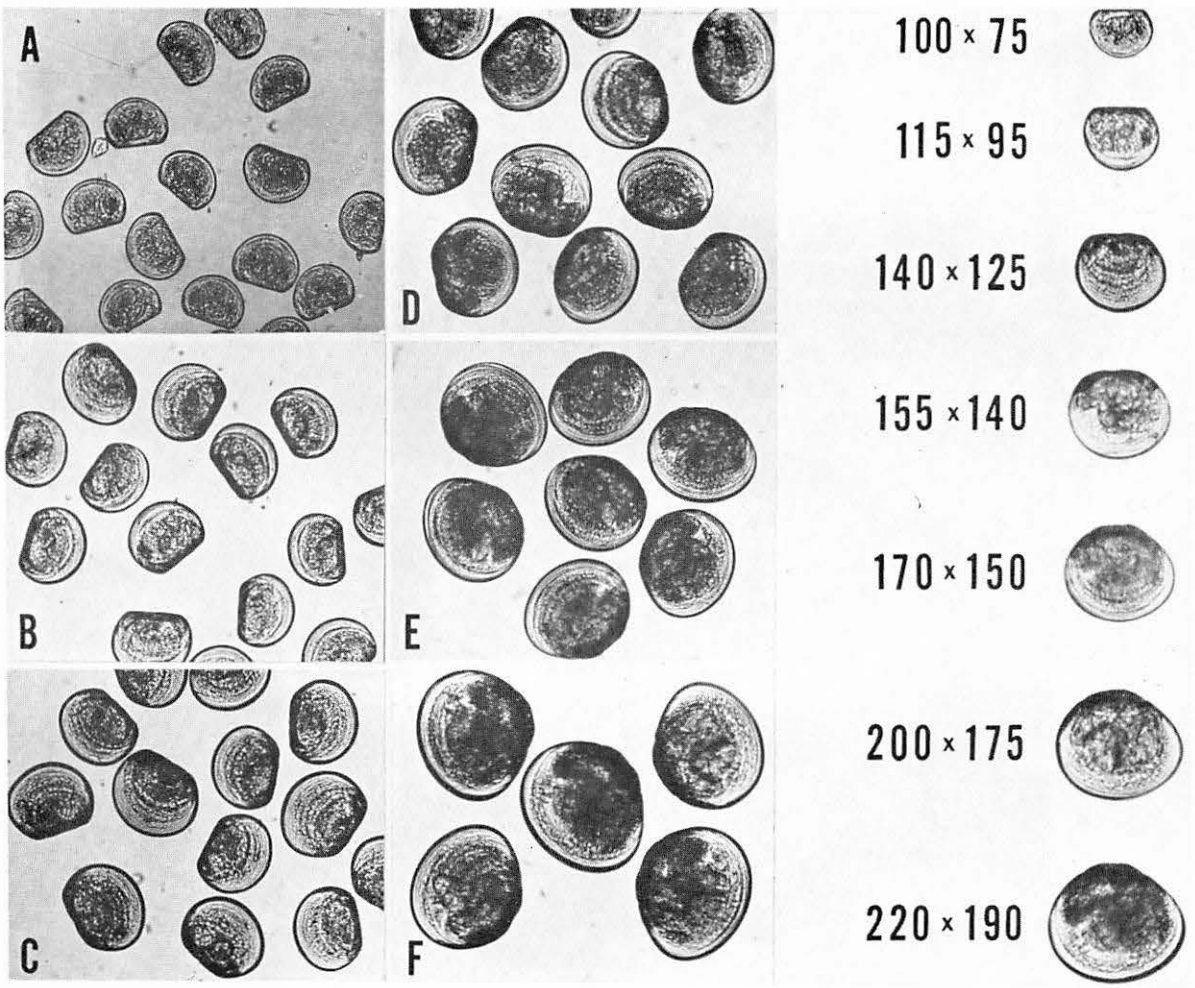

FIG. 2. *Photomicrographs of* B. recurvus *larvae. Length x height measurements are given in microns under larvae at right. These larvae are arranged with anterior end right. A. One-day old larvae about 100-110 μ long. B. Four-day old larvae about 115-125 μ long. C. Five-day old larvae about 130-140 μ long. D. Larvae about 140-160 μ long. E. Larvae about 165-175 μ long. F. Larvae about 195-215 μ long.*

than length; L—23 μ = H $\pm$ 9; L—52 μ = D $\pm$ 13 μ. Hinge line initially 68-76 μ, increasing to 72-84 μ at L = 120 μ.

