

## Mollusca: Bivalvia

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The bivalves (also known as lamellibranchs or pelecypods) include such groups as the clams, mussels, scallops, and oysters. The class Bivalvia is one of the largest groups of invertebrates on the Pacific Northwest coast, with well over 150 species encompassing nine orders and 42 families (Table 1). Despite the fact that this class of mollusc is well represented in the Pacific Northwest, the larvae of only a few species have been identified and described in the scientific literature. The larvae of only 15 of the more common bivalves are described in this chapter. Six of these are introductions from the East Coast. There has been quite a bit of work aimed at rearing West Coast bivalve larvae in the lab, but this has led to few larval descriptions.

### Reproduction and Development

Most marine bivalves, like many marine invertebrates, are broadcast spawners (e.g., *Crassostrea gigas*, *Macoma balthica*, and *Mya arenaria*); the males expel sperm into the seawater while females expel their eggs (Fig. 1). Fertilization of an egg by a sperm occurs within the water column. In some species, fertilization occurs within the female, with the zygotes then

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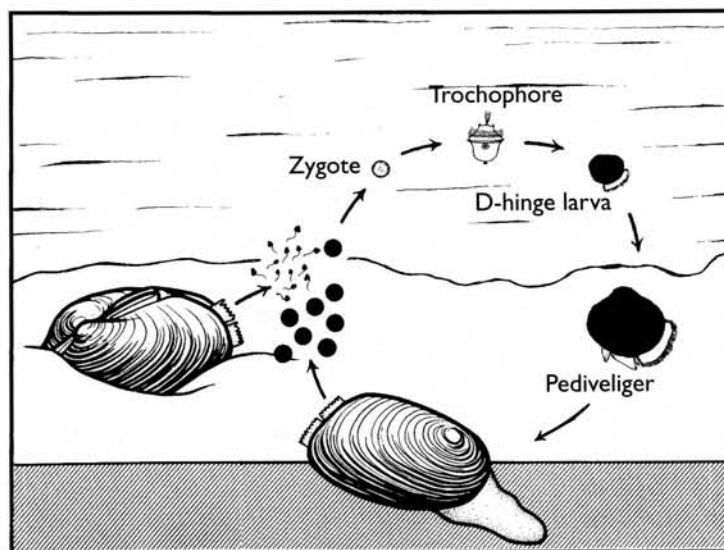


Fig. 1. Generalized life cycle of marine bivalves (not to scale).

**Table 1. Species in the class Bivalvia from the Pacific Northwest (local species list from Kozloff, 1996). Species in bold indicate larvae described in this chapter.**

Order, Family	Species	Life History <sup>1</sup>	References for Larval Descriptions
<b>Nuculoida</b>			
Nuculidae	<i>Nucula tenuis</i>		
	<b><i>Acila castrensis</i></b>	FSP	Strathmann, 1987; Zardus and Morse, 1998
Nuculanidae	<i>Nuculana hamata</i>		
	<i>Nuculana minuta</i>		
	<i>Nuculana cellutita</i>		
Yoldiidae	<i>Yoldia amygdalea</i>		
	<i>Yoldia scissurata</i>		
	<i>Yoldia thraciaeformis</i>		Hutchings and Haedrich, 1984
	<i>Yoldia myalis</i>		
<b>Solemyoida</b>			
Solemyidae	<b><i>Solemya reidi</i></b>	FSP	Gustafson and Reid, 1986
<b>Arcoidea</b>			
Glycymerididae	<i>Glycymeris subboleta</i>		
	<i>Glycymeris corteziana</i>		
Philobryidae	<i>Philobrya setosa</i>		
<b>Mytiloida</b>			
Mytilidae	<b><i>Mytilus californianus</i></b>	FSV	Lutz et al., 1982; Shaw et al., 1988; Strathmann, 1987; Martel et al., 2000
	<b><i>Mytilus trossulus</i></b> ( <i>edulis</i> )	FSV	Stafford, 1912; Sullivan, 1948; Rees, 1950; Loosanoff et al., 1966; Chanley and Andrews, 1971; Bayne, 1971; Epifanio et al., 1975; De Schweinitz and Lutz, 1976; Le Pennec, 1980; Shaw et al., 1988; Martel et al., 2000
	<i>Crenella decussata</i>		
	<i>Lithophaga plumula</i>		
	<i>Adula californiensis</i>	FSV	Morris et al., 1980
	<i>Adula falcata</i>		
	<i>Adula diegensis</i>	FSV	Lough and Gonor, 1971; Strathmann, 1987
	<b><i>Modiolus modiolus</i></b>	FSV	Rees, 1950; Chanley and Andrews, 1971; De Schweinitz and Lutz, 1976
	<i>Modiolus rectus</i>		
	<i>Musculista senhousia</i>		
	<i>Musculus niger</i>		
	<i>Musculus discors</i>		
	<i>Musculus taylori</i>		
	<i>Dacrydium pacificum</i>		
	<i>Megacrenella columbiana</i>		
<b>Limoida</b>			
Limidae	<i>Limatula subauriculata</i>		
<b>Ostreoida</b>			
Pectinidae	<i>Patinopecten caurinus</i>	FSV	Bronson et al., 1984; Strathmann, 1987
	<i>Chlamys hastata</i>	FSV	Strathmann, 1987; Hodgson and Bourne, 1988
	<i>Chlamys rubida</i>		
	<i>Chlamys behringiana</i>		
	<i>Hinnites gigantea</i>	FSV	Bronson et al., 1984; Strathmann, 1987
	<i>Delectopecten randolphi</i>		
	<i>Delectopecten vancouverensis</i>		
	<i>Parvamussium alaskensis</i>		

