18

Echinodermata

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The phylum Echinodermata is a morphologically, ecologically, and taxonomically diverse group. Within the nearshore waters of the Pacific Northwest, representatives from all five major classes are found—the Asteroidea (sea stars), Echinoidea (sea urchins, sand dollars), Holothuroidea (sea cucumbers), Ophiuroidea (brittle stars, basket stars), and Crinoidea (feather stars). Habitats of most groups range from intertidal to beyond the continental shelf; this discussion is limited to species found no deeper than the shelf break, generally less than 200 m depth and within 100 km of the coast.

Reproduction and Development

With some exceptions, sexes are separate in the Echinodermata and fertilization occurs externally. Intraovarian brooders such as *Leptosynapta* must fertilize internally. For most species reproduction occurs by free spawning; that is, males and females release gametes more or less simultaneously, and fertilization occurs in the water column. Some species employ a brooding strategy and do not have pelagic larvae. Species that brood are included in the list of species found in the coastal waters of the Pacific Northwest (Table 1) but are not included in the larval keys presented here.

The larvae of echinoderms are morphologically and functionally diverse and have been the subject of numerous investigations on larval evolution (e.g., Emlet et al., 1987; Strathmann et al., 1992; Hart, 1995; McEdward and Jamies, 1996) and functional morphology (e.g., Strathmann, 1971, 1974, 1975; McEdward, 1984, 1986a,b; Hart and Strathmann, 1994). Larvae are generally divided into two forms defined by the source of nutrition during the larval stage. Planktotrophic larvae derive their energetic requirements from capture of particles, primarily algal cells, and in at least some forms by absorption of dissolved organic molecules. These larvae are characterized by a bilaterally symmetrical arrangement of ciliated arms that form an elaborate feeding structure to capture, sort, and direct food particles toward the mouth (see Figs. 1, 3, 4, 7). These ciliated structures also provide propulsion and steering functions. Ingested food particles are processed within a simple gut, and fecal pellets are expelled through a

Table 1. Species in the phylum Echinodermata from the Pacific Northwest

	Larval Development Mode	*Spawning Period*
Class Echinoidea		
Order Clypeasteroida		
Dendraster excentricus (Eschscholtz, 1831)	pelagic, planktotrophic	Feb-Sep
Order Echinoida		
Allocentrotus fragilis (Jackson, 1912)	pelagic, planktotrophic	Late-Spr.
Strongylocentrotus franciscanus (A. Agassiz, 1863)	pelagic, planktotrophic	Mar-Jul
Strongylocentrotus purpuratus (Stimpson, 1857)	pelagic, planktotrophic	Dec-Jun
Strongylocentrotus droebachiensis (O.R. Muller, 1776)		
Order Spatangoida		
Brisaster latifrons (A. Agassiz, 1898)	pelagic, lecithotrophic	Spr.-Sum.
Class Asteroidea		
Order Forcipulatida		
Evasterias troschelii (Stimpson, 1862)	pelagic, planktotrophic	Apr-Jun
Leptasterias hexactis (Stimpson, 1862)	brooder, lecithotrophic	Nov-Apr
Orthasterias koehleri (de Loriol, 1897)	pelagic, planktotrophic	May-Aug
Pisaster brevispinus (Stimpson, 1857)	pelagic, planktotrophic	Apr-Jun
Pisaster giganteus (Stimpson, 1857)	pelagic, planktotrophic	Apr-Jun
Pisaster ochraceus (Brandt, 1835)	pelagic, planktotrophic	Apr-Jun
Pycnopodia helianthoides (Brandt, 1835)	pelagic, planktotrophic	Mar-Jul
Stylasterias forreri (de Loriol, 1887)	pelagic, planktotrophic	Apr-Jun
Order Platyasterida		
Luidia foliolata Grube, 1886	pelagic, planktotrophic	Apr-Jun
Order Spinulosida		
Solaster dawsoni Verrill, 1880	pelagic, lecithotrophic	Mar-Jun
Solaster stimpsoni Verrill, 1880	pelagic, lecithotrophic	Mar-Jun
Pteraster tesselatus Ives, 1888	pelagic, lecithotrophic	Jun-Aug
Crossaster borealis (Fisher, 1906)		
Henricia spp.	brooders/pelagic, lecithotrophic	Win.-Spr.
Order Valvatida		
Ceramaster articus (Verrill, 1909)		
Ceramaster patagonicus (Sladen, 1889)		
Hippasteria spinosa Verrill, 1909	pelagic, planktotrophic	
Mediaster aequalis Stimpson, 1857	pelagic, lecithotrophic	Apr-Jun
Asterina miniata (Brandt, 1835)	pelagic, planktotrophic	May-Jul
Dermasterias imbricata (Grube, 1857)	pelagic, planktotrophic	Apr-Aug
Class Holothuroidea		
Order Aspidochirotida		
Parastichopus californicus (Stimpson, 1857)	pelagic, planktotrophic	Apr-Aug
Parastichopus leukothele Lambert, 1986	pelagic, planktotrophic	?
Parastichopus parvimensis H. L. Clark, 1913	pelagic, planktotrophic	?
Order Dendrochirotida		
Psolidium bulatum Ohshima, 1915		
Psolus squamatus (Koren, 1844)		
Psolus chitonoides H. L. Clark, 1901	pelagic, lecithotrophic	Mar-May