Umbo stage: L = 135-220 μ; H = 101-199 μ; D = 81-184 μ; L—23 μ = H $\pm$ 11 μ; L—56 μ = D $\pm$ 12 μ.

Pediveliger stage: Minimum length with functional foot = 165 μ. Maximum length with functional velum = 220 μ.

Larval shape (Fig. 2)

Straight-hinge stage: Larvae D-shaped; hinge line proportionately long; shoulders almost straight, sloping steeply, posterior shoulder shorter and sloping more steeply than anterior; ends blunt, posterior higher and more pointed than anterior; anterior slightly longer than posterior in late straight-hinge stages; ventral margin rounded, but elongated, not hemispherical.

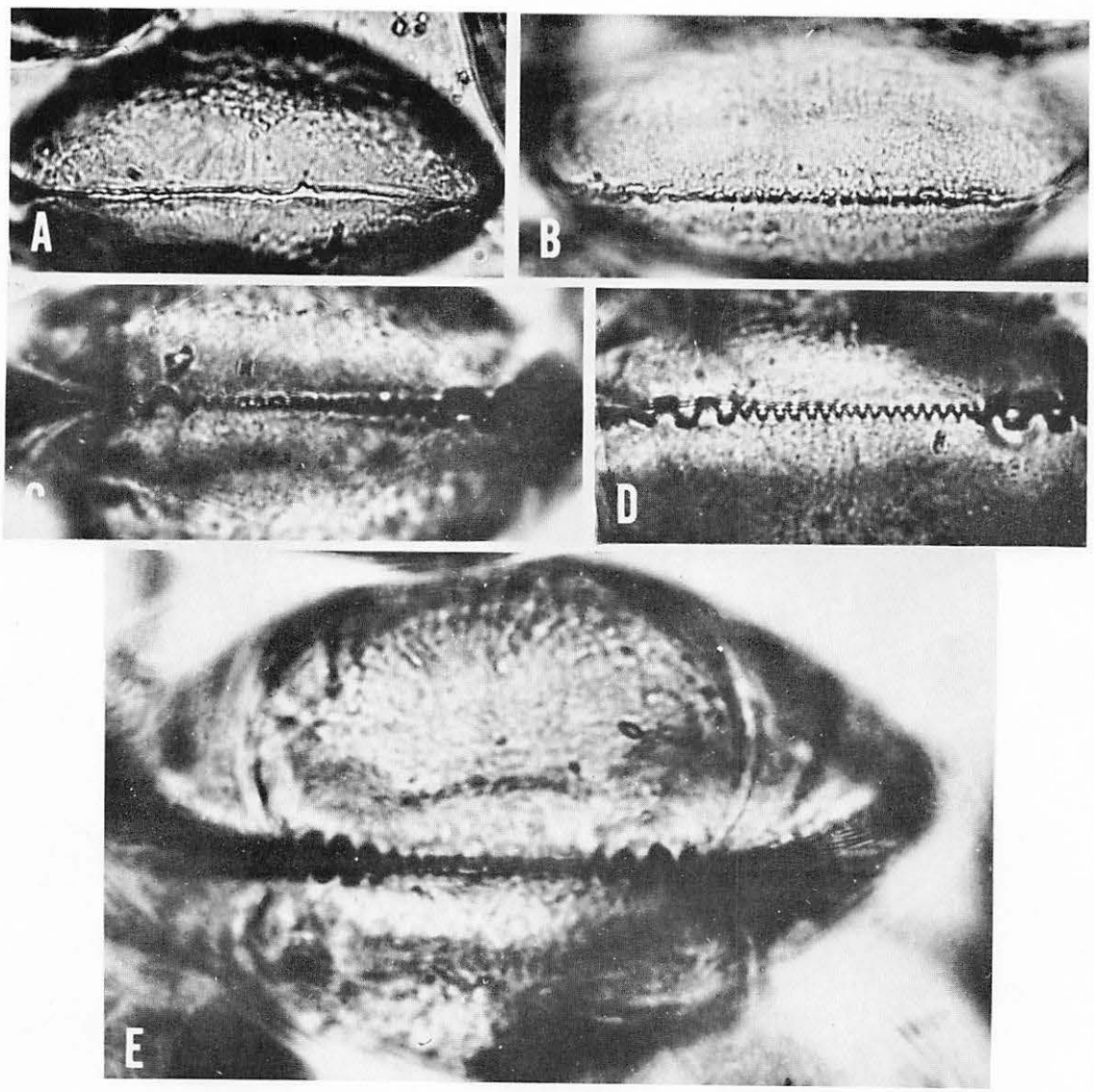

FIG. 3. *Hinge structure of larval* B. recurvus. *Anterior end is left. A. Dorsal view of hinge of larvae 105 μ long. B. Ventral view of hinge of larva 105 μ long. C. Dorsal view of hinge of larva 120 μ long. D. Dorsal view of hinge of larva 135 μ long E. Dorsal view of hinge of larva 180 μ long.*