Order, Family	Species	Life History <sup>1</sup>	References for Larval Descriptions
Anomiidae	<i>Pododesmus cepio</i>	FSV	Leonard, 1969; Strathmann, 1987
Ostreidae	<b><i>Ostrea lurida</i></b>	BV	Hori, 1933; Hopkins, 1936; Loosanoff et al., 1966; Strathmann 1987
	<i>Ostrea conchaphilia</i>		
	<b><i>Crassostrea virginica</i></b>	FSV	Sullivan, 1948; Loosanoff et al., 1966; Chanley and Andrews, 1971; Epifanio et al., 1975; Lutz et al., 1982
	<b><i>Crassostrea gigas</i></b>	FSV	Loosanoff et al., 1966; Epifanio et al., 1975; Le Pennec, 1980; Pauley et al., 1988
<b>Veneroida</b>			
Lucinidae	<i>Lucina tenuisculpta</i>		
	<i>Lucinoma annulata</i>		
Thyasiridae	<i>Thyasira cygnus</i>		
	<i>Thyasira gouldii</i>	BV or BJ ?	Blacknell and Ansell, 1974, 1975
	<i>Thyasira barbarensis</i>		
	<i>Axinopsida serricata</i>		
	<i>Axinopsida viridis</i>		
	<i>Conchocele bisecta</i>		
Ungulinidae	<i>Diplodonta orbellus</i>		
	<i>Diplodonta impolita</i>		
Chamidae	<i>Chama arcana</i>		
	<i>Pseudochama exogyra</i>		
Kelliidae	<b><i>Kellia suborbicularis</i></b>	BV	Lebour, 1938 a,b; Rees, 1950; Strathmann, 1987
	<i>Rhamphidonta retifera</i>		
	<i>Odontogena borealis</i>		
Lasaeidae	<i>Lasaea subviridis</i>	BV	Strathmann, 1987
Galeommatidae	<i>Scintillona bellerophon</i>		
Montaculidae	<i>Pseudopythina rugifera</i>	BV	Strathmann, 1987
	<i>Pseudopythina compressa</i>		
	<i>Mysella tumida</i>	BV	O'Foighil, 1985; Strathmann, 1987
Turtoniidae	<i>Turtonia minuta</i>		Matveeva, 1976
Carditidae	<i>Glans carpenteri</i>	BJ	Morris et al., 1980
	<i>Miontodiscus prolongatus</i>		
	<i>Cyclocardia ventricosa</i>		
	<i>Cyclocardia crebricostata</i>		
	<i>Crassicardia crassidens</i>		
Astartidae	<i>Astarte esquimalti</i>		
	<i>Astarte compacta</i>		
	<i>Astarte undata</i>		
	<i>Tridonta alaskensis</i>		
Cardiidae	<i>Nemocardium centrifilosum</i>		
	<i>Clinocardium nuttalli</i>	FSV	Gallucci and Gallucci 1982; Strathmann, 1987
	<i>Clinocardium blandum</i>		
	<i>Clinocardium cliatum</i>		
	<i>Clinocardium californiense</i>		
	<i>Clinocardium fucanum</i>		
	<i>Serripes groenlandicus</i>		
Mactridae	<i>Mactra californica</i>		
	<i>Spisula falcata</i>		

table continues

Order, Family	Species	Life History <sup>1</sup>	References for Larval Descriptions
Cultellidae	<i>Tresus nuttalli</i>	FSV	Morris et al., 1980
	<b><i>Tresus capax</i></b>	FSV	Bourne and Smith, 1972a,b; Strathmann, 1987
	<i>Siliqua patula</i>	FSV	Breese and Robinson, 1981; Lassuy and Simons, 1989; Morris et al., 1980
Solenidae	<i>Siliqua lucida</i>		
	<i>Siliqua sloati</i>		
Tellinidae	<i>Solen sicarius</i>		
	<i>Tellina bodegensis</i>		
Macomidae	<i>Tellina carpenteri</i>		
	<i>Tellina modesta</i>		
	<i>Tellina nuculeoides</i>		
	<b><i>Macoma balthica</i></b>	FSV	Sullivan, 1948; Strathmann, 1987
	<i>Macoma calottensis</i>		
	<i>Macoma eliminata</i>		
	<i>Macoma nasuta</i>	FSV	Marriage, 1954; Rae, 1978, 1979
	<i>Macoma secta</i>	FSV	Marriage, 1954; Rae, 1978, 1979
	<i>Macoma yoldiformis</i>		
	Psammobiidae	<i>Gari californica</i>	FSV
Scrobiculariidae	<i>Semele rubropicta</i>		
	<i>Cumingia californica</i>		
Solecurtidae	<i>Tagelus californianus</i>		
Corbiculidae	<b><i>Corbiucla fluminea</i></b>	BJ	Kennedy and Van Huekelem, 1985; Kennedy et al., 1991
	<i>Protothaca staminea</i>	FSV	Marriage, 1954; Nickerson, 1977; Chew and Ma, 1987; Strathmann, 1987
Veneridae	<i>Protothaca tenerrina</i>		
	<i>Humilaria kenerlyi</i>		
	<i>Tapes philippinarum</i>	FSV	Bourne, 1982; Strathmann, 1987
	<i>Psephidia ovalis</i>		
	<i>Psephidia lordi</i>	BV	Strathmann, 1987
	<i>Transenella confusa</i>		Gray, 1982
	<i>Transenella tantilla</i>	BG	Strathmann, 1987
	<i>Lyocyma fluctuosa</i>		
	<b><i>Saxidomus giganteus</i></b>	FSV	Fraser, 1929; Breese and Phibbs, 1970; Nickerson, 1977; Strathmann, 1987
	Petricolidae	<i>Compsomyax subdiaphana</i>	
<i>Petricola carditoides</i>			
Cooperellidae	<b><i>Petricola pholadiromis</i></b>	FSV	Chanley and Andrews, 1971
	<i>Cooperella subdiaphana</i>		
Thraciidae	<i>Thracia beringi</i>		
	<i>Thracia curta</i>		
	<i>Thracia trapezoides</i>		
	<i>Thracia challisiana</i>		
<b>Myoida</b>			
Myidae	<b><i>Mya arenaria</i></b>	FSV	Stafford, 1912; Sullivan, 1948; Marriage, 1954; Loosanoff et al., 1966; Chanley and Andrews, 1971; Savage and Goldberg, 1976; Lutz et al., 1982
	<i>Mya truncata</i>		
	<i>Cryptomya californica</i>		
	<i>Platyodon cancellatus</i>		
	<i>Sphenia ovoidea</i>		