table continues

Table 1 continued. Species in the phylum Echinodermata from the Pacific Northwest

	Larval Development Mode	*Spawning Period*
Eupentacta pseudoquinquesemita Deichmann, 1938		
Eupentacta quinquesemita (Selenka, 1867)	pelagic, lecithotrophic	Mar-May
Pentamera lissoplaca (H.L. Clark, 1924)		
Pentamera populifera (Stimpson, 1864)		
Pentamera pseudocalciegera Deichmann, 1938		
Pentamera trachyplaca (H.L. Clark, 1924)		
Havelockia benti (Deichmann, 1937)		
Cucumaria miniata (Brandt, 1835)	pelagic, lecithotrophic	Mar-May
Cucumaria piperata (Stimpson, 1864)	pelagic, lecithotrophic	Mar-May
Cucumaria pseudocurata Deichmann, 1938	brooder, lecithotrophic	Dec-Jan
Cucumaria fallax Ludwig, 1894		
Cucumaria lubrica H.L. Clark, 1901		
Order Molpadiida		
Molpadia intermedia (Ludwig, 1894)		
Paracaudina chilensis (J. Müller, 1850)	pelagic, lecithotrophic	Mar-Apr
Order Apodida		
Leptosynapta clarki Heding, 1928		
Leptosynapta roxtona Heding, 1928		
Leptosynapta transgressor Heding, 1928		
Class Ophiuroidea		
Order Ophiurida		
Ophiopholis aculeata (Linnaeus, 1767)	pelagic, planktotrophic	Spr.-Fall
Amphipholis squamata (Delle Chiaje, 1829)	ovoviviparous brooder	Sum.-Fall
Amphipholis pugetana (Lyman, 1860)	pelagic, planktotrophic	?
Amphioplus macraspis (H.L. Clark, 1911)		
Amphioplus strongyloplax (H.L. Clark, 1911)		
Amphiodia occidentalis (Lyman, 1860)	benthic, lecithotrophic	Spr.-Sum.
Amphiodia urtica (Lyman, 1860)	pelagic, planktotrophic	?
Gorgonocephalus eucnemis (Müller & Troschel, 1842)	benthic, lecithotrophic	Winter
Ophiopteris papillosa (Lyman, 1875)	pelagic, planktotrophic	?
Ophiura leptoctenia H.L. Clark, 1911		
Ophiura lütkeni (Lyman, 1960)		
Ophiura sarsi Lütkeni, 1855		
Class Crinoidea		
Florometra serratissima (A. H. Clark, 1907)	pelagic, lecithotrophic	all year

ventral anus. Because development of these larvae is dependent on an external food source, few lipid reserves are provided in the egg, and species with this type of larval form generally produce relatively large numbers of small eggs (80–170 µm in echinoids, 120–200 µm in asteroids). Temperature and food supply influence larval development rate, which determines the length of time required to reach the stage at which larvae are competent to settle and metamorphose to the benthic juvenile stage. In the northeast Pacific, this larval period may last from three weeks to several months. Planktotrophy is common within the echinoids, asteroids, and ophiuroids but rare within the holothuroids and absent in the crinoids.

