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

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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 $23 \pm 10 \mu$ less than length. Depth was $54 \pm 15 \mu$ 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. Brachidontes 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; Nughabhusanam, 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
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 *Mucocystis* 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

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

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

Pediveliger stage: Minimum length with functional foot = 165 $\mu$. Maximum length with functional velum = 220 $\mu$.

**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 $\mu$ long.
- B. Ventral view of hinge of larva 105 $\mu$ long.
- C. Dorsal view of hinge of larva 120 $\mu$ long.
- D. Dorsal view of hinge of larva 135 $\mu$ long.
- E. Dorsal view of hinge of larva 180 $\mu$ long.
Umbo and pediveliger stages: Umbo appearing as rounding of hinge line at about 150 \( \mu \), 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 \( \mu \) long; larvae dark, brown, antero-ventral margin frequently darker and reddish brown in larvae over 165 \( \mu \); eyespot appearing at 165 \( \mu \), small, indistinct but becoming conspicuous at about 180 \( \mu \), eventually 10 \( \mu \) 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 \( \mu \). 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 \( \mu \)) 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 \( L = 220 \mu \). 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 \( \mu \). In earlier stages the straight hinge line of larval *M. demissus* is longer (85 \( \mu \)) and the umbo appears somewhat later. *M. demissus* larvae have a minimum length of about 105 \( \mu \) and a maximum of about 300 \( \mu \). Their hinge structure has not been described.

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

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**


LARVAL DEVELOPMENT OF BRACHIDONTES RECURVUS


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

<table>
<thead>
<tr>
<th>Nominal Taxa</th>
<th>Reference</th>
<th>Descriptions</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Adula simpsoni</em> (Marshall)</td>
<td>Rees (1950)</td>
<td>Large (figured specimen over 300 μ) rich brown larvae. Length considerably greater than height.</td>
</tr>
<tr>
<td><em>Brachidontes senhausi</em> (Reeve)</td>
<td>Yoshida (1937; 1953)</td>
<td>Length to at least 240 μ. Height about 30 μ less. Pediveligers 230 to 290 μ with pigmented eyespot. Many minute teeth along hinge.</td>
</tr>
<tr>
<td><em>Crenella decussata</em> (Montagu)</td>
<td>Jørgensen (1946)</td>
<td>Prodissocochn is 750 μ.</td>
</tr>
<tr>
<td><em>Modiola adriatica</em> (Lamarck)</td>
<td>Jørgensen (1946)</td>
<td>Development probably non-pelagic. Prodissocochn about 1 mm.</td>
</tr>
<tr>
<td><em>Modiolaria discors</em> (L.)</td>
<td>Sullivan (1935)</td>
<td>Prodissocochn about 400 μ.</td>
</tr>
<tr>
<td><em>Modiolaria marmorata</em> (Forbes)</td>
<td>Lovén (1948)</td>
<td>Non-pelagic larvae.</td>
</tr>
<tr>
<td></td>
<td>Jørgensen (1946)</td>
<td>Minimum size 80 μ.</td>
</tr>
<tr>
<td></td>
<td>Loosanoff and Davis (1963)</td>
<td>Length 105-305 μ. Height 20-60 μ less; difference increasing with growth. Dark brown. Long hinge line becomes rounded at 180 μ and knobby at about 220 μ. Pediveliger 200-305 μ. Most set at 275 μ.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Umbo more pronounced and shell more massive than <em>M. edulis</em>.</td>
</tr>
</tbody>
</table>
**LARVAL DEVELOPMENT OF BRACHIDONTES RECURVUS**