Order, Family	Species	Life History <sup>1</sup>	References for Larval Descriptions
Hiatellidae	<b>Hiatella arctica</b>	FSV	Lebour, 1938b; Sullivan, 1948; Rees, 1950; Savage and Goldberg, 1976
	<i>Panope abrupta</i>	FSV	Marriage, 1954; Goodwin, 1973; Strathmann, 1987
Pholadidae	<i>Panomya chrysis</i>		
	<i>Barnea subtruncata</i>		
	<i>Zirfaea pilsbryi</i>		
	<i>Penitella conradi</i>		Wilson and Kennedy, 1984
	<i>Penitella gabbii</i>		
	<i>Penitella penita</i>	FSV	Morris et al., 1980
	<i>Penitella turnerae</i>		
Xylophagidae	<i>Netastoma rostrata</i>		
Teredinidae	<i>Xylophaga washingtona</i>		
	<b>Teredo navalis</b>	FSV	Sullivan, 1948; Loosanoff et al., 1966; Chanley and Andrews, 1971; Culliney, 1975; Quayle, 1992
	<b>Bankia setacea</b>	FSV	Quayle, 1953, 1959, 1992; Townsley et al., 1966; Haderlie, 1983
<b>Pholadomyoidea</b>			
Lyonsiidae	<i>Lyonsia californica</i>	FSV	Strathmann, 1987
	<i>Entodesma pictum</i>		
	<i>Mytilimeria nuttalli</i>	FSV	Yonge, 1952; Strathmann, 1987
Pandoridae	<i>Agriodesma saxicola</i>		
	<i>Pandora bilirata</i>		
	<i>Pandora filosa</i>		Thomas, 1994
	<i>Pandora punctata</i>		
	<i>Pandora wardiana</i>		
	<i>Pandora glacialis</i>		
<b>Septibranchida</b>			
Cuspidariidae	<i>Cardiomya oldroydi</i>		
	<i>Cardiomya pectinata</i>	BEC	Gustafson et al., 1986; Strathmann, 1987
	<i>Cardiomya planetica</i>		
	<i>Cardiomya californica</i>		
	<i>Plectodon scaber</i>		

<sup>1</sup>Life History: FSV, free-spawning veliger larvae; FSP, free-spawning periclymna larvae; BV, brooded to veliger; B], brooded to juvenile; BEC, benthic egg capsule.

expelled into the surrounding water column. After fertilization of the egg, the zygote first develops into a planktonic trochophore and then into a shelled veliger larva with a ciliated velum used for swimming and respiration. This planktonic larval stage can last from a few days to months, depending on the species. Just prior to metamorphosis the foot develops, at which time the larva is called a pediveliger. After settling on the bottom, loss of the ciliated swimming velum takes place and the post-larval bivalve is able to dig and crawl around using its now fully functional foot. At this stage, these post-larval individuals are referred to as "spat," or juveniles.

In contrast, some bivalve species brood their larvae either within the mantle cavity or attached to the external shell surface (Strathmann, 1987). The developmental stage at which these larvae are released is species specific; some species release their young at the early veliger stage (i.e., *Kellia suborbicularis*, at ca 72  $\mu\text{m}$ ; Strathmann, 1987), but others retain the larvae until they are ready to live as juveniles on the bottom (i.e., *Corbicula fluminea*, at ca 210  $\mu\text{m}$ ; V. Kennedy, pers. comm.).

Finally, some species in the orders Nuculoida and Solemyoida produce non-feeding (lecithotrophic) larvae with unique morphology, the periclymma larva (see Fig. 3). The larvae are barrel-shaped with prominent apical tufts and are propelled by cilia. The outer cellular body, or test, is ovoid and completely surrounds the shell. The test is cast off at metamorphosis when the juvenile clam begins its benthic existence. Two local species with this mode of development have thus far been described (*Acila castrensis* and *Solemya reidi*).

Occasionally post-settlement-sized "larvae" are found in plankton samples, especially those samples taken near the bottom. These are individuals that have already metamorphosed and taken up residence on the bottom. Non-planktonic individuals are occasionally found in plankton samples for one of three reasons: (1) They were stirred up from the bottom by the currents. (2) They are byssus thread drifters. Byssus thread drifting occurs when post-settlement bivalves extend a byssus thread and the drag on the thread causes the individual to become resuspended in the water column. This is a common way for post-larval bivalves (and occasionally gastropods) to further their dispersal (Lane et al., 1985; Martel and Chia, 1991; Cummings et al., 1993). (3) Less likely, these individuals have not found suitable settlement sites and are able to delay metamorphosis (Bayne, 1965).

## Identification and Description of Local Taxa

Sampling of bivalve larvae is best accomplished with a plankton net that has a mesh size small enough to retain the smallest larvae one wishes to study. Larvae smaller than about 100  $\mu\text{m}$  are nearly impossible to identify without the aid of a scanning electron microscope. The larval shells are surprisingly strong and thus can be sampled either by a towed plankton net or through an electric or gas-powered pump with minimal damage to the shells. For short-term storage (on the order of months), 5% formalin buffered with calcium carbonate works well for preservation; buffering prevents low pH that causes shells to dissolve. If longer storage is necessary (months to years), 70% ethanol is recommended to prevent shell loss.

Because plankton samples are typically kept in buffered formalin, the bodies of the bivalve larvae are often shriveled while the shell has remained intact. For some larvae, shell color is helpful for identification. Depending on how long the sample has been stored, however, this color may not have survived, and shell shape is the primary tool for identification, not shell or body color. Color characteristics can be useful as a backup to help confirm an identification.

Use cross-polarized light to view larvae. Place a polarizing filter below the stage on the microscope and a second filter between the sample and the lens of the microscope. Rotate one of the filters until the background becomes dark and the bivalve shells "light up." The crossed polarization causes birefringence due to the microcrystalline aragonitic structure of the larval shells (Gallager et al., 1989) and dramatically aids finding and identifying larvae within a sample.

At all developmental stages (veliger or pediveliger) regardless of size, the shape of the umbo is most useful for identification (Fig. 2). The umbo can take on a variety of shapes and sizes, most of which are species-specific. Prior to the development of the umbo, during the early veliger or D-hinge stage, larvae can be extremely difficult to differentiate and, without the use of scanning electron microscopy, probably cannot be taken down to species. Aside from the umbo, the length and slope of the shoulders can also be helpful in identification. The shoulders typically become prominent during the veliconcha stage.

### Periclymma Larvae

There are probably 12 local bivalve species that produce periclymma larvae. The larvae of two of these species have been described, and illustrations of several additional periclymma are available (Fig. 3).