Umbo and pediveliger stages: Umbo appearing as rounding of hinge line at about 150 μ, becoming more conspicuous and broadly rounded in late stages; shoulders almost straight, anterior longer than posterior and not sloping as steeply; posterior end blunt, anterior end longer and more sharply pointed; ventral margin markedly elongated, but still rounded, not hemispherical.

Anatomy

Shell appearing heavy and thick; apical flagellum present, but rarely displayed; velar cilia about 25 μ long; larvae dark, brown, antero-ventral margin frequently darker and reddish brown in larvae over 165 μ; eyespot appearing at 165 μ, small, indistinct but becoming conspicuous at about 180 μ, eventually 10 μ in diameter; pediveligers first appearing in 11 days.

Hinge structure (Fig. 3)

Hinge originally undifferentiated (Fig. 3A); within one or two days many small taxodont central teeth and two larger teeth develop at both ends of hinge line in each valve (Fig. 3B), increasing to 3 or 4 large teeth with growth (Figs. 3C, 3D, 3E). No ligament evident.

DISCUSSION

Larvae of many mytilid species have been described (Table 1). Some have non-pelagic development (Thorson, 1935); others differ widely in shape. However, most pelagic larval Mytilidae have many common characteristics. The hinge line is long, in relation to other dimensions, and increases in length with larval growth. Hinge-line length does not increase with growth in larvae of most bivalves. Dentition, in mytilid larvae, usually consists of a series of taxodont teeth over the entire hinge line, but with larger teeth near the ends. The umbo is usually late in developing and remains low, rounded, and inconspicuous. The larval umbo is more pronounced in the genus *Modiolus*. The anterior end is rounded but not nearly as blunt as the posterior. This and the inconspicuous umbo give larvae a decided egg shape. The color is usually "dark" or some shade of brown. Mytilid larvae attain a comparatively large pelagic size, frequently in excess of 300 μ. Juveniles remaining pelagic by means of entrapped air, byssus floats or drifting algal substrates (Nelson, 1928; Bayne, 1964) have been taken in plankton samples and have undoubtedly led to some reports of extremely large larvae. Nonetheless, larvae of mytilids generally set at larger sizes than do larvae of most other bivalves. There is frequently much variation in setting size among larvae of the same species (Nelson, 1928; Bayne, 1965).

Larvae of *B. recurvus* have many characteristics common to larval Mytilidae. For example, the hinge line is long and has a typical mytilid dentition, larvae appear dark or coarse and thick shelled and the ends are rounded, with the anterior more pointed than the posterior. When they first develop a shell, *B. recurvus* larvae are not appreciably smaller than most mytilid larvae. However, they set at a smaller size (165-220 μ) and develop a broader, more conspicuous umbo at a smaller size than most mytilid larvae.

Other species of Mytilidae that occur in the same geographic range as *B. recurvus* include *Mytilus edulis, Modiolus demissus* and *Amygdalum papyria.* Larvae of *M. edulis* can be readily differentiated by their more rounded ventral margin and less conspicuous umbo, which is no more than a rounding of the hinge line below L = 220 μ. The hinge structure of larval *M. edulis* is also much weaker. Teeth are lacking in the central portion of the hinge and are small at the ends.

Larval *M. demissus* are similar to *B. recurvus* in appearance and are virtually indistinguishable from L = 150 to 200 μ. In earlier stages the straight hinge line of larval *M. demissus* is longer (85 μ) and the umbo appears somewhat later. *M. demissus* larvae have a minimum length of about 105 μ and a maximum of about 300 μ. Their hinge structure has not been described.

A. papyria larvae have a more pointed anterior end, and a shorter hinge line (50-70 μ) than larval *B. recurvus.* They develop a broad knobby umbo at only 110-125 μ.

Larvae of *B. recurvus* can be distinguished from most other bivalve larvae by their hinge, heavy appearance and dimensions. They resemble larval *M. mercenaria* and other venerid larvae in shape and dimensions but have a much flatter ventral margin and entirely different hinge structure.