Lecithrotrophic, or non-feeding, larvae derive their nutritional requirements from yolk and lipid reserves supplied in the egg. Because these reserves must be sufficient to supply all the energetic requirements until metamorphosis, eggs from lecithotrophic species are larger (400–625 µm in holothuroids, 750–1,500 µm in asteroids) and fewer in number than eggs of species with feeding larvae. At least in the echinoids and ophiuroids, lecithotrophic larvae have evolved from species with feeding larval forms and, in some cases, have retained internal vestiges of larval feeding arms (Hendler, 1978, 1982; Amemiya and Emlet, 1992; Emlet, 1995). Because feeding from external sources does not occur, these larvae do not develop elaborate feeding and propulsion structures. The larval body either is evenly covered with cilia or has well-defined rows of cilia, providing swimming propulsion (see Figs. 5, 6, and Emlet, 1994a). This larval form is found throughout each class of echinoderms but is most prevalent within the holothuroids and is found exclusively within the crinoids. Larvae that are brooded by the adult are also non-feeding. Brooding is most common in the ophiuroids, crinoids, and some groups of asteroids.

A third type of larval form, the facultative planktotroph, has characteristics of both feeding and non-feeding larvae. This larval form may develop by feeding in the plankton, but if deprived of food it is capable of developing through metamorphosis on energy and material provided in the egg (Emlet, 1986; Hart, 1996). This type of larva is represented in local waters by one echinoid species, the heart urchin, *Brisaster latifrons* (Strathmann, 1979; Hart, 1996).

Although the type of larval form (feeding or non-feeding) is known for most nearshore species of echinoderms, published descriptions of larval morphology for some groups are incomplete. Larvae described in the literature include most of the shallow-water echinoids and holothuroids found off the Pacific Northwest. The majority of ophiuroid larvae have not been described. The larvae of some asteroid species have been described, particularly the non-feeding and brooding forms, but little has been published on species with planktotrophic forms.

The biology of echinoderms is reviewed in Hyman (1955), and reproduction and development is reviewed in Okazaki (1975) and Giese et al. (1991). Most of the following discussion on development and larval morphology of local species is taken from Strathmann (1987), which provides the most comprehensive reference on reproduction and development of echinoderms found in the northeast Pacific.

Collecting and Observing Echinoderm Larvae

Echinoderm larvae, particularly species with an extended spawning period (e.g., *Dendraster excentricus*), can be found in the nearshore plankton from late winter through fall. Echinoplutei are most abundant at depths of 5–10 m. Nearshore, both asteroid and ophiuroid larvae can be found at most depths but are frequently most abundant slightly deeper (10–20 m) in the water column, closer to the pycnocline. Early stages of most holothuroid larvae are positively buoyant and, hence, are most abundant near the surface. Holothuroid larvae at advanced stages of development may be found at all depths (Miller, 1995).

A plankton net and cod-end bucket with 202 µm mesh will capture larvae as small as four-arm and most prism-stage pluteus larvae. Handling live larvae in the laboratory should be done with 100 µm mesh or finer, to minimize damage to the arm epithelia and surface cilia. Undamaged bipinnariae, brachiolariae, and pluteus larvae may be kept in the laboratory for several days without feeding. For observation of later stages, larvae must be fed and the water in culture jars stirred and changed periodically. Refer to Strathmann (1987) and Leahy (1986) for laboratory culture of echinoderm larvae. With careful culture techniques (and, perhaps, a bit of luck) larvae (feeding and non-feeding forms) may complete development through metamorphosis in the laboratory. Competent stages of most echinoid and holothuriod larvae, and some asteroid larvae, can be induced to metamorphose in the laboratory if provided with a substrate covered with a bacterial film. For many species, natural rock covered with coralline algae is sufficient to induce metamorphosis (Miller, 1995).

Material that is to be preserved should be immediately transferred to 1.5% buffered formaldehyde (5% formalin). An excess of sodium borate (widely available as Borax) added to the stock formaldehyde solution is an adequate buffer. The calcareous parts of echinoderm larvae dissolve quickly in formalin solutions that are not buffered. Larvae preserved in this manner will retain their color for several weeks and remain in good condition for at least several months. Larvae that are to be kept for longer periods should be transferred to buffered ethanol after fixing in formalin.