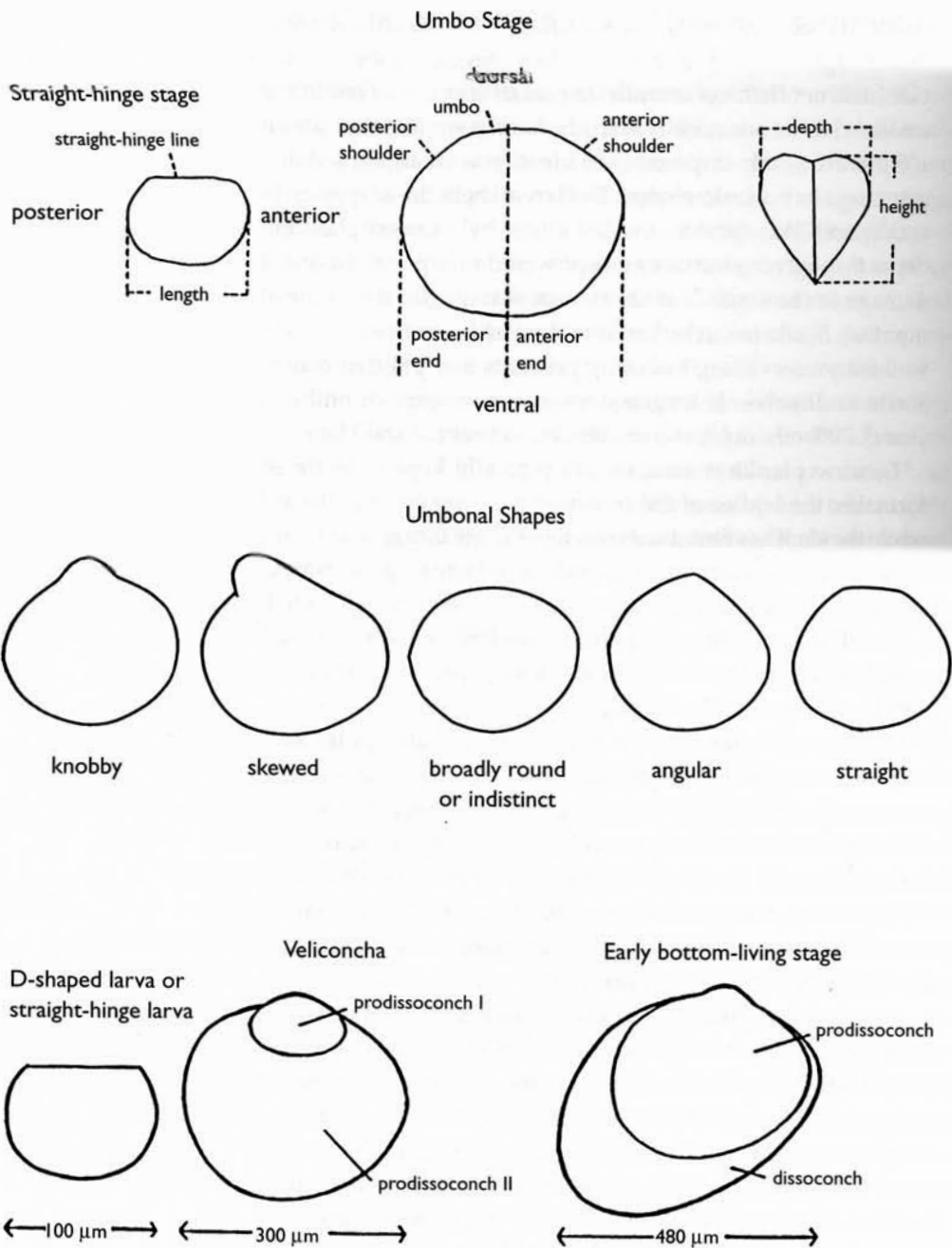


Fig. 2. Terminology used to describe dimensions and shapes of bivalve larvae. The posterior end of the larval shell is typically blunter and shorter than the anterior end and has a higher shoulder. (Adapted from Chanley and Andrews, 1971; Rees, 1950)



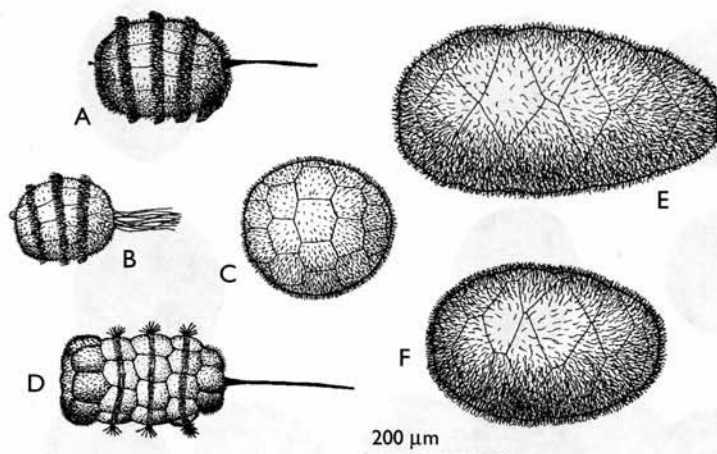


Fig. 3. Periclymma larvae. (A) ***Acila castrensis***. (B) ***Nucula proxima***. (C) ***Nucula delphinodonta***. (D) ***Yoldia limatula***. (E) ***Solemya reidi***. (F) ***Solemya velum***. Local genera and species are in bold. (From Zardus and Morse, 1998, Fig. 54)

### Key to bivalve periclymma larvae

- 1a. Test with 3 transverse bands of cilia and apical tuft of accessory cilia. Late-stage larvae laterally compressed with shell development. Test shed at metamorphosis (Fig. 3A) ..... *Acila castrensis*
- 1b. Test entirely covered with cilia. Length varies, 360–440  $\mu\text{m}$  (Fig. 3E) ..... *Solemya reidi*

### Veliger Larvae

The subtle differences in larval shell shape between bivalve species do not lend themselves to the normal dichotomous key. What works better is a pictorial guide. We have modeled this identification guide after Chanley and Andrews's (1971) guide to the bivalve larvae of the Virginia coast. Because of the difficulty in distinguishing straight-hinge or D-larvae, this section describes only larvae in which the umbo has become rounded. Use this section as follows: (1) Use the ocular micrometer on the dissection microscope to determine the length of the larva in question. (2) Find this length in Fig. 4. (3) Match the shape of the specimen's larval shell. (4) Find details of the selected species in the following descriptions.