ACKNOWLEDGMENTS

I am grateful to Mrs. Juanita Tutt, Miss Judy Ward and Mrs. Phyllis Howard of the Microbiology Department of the Virginia Institute of Marine Science for providing the algal food and helping culture and measure the larvae. I am also indebted to Mrs. Jane Davis, also at the Virginia Institute of Marine Science, for preparing the illustrations.

LITERATURE CITED

Abbott, R. T. 1954. American Seashells. Van Nostrand, Princeton, N. J., 541 p.

Allen, J. F. 1960. Effect of low salinity on survival of the curved mussel *Brachidontes recurvus.* Nautilus, 74:1-8.

Allen, J. F. 1962. Gonad development and spawning of *Brachidontes recurvus* in Chesapeake Bay. Nautilus, **75**:149-156; (continued) **76**:9-16.

Bayne, B. 1964. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). J. Anim. Ecol. **33**:513-523.

Bayne, B. 1965. Growth and delay of metamorphosis of the larvae of *Mytilus edulis* (L.). Ophelia, **2**:1-47.

Borisiak, A. 1909. Pelecypoda du plankton de la Mer Noire. Bull. Sci. Fr. Belg. **42**:149-181.

Breese, W. P., R. E. Williamson and R. E. Dimick. 1963. Stimulation of spawning in the mussels, *Mytilus edulis* Linnaeus and *Mytilus californianus* Conrad, by kraft mill effluent. Biol. Bull. **125**:197-205.

Carriker, M. R. 1950. Killing and preservation of bivalve larvae in fluids. Nautilus, **64**:14-17.

Chanley, P. 1958. Survival of some juvenile bivalves in water of low salinity. Proc. Nat. Shellfish. Ass. **48**:52-65.

Chanley, P. and J. D. Andrews. (In press). Aids for identification of bivalve larvae of Virginia. Malacologia.

Chanley, P. and W. A. Van Engel. 1969. A three-dimensional representation of measurement data. Veliger, **12**:78-83.

Culliney, J. (In press). Laboratory rearing of the larvae of the mahogany date mussel, *Lithophaga bisulcata*. Bull. Mar. Sci.

Field, I. A. 1923. Biology and economic value of the sea mussel *Mytilus edulis*. Bull. U.S. Bur. Fish. **38**:127-259.

Hayashi, T. and K. Terai. 1964. Study on the larvae and youngs of Japanese surf clam, *Spisula (S) sachalinensis* (Schrenck), at Shikuzu, Muroran City. I. Taxonomy of the Pelecypoda's veliger larvae in plankton. Sci. Rep. Hokkaido Fish. Exp. Sta. **2**:7-38.

Jørgensen, C. B. 1946. Reproduction and larval development of Danish marine bottom invertebrates. 9. Lamellibranchia. Medd. Komm. Havundersøg. Kbh., Ser. (d): Plankton, **4**:277-311.

Kändler, R. 1926. Muschellarven aus dem Helgoländer Plankton. Bestimmung ihrer Artzugehörigkeit durch Aufzucht. Wiss. Meeresunters., N.F. Abt. Helgoland, **16**(5):1-8.

Loosanoff, V. L. and H. C. Davis. 1963. Rearing of bivalve mollusks. Advan. Mar. Biol. **1**:136.

Loosanoff, V. L., H. C. Davis and P. Chanley. 1966. Dimensions and shapes of larvae of some marine bivalve mollusks. Malacologia, **4**:351-435.

Lovén, S. 1848. Bidrag till Kännedomen om Utvecklingen af Mollusca. Acephala Lamellibranchiata. Stockholm.

Matthews, A. 1913. Notes on the development of *Mytilus edulis* and *Alcyonium digitatum* in the Plymouth Laboratory. J. Mar. Biol. Ass. U.K. **9**:557-560.

Miyazaki, I. 1935. On the development of some marine bivalves, with special reference to the shelled larvae. J. Imp. Fish. Inst. **31**:1-10.

Nagabhushanam, R. 1965. The influence of salinity and temperature upon the heart rate in the bivalve mollusc, *Brachidontes recurvus*. Sci. Cult. **31**:318-319.

Nelson, T. C. 1928. Pelagic dissoconchs of the common mussel, *Mytilus edulis*, with observations on the behavior of the larvae of allied genera. Biol. Bull. **55**:180-192.

Newell, G. E. and R. C. Newell. 1963. Marine Plankton. Hutchinson Educational Ltd., London, 207 p.