The calcareous arm spicules and ossicles of echinoderm larvae can be difficult to see under normal transmitted light. To highlight the birefringent skeletal rods and ossicles, larvae are best observed with substage illumination and cross-polarized light. Polarizing filters are placed above and below the sample and oriented such that the planes of light transmission are 90° to each other. Polarizing filter accessories are available from some microscope companies; however, a more economical approach is to mount a standard rotating polarizing filter designed for camera lenses onto the bottom of the microscope objective. A mount can be readily made by cutting a section of PVC pipe that will slip over the outside of the objective lens and gluing the filter onto the bottom of the PVC section. Make sure the glue does not prevent the filter from rotating. The mount can be tapped for a set screw to hold it in place on the microscope objective. There must also be polarizing film below the material to be viewed. Plastic polarizing film is available at most photography suppliers and can be ordered from Edmund Scientific Company, Barrington, New Jersey. Cut a piece of this film to fit under the microscope stage. If heat from substage illumination is a problem, place the filter on top of the stage and cover it with a sheet of glass. In use, the filter mounted on the objective is rotated until the background is dark and calcareous structures become refractive, that is, until they appear illuminated against a dark background. Under cross-polarized light, other characteristics such as color are difficult to discern, so it may be necessary to alternate between polarized and incident light by rotating the filter on the microscope objective. A secondary fiber optic light for incident light is helpful. This method is useful for sorting and identification of any larvae or material with calcareous parts, such as mollusc larvae and some sponge spicules.

Morphology

Class Echinoidea

Local echinoids include three species of sea urchins (*Strongylocentrotus franciscanus, S. purpuratus, Allocentrotus fragilis*), a sand dollar (*Dendraster excentricus*), and a heart urchin (*Brisaster latifrons*) (Table 1). All are free-spawning and have pelagic larvae called echinoplutei (Fig. 1). Larvae from at least one of these species can be found from late winter through fall. Natural spawning of each species occurs over a period of one to several months, and some populations may shed gametes several times during a season (Chatlynne, 1969; Gonor, 1973; Cameron and Rumrill, 1982). With the exception of *B. latifrons*, local species have small eggs, 80–170 µm diameter.

Cleavage is radial and holoblastic. At 12°C, a ciliated blastula hatches at ca 24 hours after fertilization. The hatched swimming blastula has a thick posterior vegetal pole where gastrulation by invagination begins. Gastrulation proceeds until the archenteron fills almost three-fourths the length of the blastula. The archenteron then turns toward one side, which becomes the flat ventral side of the prism stage of the larva. At the base