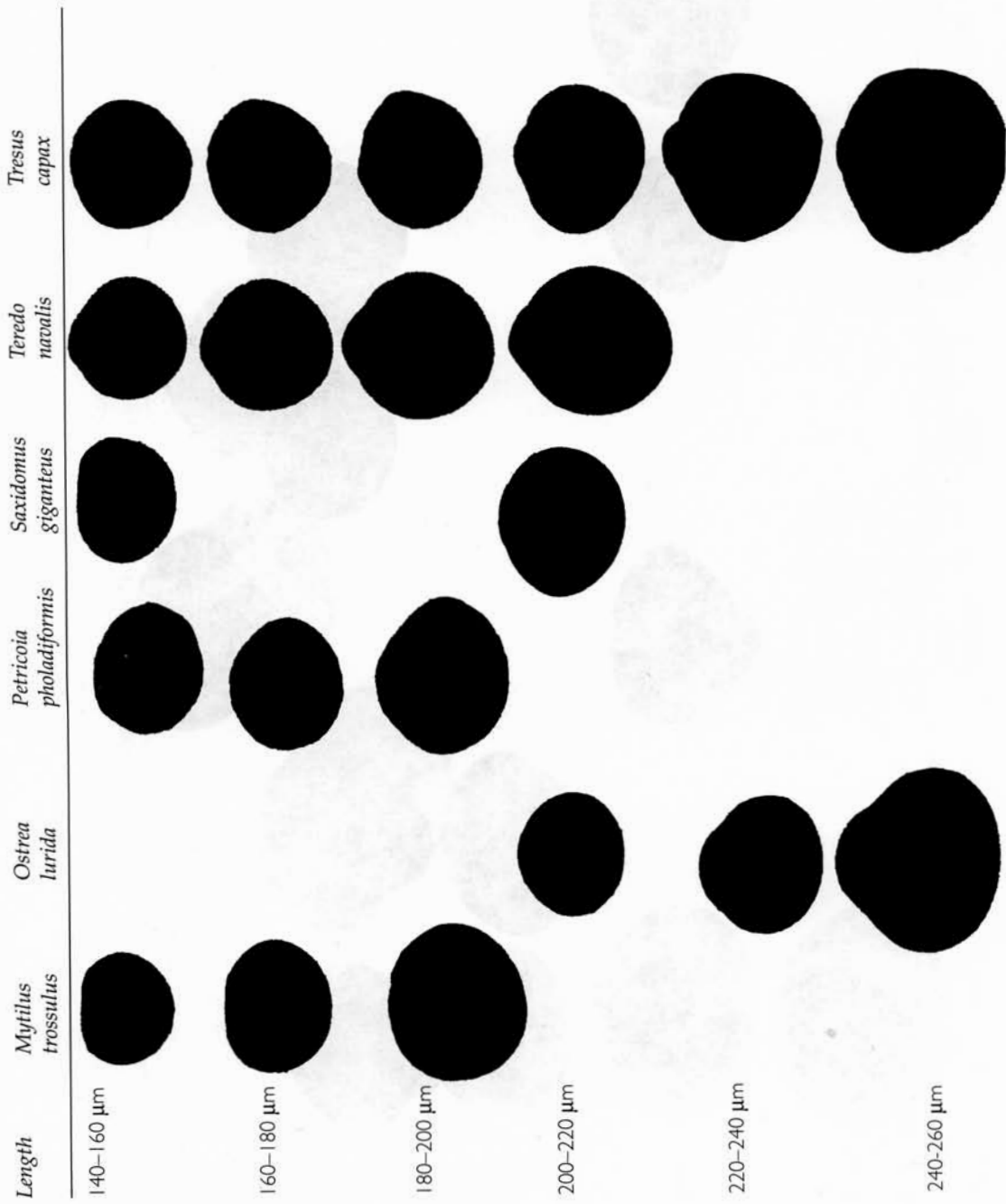
The correct identification of larval bivalves takes considerable time and patience. Differences in shell shape among species are in most cases extremely subtle. It is particularly important to remember that few of the bivalve species common to the Pacific Northwest coast have published descriptions of their larvae (see Table 1).

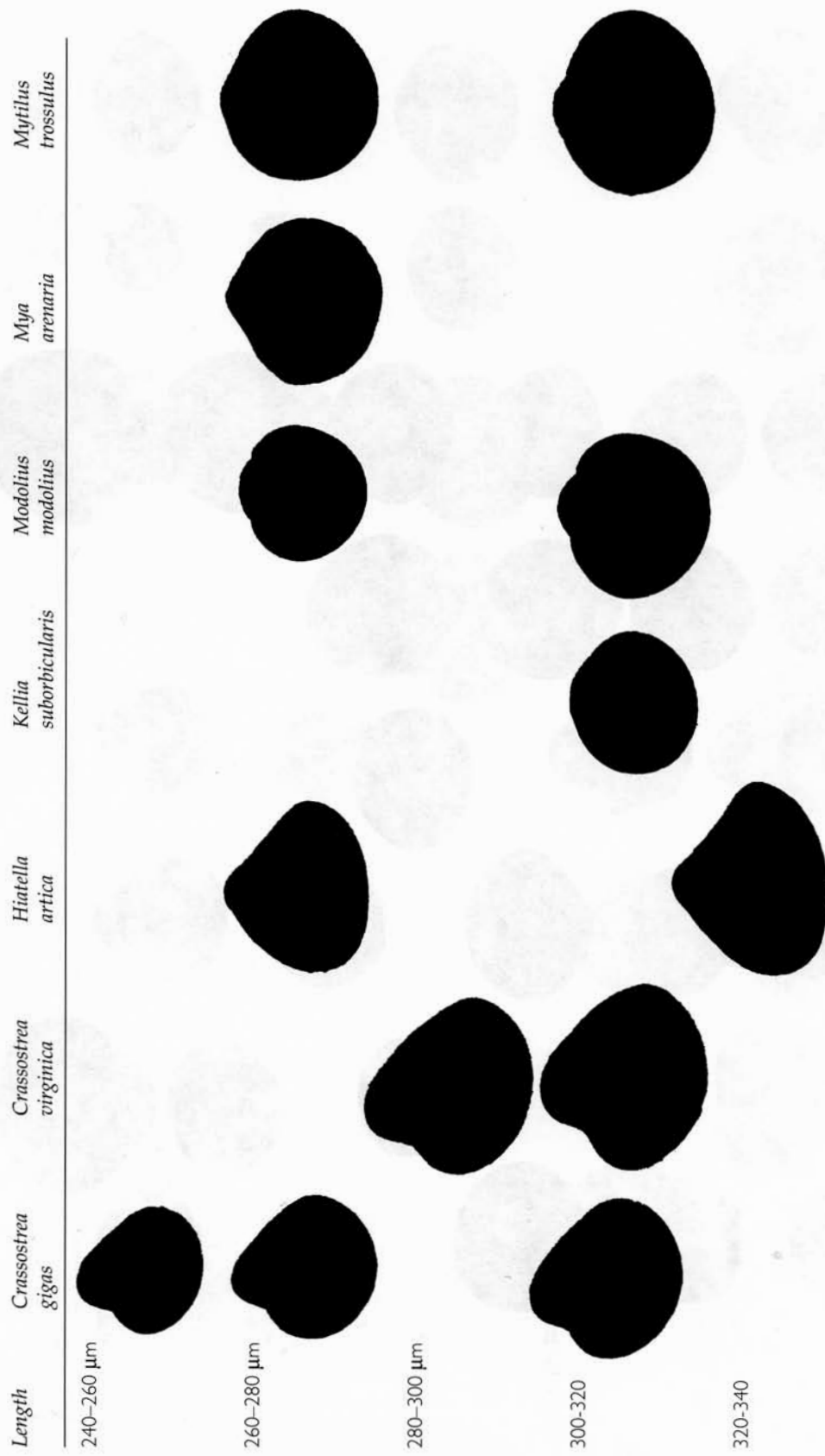
*Bankia setacea*, **Feathery Shipworm** (Order Myoida, Family Teredinidae). Characteristic dark rim around the margin of the