Odhner, N. H. 1914. Notizen über die Fauna der Adria bei Rovigno. Beiträge zur Kenntnis der marinen Molluskenfauna von Rovigno in Istrien. Zool. Anz. **44**:156-170.

Rees, C. B. 1950. The identification and classification of lamellibranch larvae. Hull Bull. Mar. Ecol. **4**(27):21-46.

Stafford, J. 1912. On the recognition of bivalve larvae in plankton collections. Contrib. Can. Biol. 1906-1910:221-242.

Sullivan, C. M. 1948. Bivalve larvae of Malpeque Bay, P.E.I. Bull. Fish. Res. Bd. Can. No. 77, 36 p.

Thorson, G. 1935. Biologische Studien uber die Lamellibranchier *Modiolaria discors* L. und *Modiolaria nigra* Gray in Ostgrönland. Zool. Anz. **111**:297-304.

Wells, W. F. 1927. Report of experimental shellfish station. Sixteenth Annu. Rep. N.Y. State Conserv. Dep., p. 5-22.

Werner, B. 1939. Über die Entwicklung und Artunterscheidung von Muschellarven des Nordseeplanktons unter besonderer Berücksichtigung der Schalenentwicklung. Zool. Jahrb., Abt. Anat. Ontog. **66**:1-54.

Yoshida, H. 1936. On the pelagic larvae and youngs of *Mytilus crassitesta* Lischke. Venus, **6**:22-31.

Yoshida, H. 1937. On the pelagic larvae and youngs of *Brachidontes senhausi* (Reeve). Venus, **7**:121-128.

Yoshida, H. 1953. Studies on larvae and young shells of industrial bivalves in Japan. J. Shimonoseki Coll. Fish. **3**:1-106.

Zakhvatkina, K. A. 1959. Larvae of bivalve mollusks of the Sevastopol region of the Black Sea. Akademia Nauk SSSR. Trudy Sevastopol'skoi Biologischeskoi Stantsii **11**:108-152. (Translated by E. Wells. Virginia Institute of Marine Science Translation Series No. 15, 1966)

TABLE 1. *A Summary of Published Descriptions of Larval Mytilidae*

Nominal Taxa	Reference	Descriptions
Adula simpsoni (Marshall)	Rees (1950)	Large (figured specimen over 300 μ) rich brown larvae. Length considerably greater than height.
Brachidontes senhausi (Reeve)	Yoshida (1937; 1953)	Length to at least 240 μ. Height about 30 μ less. Pediveligers 230 to 290 μ with pigmented eyespot. Many minute teeth along hinge.
Crenella decussata (Montagu)	Jørgensen (1946)	Prodissoconch is 750 μ.
Lithophaga bisulcata (Orbigny)	Culliney (in press)	Length 92-400 μ. Hinge line 66μ. Umbo develops at 140-160 μ. Pediveliger 300-400 μ.
Modiola adriatica (Lamarck)	Jørgensen (1946)	Development probably non-pelagic. Prodissoconch about 1 mm.
	Zakhvatkina (1959)	Length to 378 μ. Anterior end longer and narrower than posterior. Umbo low, wide and distinct. Hinge with taxodont dentition. Teeth at ends larger than distinct central teeth.
Modiola modiolus (L.)	Jørgensen (1946)	Prodissoconch about 400 μ.
Modiolaria discors (L.)	Thorson (1935)	Non-pelagic larvae.
Modiolaria marmorata (Forbes)	Lovén (1848) Jørgensen (1946)	Minimum size 80 μ. Larvae set at 320-400 μ. Shells orange with purple flat umbo. Anterior end more pointed and shorter than posterior. Eyespot and statocyst evident. Hinge with taxodont dentition and central ligament. Teeth larger at both ends of hinge.
Modiolaria nigra (Gray)	Thorson (1935)	Non-pelagic. Lengths 112 to 205 μ. Height 20-25 μ.
Modiolus demissus (Dillwyn)	Sullivan (1948)	Length 112-205 μ. Height 20-25 μ less. Bulky thick shell with dark outline. Heavy yellow brown. Posterior shoulder higher and steeper than anterior. Umbones project prominently.
	Loosanoff and Davis (1963)	Length 105-305 μ. Pediveligers with eyespots 220-305 μ. Most set at 275 μ.
	Loosanoff, Davis and Chanley (1966)	Length 105-305 μ. Height 20-60 μ less; difference increasing with growth. Dark brown. Long hinge line becomes rounded at 160 μ and knobby at about 220 μ. Pediveliger 200-305 μ. Most set at 275 μ.
Modiolus modiolus (L.)	Rees (1950)	Length to 315 μ. One end pointed. Knobby umbo in late stages. Blunt end droops ventrally.
	Newell and Newell (1963)	Umbo more pronounced and shell more massive than *M. edulis*.