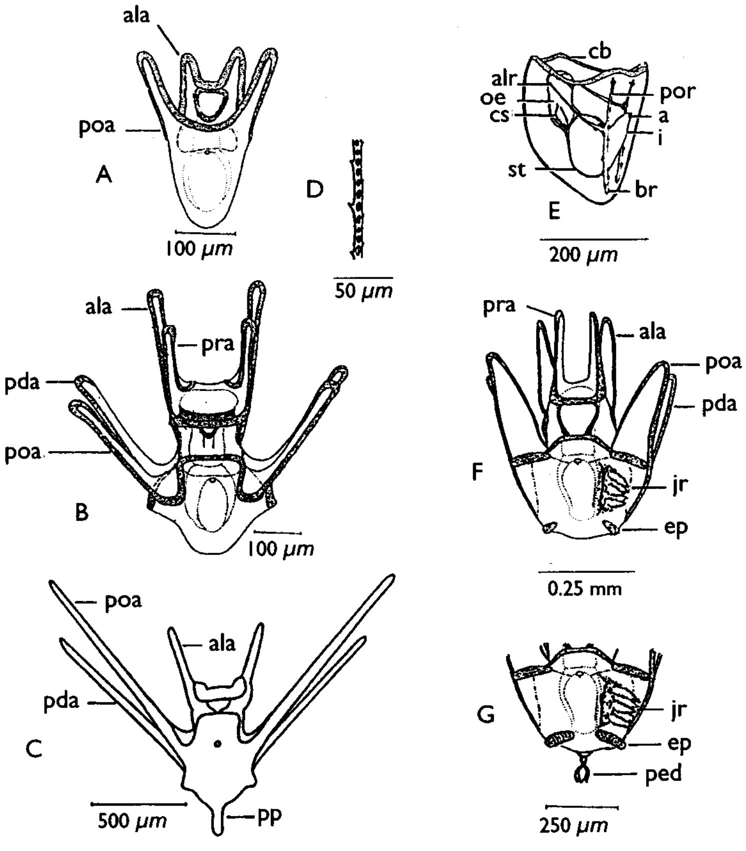

Fig. 1. Echinoplutei. (A) *Dendraster excentricus*, four-armed stage. (B) *Dendraster excentricus*, eight-armed stage. (C) *Brisaster latifrons*, six-armed stage. (D) Fenestrated arm rod of *D. excentricus*. (E) *Strongylocentrotus* sp., late prism–early pluteus stage. (F) *Strongylocentrotus purpuratus*, eight-armed stage. (G) *Strongylocentrotus franciscanus*, eight-armed stage, only posterior region and posterior pedicellaria shown. (A–D, F–G, ventral view; E, right lateral view. Abbreviations: anus (a), anterolateral arm (ala), anterolateral rod (alr), body rod (br), ciliated band (cb), epaulette (ep), intestine (i), juvenile rudiment (jr), oesophagus (oe), pedicellariae (ped), posterodorsal arm (pda), postoral arm (poa), postoral rod (por), preoral arm (pra), posterior process (pp). (Adapted from Strathmann, 1971, 1979, 1987)

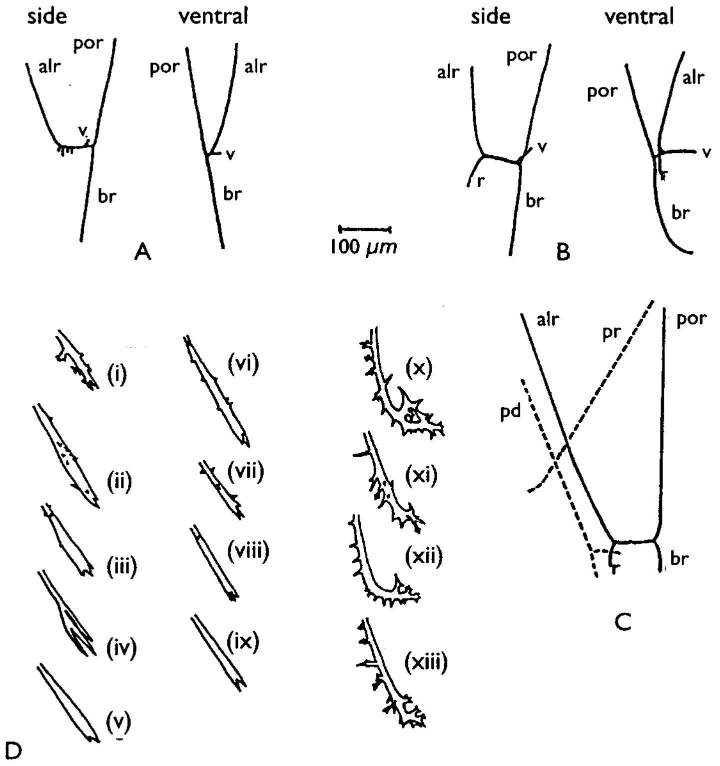

Fig. 2. Calcareous skeletal rods of strongylocentrotids in the four-armed stage, side view on left, ventral view on right. (A) Arrangement in *Strongylocentrotus purpuratus* and *Allocentrotus fragilis*, four-armed stage. (B) Arrangement in *Strongylocentrotus franciscanus*, four-armed stage. (C) Arrangement in *Strongylocentrotus franciscanus*, eight-armed stage. (D) Distal ends of body rods in four-armed and early six-armed stages; (i)–(v), *S. purpuratus;* (vi)–(ix), *A. fragilis;* (x)–(xiii), *S. fransicanus.* Abbreviations: anterolateral rod (alr), body rod (br), posterodorsal rod (pd), postoral rod (por), preoral rod (pr), recurrent rod (r), ventral transverse rod (v). (Adapted from Strathmann, 1979)

of the archenteron, the primary mesenchyme cells aggregate into two masses within which the triradiate primary spicules of the larval skeleton are secreted. These calcareous spicules, which eventually form the supportive structures for the larval arms, are key diagnostic traits for distinguishing between echinoid species (Fig. 2).

By four to seven days (depending on species and temperature), an early four-armed pluteus larva has formed. Larval growth involves both the addition of arms and increase in their size. The anterolateral and postoral pairs of arms appear first, with a third rod extending posteriorly from each primary spicule to form a body rod (Fig. 1E). Small medially projecting rods, the ventral transverse rods, also develop from the primary spicules. Next, the larva develops a pair of posterodorsal arms and a dorsal skeletal arch with arms that extend into the oral lobe and become the preoral arms of the eight-armed echinopluteus (e.g., Fig. 1B, 1F). The body rods thicken and elaborate posteriorly; and in *Dendraster excentricus* they form a basket-like structure. The larva of *Brisaster latifrons* also develops a single posterior process supported by a calcareous rod (Fig. 1C).