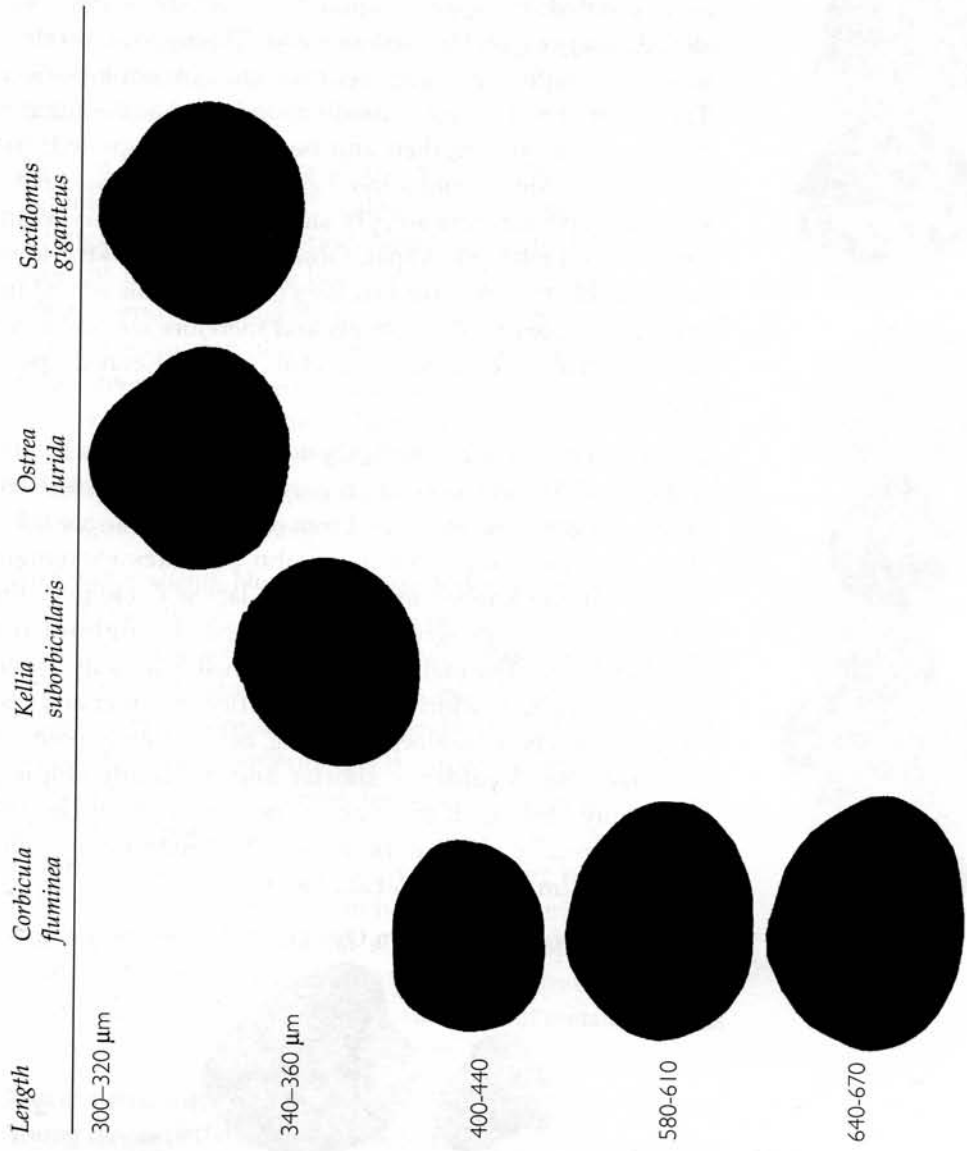
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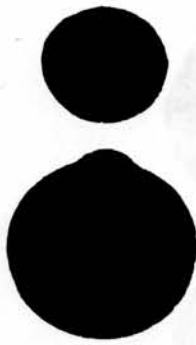
Fig. 4 (overleaf). Comparative drawings of 15 species of larval bivalves.

Length	<i>Bankia setacea</i>	<i>Corbicula fluminea</i>	<i>Crassostrea gigas</i>	<i>Crassostrea virginica</i>	<i>Hiatella artica</i>	<i>Macoma balthica</i>	<i>Modiolus modiolus</i>	<i>Mya arenaria</i>
140-160 $\mu$ m								
160-180 $\mu$ m								
180-200 $\mu$ m								
200-220 $\mu$ m								
220-240 $\mu$ m								

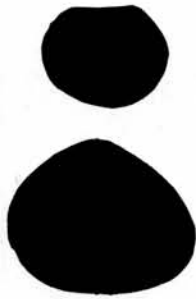




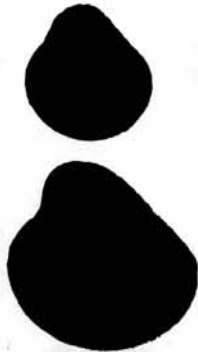




larval shell; at a length of ca 140  $\mu\text{m}$ , a dark line appears just inside the edge of the shell and runs parallel to the rim of the shell. Before the appearance of the knobby umbo at ca 150  $\mu\text{m}$ , the shell is nearly round and the shoulders are gradually sloping. The shell gets progressively yellower in color throughout the larval period. The shell becomes as tall if not taller than it is long; the shell depth becomes nearly as great as the length. Size at metamorphosis, ca 245  $\mu\text{m}$  (Quayle, 1953).