Musculus marmoratus (Forbes)	Rees (1950)	One end pointed, other blunt and drooping ventrally. Umbo knobby but inconspicuous at 260 μ.
Mytilacea	Rees (1950)	Distinctive hinge with minute taxodont teeth over entire hinge line. Teeth larger near ends. Ligament posterior.
Mytilaster lineatus (Gmelin)	Zakhvatkina (1959)	Length 105-312 μ. Height 96-290 μ. Hinge line 95 μ. Anterior end longer and narrower than posterior. Hinge taxodont with larger teeth at both ends.
Mytilidae	Odhner (1914)	Characterized by medium umbo, taxodont hinge and eyed stage.
	Hayashi and Terai (1964)	Three types of larvae shown. Lengths 283-413 μ. Height 10-45 μ less. One type with small umbo. Pediveliger over 400 μ had large umbo and straight ventral margin. All with anterior more pointed than posterior.
Mytilus californianus (Conrad)	Breese, Williamson and Dimick (1963)	Length of straight-hinge larvae much longer than height. Hinge line long.
Mytilus crassitesta (Lischke)	Miyazaki (1935)	Length 95-203 μ. Height 23-33 μ less. Hinge line 71 μ increasing to 85 μ. Umbo small, yellow, inconspicuous. Anterior end more pointed than posterior. Eyespots and statocyst present in pediveliger.
	Yoshida (1936; 1953)	Larvae set at 280-320 μ. Height about 30 μ less than length. Umbo small. Anterior end more pointed than posterior.
Mytilus edulis (Linné)	Borisiak (1909)	Taxodont hinge teeth, long hinge line. Anterior end more pointed than posterior.
	Stafford (1912)	Length to 400 μ. Hinge line long. Length much greater than height. Umbo appears at about 140 μ. Posterior much deeper than anterior at 172 μ as foot and gills appear. At 275 μ pediveligers have byssus gland, statocysts and eyespots.
	Mathews (1913)	Set from 210-380 μ. Height 20-60 μ less than length. Cockle-shaped.
	Field (1923)	Figures straight hinge stage at 60 hours.
	Kändler (1926)	Recognizable at 225 μ. Have statocyst with multiple statoliths and eyespot. Pediveligers at 290 μ.
	Wells (1927)	Long hinge line; low, rounded umbo. Anterior end more pointed than posterior. Umbones small; color, horn yellow.

	Nelson (1928)	Length to 376 μ. Height 20-40 μ less. Vary considerably in size at setting. Anterior end more pointed than posterior. Umbones small. Color, horn yellow.
	Werner (1939)	Length proportionately long, about 113-299 μ. Height 30-40 μ less. Hinge line 93 μ. Multiple statoliths. Eyespot. Taxodont hinge with larger teeth at both ends. Anterior end more pointed than posterior.
	Jørgensen (1946)	Length 90-400 μ. Egg-shaped with anterior end more pointed than posterior. Umbo low indistinct. Deep orange, almost opaque. Variable in shape, color and development. Hinge taxodont. Weak teeth in center with 6-8 stronger teeth at both ends.
	Sullivan (1948)	Length 155-320 μ. Height 35-65 μ less. Umbo low and rounded. Statocyst in foot. Anterior end more pointed than posterior.
	Rees (1950)	Umbo inconspicuous. Photomicrographs.
	Newell and Newell (1963)	Ovoid shape. Taxodont hinge with posterior ligament.
	Loosanoff and Davis (1963)	Length 93-300 μ. Height 14-30 μ less. Eyespot appears at about 215 μ. Larvae set from 215-300 μ.
	Loosanoff *et al.* (1966)	Length 80-348 μ. Height 65-304 μ Eyespot appears at 215 μ. Pediveligers from 210 μ. Photomicrographs.
Mytilus galloprovincialis (Lamarck)	Zakhvatkina (1959)	Length 80-348 μ. Height 65-304 μ Hinge line 71-94 μ. Pediveligers with numerous statoliths. Taxodont dentition with 7-8 large teeth at each end of hinge line. Umbo low, broad. Anterior end more pointed than posterior.