The larval arms and the preoral lobe support a band of ciliated cells that form a continuous loop that extends over the ciliated oral region and mouth. This ciliated band is used for feeding and swimming. Larvae of the three species of sea urchin also develop two additional bands of cilia located posterially, epaulettes, which are important for locomotion.

After development of eight arms, a juvenile rudiment begins to form on the left side of the larva, between the postoral and posterodorsal arms. The juvenile rudiment is the developing cell mass that forms all the structures of the juvenile sea urchin. The rudiment forms within an invagination of the body wall, the vestibule. Five primary tube feet (podia) of the developing juvenile can extend from the vestibule and are used to attach to the substratum when the larva is ready to metamophose. The primary spines of the juvenile may also be seen protruding from the vestibule.

In larvae competent to metamorphose, the rudiment may be viewed as an "inside-out" juvenile sea urchin, attached to the larval body. The primary tube feet extend from what will become the oral surface, and the primary spines originate from what will become the aboral surface of the juvenile. Upon settlement and metamorphosis, most of the larval body is resorbed, including the arm tissues, and the rudiment tissues evert in such a manner to cover the aboral surface with the calcareous plates associated with each primary spine. For a detailed description of echinoid metamorphosis, see Chia and Burke (1978).

Key to echinoid larvae (modified from Strathmann, 1979)

1a. Postoral and posterodorsal arm rods fenestrated (Fig. 1D) 2
1b. Arm rods not fenestrated 3

2a. Larvae opaque, with orange-red pigment spots (when living, and for several weeks when preserved in buffered formalin); posterior process present by late 4-armed stage .... *Brisaster latifrons*
2b. Most of larval surface transparent, typically with pale green pigment spots; no posterior process; posterior distal ends of body and arm rods curve inward to form basket-like structure in 8-armed stage; no posterior epaulettes in 4-armed stage (Fig. 1B) .... *Dendraster excentricus*

3a. With 4 or 6 arms 4
3b. With 8 arms 6

4a. Ventral transverse rod prominent and meeting at midline in 4- and early 6-armed stage (Fig. 2B); recurrent rods prominent; distal end body rods very thorny and curved toward midline (before late 6-armed stage, Fig. 2D); small pigment spots deep red .... *Strongylocentrotus franciscanus*

4b. Ventral transverse rods short and not meeting at midline; recurrent rods absent or not prominent; body rods not curved toward midline; no posterior pedicellariae; small pigment spots may be other than deep red 5

5a. Pigment spots (deep red) over most of larval surface .... *Strongylocentrotus purpuratus*
5b. Pigment spots few and inconspicuous; pink or orange pigment spots only in arms, or near ciliated band .... *Allocentrotus fragilis*

6a. Recurrent rod still present in early 8-armed stage; 1 pedicellaria forms at posterior and 2 on right side during 8-armed stage; posterior transverse rod present and associated with developing posterior pedicellaria; with epaulettes; pigment spots deep red .... *Strongylocentrotus franciscanus*
6b. Recurrent rods absent or not prominent; no pedicellaria form on larva prior to metamorphosis; posterior spicules (if present) not extended as transverse rod; with epaulletes; pigment spots may not be deep red 7

7a. Pigment spots deep red .... *Strongylocentrotus purpuratus*
7b. Pigment spots orange or pink .... *Allocentrotus fragilis*

Class Asteroidea

Sea stars found in nearshore waters of the Pacific Northwest are represented by four orders: Platyasterida, Valvatida, Spinulosida, and Forcipulatida (Table 1). Two species brood