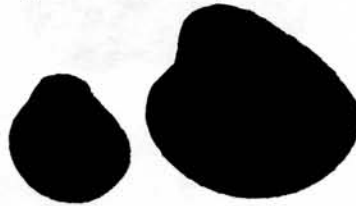


*Corbicula fluminea*, **Asiatic Freshwater Clam** (Order Veneroidea, Family Corbiculidae). Larvae are brooded within the adult clam until ca 210  $\mu\text{m}$  length. Upon release the spat have a long, straight umbo, a steeply sloping posterior shoulder, and rounded posterior end; the anterior end is slightly longer and more pointed; the anterior shoulder is steeply sloping but slightly longer than the posterior end. Throughout development, the length of the umbo shortens and remains indistinct. The posterior end remains broadly rounded while the anterior end continues to lengthen and become more pointed; the anterior shoulder becomes more gradually sloping while the posterior end remains steeply sloping. Because larvae are brooded and released as spat, those caught in plankton tows are probably byssus thread drifters or individuals stirred up from the bottom by the currents and therefore are no longer considered true larvae (Kennedy et al., 1991; V. Kennedy, pers. comm.)



*Crassostrea gigas*, **Giant Pacific Oyster** (Order Osteoidea, Family Ostreidae). These larvae are nearly indistinguishable from larvae of *Crassostrea virginica*. From early on, larvae are taller than they are long, and the umbo becomes extremely prominent and knobby in even small larvae (~140  $\mu\text{m}$ ); the umbo becomes progressively skewed throughout the planktonic life. The main body of the shell is initially round until ca 200  $\mu\text{m}$ , at which time the anterior shoulder and end lengthen and become steeply sloping, being slightly pointed; the posterior shoulder is shorter and gradually sloping, eventually coming off the umbo at nearly a right angle. The shell is typically rather dark in color. Metamorphosis occurs at 275–330  $\mu\text{m}$  (Loosanoff et al., 1966).

*Crassostrea virginica*, **Eastern Oyster**. See *Crassostrea gigas*.



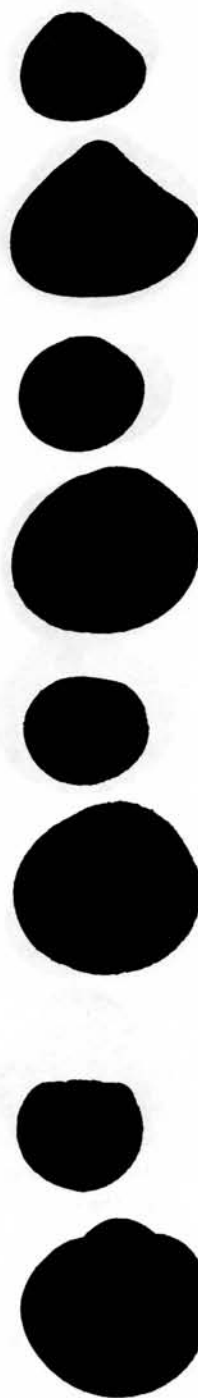
*Hiatella arctica*, **Arctic Saxicave, Little Gaper, Red Nose** (Order Myoida, Family Hiattellidae). Larvae of this species have a distinct shape: the umbo is angular and slightly knobby; the posterior shoulder is long and steeply sloping; the bottom half of the posterior end is rather squared-off. The anterior shoulder is also long and steeply sloping, but less so than the posterior end. The anterior end comes to a distinct point halfway down the height of the shell. Metamorphosis is believed to occur at ca 345  $\mu\text{m}$  (Rees, 1950).

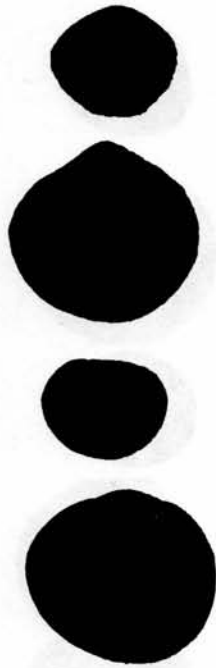
*Kellia suborbicularis*, **North Atlantic Lepton** (Order Veneroida, Family Kelliidae). Larvae of this species are large and easily recognized by their very short, straight umbo. The posterior end is broadly rounded with a long, steeply sloping shoulder. The anterior end is also broadly rounded but is slightly longer and skewed toward the anteroventral margin of the shell. Size at metamorphosis is believed to be ca 370  $\mu\text{m}$  (Rees, 1950; Strathmann, 1987).

*Macoma balthica*, **Balthica Macoma** (Order Veneroida, Family Tellinidae). These larvae retain a rather indistinct shape throughout the larval period. Young larvae (<160  $\mu\text{m}$ ) have a straight hinge and the body is broadly rounded with the anterior end only slightly longer than the posterior end. As the larvae develop, the anterior end lengthens and becomes more steeply sloped while the posterior end remains much shorter and more rounded. The result is a larval shell slightly skewed in the direction of the anterior end. The umbo remains broadly rounded and indistinct throughout development. Average size at metamorphosis is 255  $\mu\text{m}$  (Sullivan, 1948).

*Modiolus modiolus*, **Northern Horse Mussel** (Order Mytiloida, Family Mytilidae). Straight-hinge larvae of *M. modiolus* are indistinguishable from *Mytilus trossulus* (*edulis*) straight-hinge larvae. At ca 170  $\mu\text{m}$ , the umbo of *M. modiolus* becomes broadly rounded. At this size, the posterior end is short and also broadly rounded, while the anterior end is longer and slightly pointed. As size increases, the umbo becomes more prominent and knobby. The posterior shoulder is short and the posterior end is rather squared off; the anterior shoulder is longer and gradually sloping. The bottom half of the anterior end slopes sharply toward the ventral margin. This species is best distinguished from *M. trossulus* by the size of the umbo, which is longer and wider than in *M. trossulus*. Size at metamorphosis is ca 300  $\mu\text{m}$ . (De Schweinitz and Lutz, 1976).

*Mya arenaria*, **Soft-shell Clam** (Order Myoida, Family Myidae). Young larvae (<150  $\mu\text{m}$ ) have a broadly rounded umbo with a



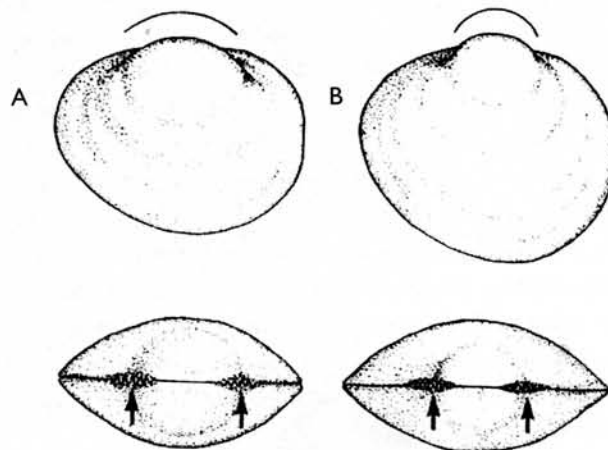


short, gradually sloping posterior shoulder and a longer, more steeply sloping anterior shoulder and end. As development proceeds, the umbo becomes angled and the shoulders become straighter and more steeply sloping. Both ends are pointed but the anterior end is slightly longer. Larvae retain this general shape throughout development. Metamorphosis occurs at 170–230  $\mu\text{m}$  (Chanley and Andrews, 1971).