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Author</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Musculus marmoratus</em> (Forbes)</td>
<td>Rees (1950)</td>
<td>One end pointed, other blunt and drooping ventrally. Umbo knobby but inconspicuous at 260 µ.</td>
</tr>
<tr>
<td><em>Mytilacea</em></td>
<td>Rees (1950)</td>
<td>Distinctive hinge with minute taxodont teeth over entire hinge line. Teeth larger near ends. Ligament posterior.</td>
</tr>
<tr>
<td><em>Mytilaster lineatus</em> (Gmelin)</td>
<td>Zakhvatkina (1959)</td>
<td>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.</td>
</tr>
<tr>
<td><em>Mytilidae</em></td>
<td>Odhner (1914)</td>
<td>Characterized by medium umbo, taxodont hinge and eyed stage.</td>
</tr>
<tr>
<td><em>Mytilus californianus</em> (Conrad)</td>
<td>Breese, Williamson and Dimick (1963)</td>
<td>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.</td>
</tr>
<tr>
<td><em>Mytilus crassitesta</em> (Lischke)</td>
<td>Miyazaki (1935)</td>
<td>Characterized by medium umbo, taxodont hinge and eyed stage.</td>
</tr>
<tr>
<td><em>Mytilus edulis</em> (Linne')</td>
<td>Borisiak (1909)</td>
<td>Larvae set at 280-320 µ. Height about 30 µ less than length. Umbo small. Anterior end more pointed than posterior.</td>
</tr>
<tr>
<td>Stafford (1912)</td>
<td></td>
<td>Taxodont hinge teeth, long hinge line. Anterior end more pointed than posterior.</td>
</tr>
<tr>
<td>Mathews (1913)</td>
<td></td>
<td>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.</td>
</tr>
<tr>
<td>Field (1923)</td>
<td></td>
<td>Set from 210-380 µ. Height 20-60 µ less than length. Cockle-shaped.</td>
</tr>
<tr>
<td>Kändler (1926)</td>
<td></td>
<td>Figures straight hinge stage at 60 hours.</td>
</tr>
<tr>
<td>Wells (1927)</td>
<td></td>
<td>Recognizable at 225 µ. Have statocyst with multiple statoliths and eyespot. Pediveligers at 290 µ.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Long hinge line; low, rounded umbo. Anterior end more pointed than posterior. Umbones small; color, horn yellow.</td>
</tr>
<tr>
<td>Authors</td>
<td>Description</td>
<td></td>
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<td>-------------------------------</td>
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</tr>
<tr>
<td>Nelson (1928)</td>
<td>Length to 376 ( \mu ). Height 20-40 ( \mu ) less. Vary considerably in size at setting. Anterior end more pointed than posterior. Umbones small. Color, horn yellow.</td>
<td></td>
</tr>
<tr>
<td>Werner (1939)</td>
<td>Length proportionately long, about 113-299 ( \mu ). Height 30-40 ( \mu ) less. Hinge line 93 ( \mu ). Multiple statoliths. Eyespot. Taxodont hinge with larger teeth at both ends. Anterior end more pointed than posterior.</td>
<td></td>
</tr>
<tr>
<td>Sullivan (1948)</td>
<td>Length 155-320 ( \mu ). Height 35-65 ( \mu ) less. Umbo low and rounded. Statocyst in foot. Anterior end more pointed than posterior.</td>
<td></td>
</tr>
<tr>
<td>Newell and Newell (1963)</td>
<td>Ovoid shape. Taxodont hinge with posterior ligament.</td>
<td></td>
</tr>
<tr>
<td>Loosanoff and Davis (1963)</td>
<td>Length 93-300 ( \mu ). Height 14-30 ( \mu ) less. Eyespot appears at about 215 ( \mu ). Larvae set from 215-300 ( \mu ).</td>
<td></td>
</tr>
<tr>
<td>Loosanoff et al. (1966)</td>
<td>Length 80-348 ( \mu ). Height 65-304 ( \mu ). Eyespot appears at 215 ( \mu ). Pediveligers from 210 ( \mu ). Photomicrographs.</td>
<td></td>
</tr>
<tr>
<td><em>Mytilus galloprovincialis</em> (Lamarck) Zakhvatkina (1959)</td>
<td>Length 80-348 ( \mu ). Height 65-304 ( \mu ). Hinge line 71-94 ( \mu ). 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.</td>
<td></td>
</tr>
</tbody>
</table>