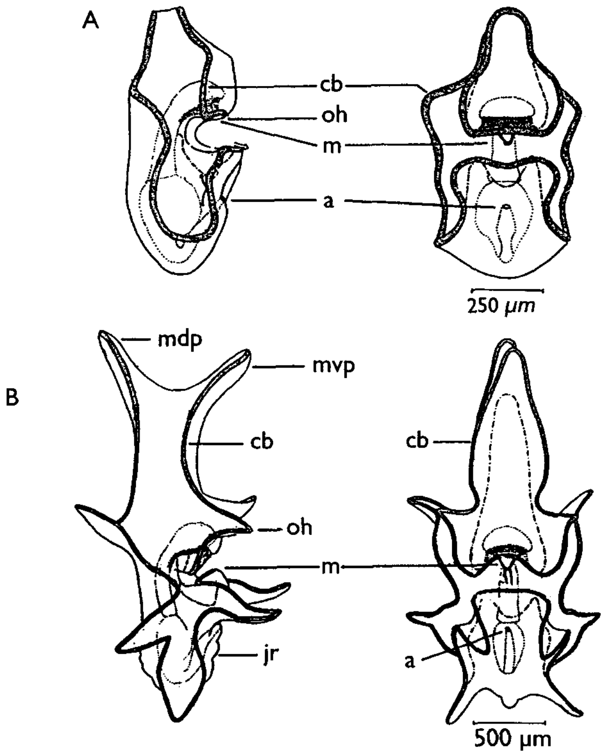

Fig. 3. Asteroid bipinnaria, lateral (left) and ventral (right) views. (A) *Asterina miniata* (general form of forcipulate bipinnaria). (B) *Luidia foliata*. Abbreviations: anus (a), ciliated band (cb), juvenile rudiment (jr), mouth (m), median dorsal process (mdp), median ventral process (mvp), oral hood (oh). (Adapted from Strathmann, 1979)

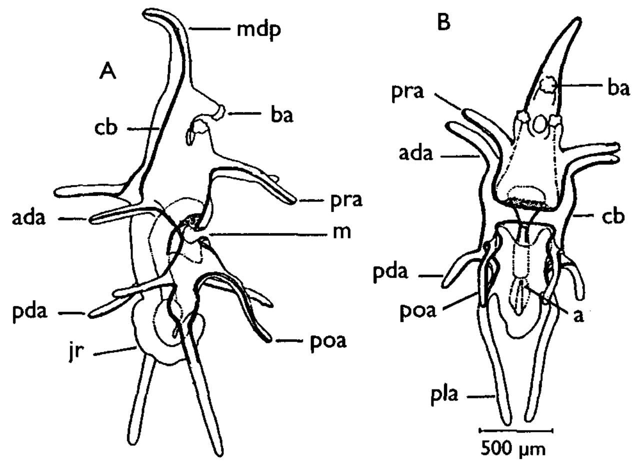

Fig. 4. Brachiolaria of *Pisaster ochcraceus* (general form of forcipulate brachiolaria), (A) lateral and (B) ventral views. Abbreviations: anus (a), adhesive disc (add), anterodorsal arm (ada), anterolateral arm (ala), brachiolar arm (ba), ciliated band (cb), mouth (m), median dorsal process (mdp), posterodorsal arm (pda), posterolateral arm (pla), postoral arm (poa), preoral arm (pra). (Adapted from Strathmann, 1971).

(*Leptasterias hexactis* and *Henricia* sp.), and the remainder have pelagic larvae. Both feeding and non-feeding larval forms are found. Feeding larvae are pelagic for one to several months; non-feeding larvae develop on the order of two to four weeks. Oguro (1989) provides a discussion of development and larval types in asteroids.

The early stage of feeding larvae is the bipinnaria (Fig. 3), and a later stage with attachment arms is the brachiolaria (Fig. 4). The bipinnaria swims and feeds by means of a ciliated band that forms a continuous loop along the sides of the body, the larval arms, and around the anus. An anterior ventral band of cilia becomes a separate loop, the preoral loop. This latter trait may be used to distinguish asteroid larvae from the similarly shaped auricularia larva of the holothuroid *Parastichopus* sp., which has only a single continuous band of cilia (see Fig. 6A). At 12° C, the common ochre seastar, *Pisaster ochraceus*, forms a feeding bipinnaria five days after fertilization (Fraser et al., 1981). In advanced larvae, the posterior left hydrocoel develops five lobes that are rudiments of the hydrocoels of the rays of the juvenile. The juvenile rudiment develops posteriorly on the left side of the larval body with the oral surface facing the left side of the body.