*Mytilus trossulus* (*edulis*), **Blue Mussel** (Order Mytiloida, Family Mytilidae). This larva retains its straight hinge much longer than other larvae, until almost 220  $\mu\text{m}$ . At this point, the umbo becomes broadly rounded and the anterior end begins to lengthen and become more pointed. Eventually a small, knobby umbo develops. The posterior end is short but steeply sloping; the anterior end is longer but slopes more gradually down to a point. The bottom half of the anterior end slopes steeply toward the ventral margin. Compare *Modiolus modiolus*. Metamorphosis occurs at 215–305  $\mu\text{m}$  (Chanley and Andrews, 1971).

Martel et al. (2000) provide a description of characteristics that can be used to differentiate between settling and early postlarval stages (e.g., prior to dissoconch secretion) of *Mytilus trossulus* and *M. californianus*. In addition, they suggest that the following characteristics can also be used to separate *M. galloprovincialis* (a species found in southern California) from *M. californianus*. *M. californianus* displayed 1) a shallower, flatter umbo (i.e., the PI curve was more pronounced, see Fig. 5), 2) the umbo was less conspicuous, barely extending above the larval hinge and only weakly curved (Fig. 5), and 3) wider separation between the provincial lateral teeth (Fig. 5).

Fig 5. Settling and early postlarval stages of (A) *Mytilus californianus* and (B) *M. trossulus* (Martel et al., 2000). The curved line above the upper figures indicates the length of the prodissoconch curve (the PI curve). Note the higher and more pronounced umbo displayed by *M. trossulus* and the closer spacing between the provincial lateral teeth (arrows) relative to *M. californianus*.



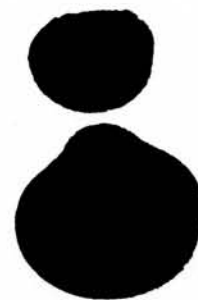
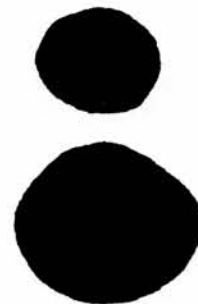
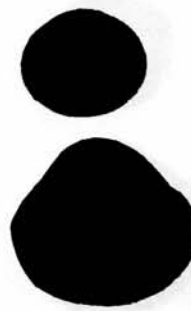
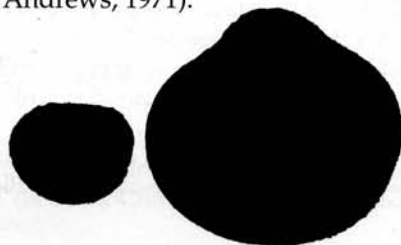


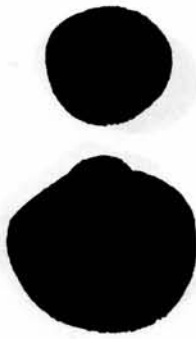
*Ostrea lurida*, **Native Pacific Oyster** (Order Ostreoida, Family Ostreidae). Larvae are brooded until 165–189  $\mu\text{m}$  (Strathmann, 1987). Larvae less than ca 200  $\mu\text{m}$  have a straight hinge, with the main body of the shell broadly rounded with ends of roughly equal length. At 200  $\mu\text{m}$ , the umbo first becomes apparent and is initially just a rounded hump atop the valves. The anterior end begins to lengthen, and the anterior shoulder gets progressively longer and more steeply sloping while the posterior shoulder becomes shorter and less steeply sloping. The anterior end is longer than the posterior end. The umbo, like that of *Crassostrea*, becomes prominent and knobby in shape throughout development, although it does not become skewed. Metamorphosis occurs at ca 320  $\mu\text{m}$  (Hori, 1933).

*Petricola pholadiformis*, **False Angle Wing** (Order Veneroida, Family Petricolidae). Larvae are free-swimming. Total length is 60–185  $\mu\text{m}$ . Straight-hinge stage ends at ca 105  $\mu\text{m}$  length, at which time a broadly rounded umbo develops. The anterior end is slightly longer than posterior. The ends of the shell are nearly equally rounded. The shoulders are straight and slope steeply. There is no distinctive color, though the margin is dark. The eye spot is not pigmented. The shell is heavier than in most clams. Metamorphosis occurs at ca 175  $\mu\text{m}$  (Chanley and Andrews, 1971).

*Saxidomus giganteus*, **Butter Clam** (Order Veneroida, Family Veneridae). Rather indistinct larvae with a straight hinge until ca 160  $\mu\text{m}$ . At this point, the anterior end is slightly longer and more pointed than the broadly rounded posterior end. As development proceeds, the umbo becomes broadly rounded as do both ends, with the anterior end being only slightly longer than the posterior end. The larvae are noticeably longer than they are tall and as a result have a rather squat appearance. Metamorphosis occurs at ca 230  $\mu\text{m}$  (Breese and Phibbs, 1970).

*Teredo navalis*, **Common Shipworm** (Order Myoida, Family Teredinidae). Larvae have a distinct walnut-shaped (oval) shell, being as tall if not taller than long and with considerable depth. The larvae have a knobby umbo and virtually no shoulders. The ends are of equal length and rounded. The shell is usually a dark brown, golden color. Metamorphosis is at 190–200  $\mu\text{m}$  (Chanley and Andrews, 1971).





*Tresus capax*, **Alaskan Gaper** (Order Veneroidea, Family Mactridae). In small larvae with straight umbos (<140  $\mu\text{m}$ ), the anterior end is slightly longer and pointed, and the posterior end is short and more broadly rounded. The bottom half of the anterior end slopes sharply toward the ventral margin. As size increases, the umbo becomes progressively more angled but never becomes conspicuous. The posterior end becomes rather squared off, while the anterior end becomes more pointed. The anterior shoulder is longer than the posterior shoulder. Metamorphosis occurs at 270  $\mu\text{m}$  (Bourne and Smith, 1972a,b).

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