In the orders Forcipulatida and Valvatida, and in some of the Spinulosida, the brachiolaria develops three anterior brachiolar arms with glandular tips surrounding a central adhesive disc (Fig. 4). These structures are used to attach to the substratum when the larva is metamorphically competent. Upon settlement, the developing juvenile has a single primary tube foot and ocellus (eye spot) on the end of each ray. In the forcipulates, six primary calcareous ossicles (one central, plus one associated with each ray) can also be seen on the aboral surface.

Pelagic non-feeding larvae are found in the orders Spinulosida (*Pteraster tesselatus, Henricia* spp., *Solaster stimpsoni, S. dawsoni*) and Valvatida (*Mediaster aequalis*). The large, yolky eggs (0.75–1.5 mm diam.) and early larvae are usually positively buoyant and can be found near the surface. The early ciliated larva is opaque and in some species colored bright red-orange. A local species of the genus *Henricia, M. aequalis, S. stimpsoni,* and *S. dawsoni* develop into modified brachiolarias with anterior brachiolar arms and an adhesive disc that differ from those found in the forcipulates (Fig. 5). *Pteraster tesselatus* does not develop brachiolar arms.

The forcipulate *Lepasterias hexactis* broods its larvae. Large yolky eggs are shed under the female body, where they are fertilized by sperm shed into the surrounding water. Larvae of *L. hexactis* are brooded under the female. They develop tube feet by 40 days and crawl away as small juveniles at two months (Chia, 1966, 1968).

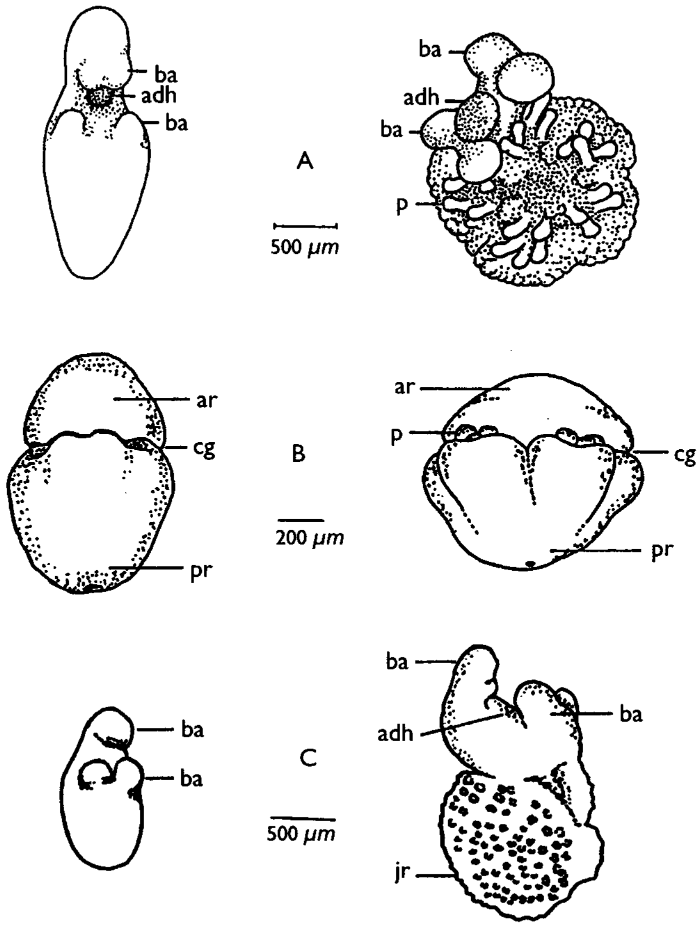

Fig. 5: Larval forms of lecithrotrophic (non-feeding) asteroids. (A) Brachiolaria of a species of *Henricia*, frontal view (left) and during metamorphosis (right), left side of larva and ventral (oral) side of juvenile. (B) *Pteraster tesselatus*, at six days (left), lateral view, and at eight days (right), lateral view. (C) *Mediaster aequalis*, brachiolaria at 10 days (left), frontal view, and advanced brachiolaria at ~25–30 days (right), right side of larva and dorsal (aboral) side of juvenile. Abbreviations: adhesive disc (add), anterior region (ar), brachiolar arm (ba), circumferential groove (cg), juvenile rudiment (jr), podium (p), posterior region (pr). A adapted from Strathmann, 1987; B adapted from McEdwards, 1992; C adapted from Birkeland et al., 1971)

Key to asteroid larvae

1a. Larval form with paired feeding arms or lobes, with 2 continuous bands of cilia along arms (e.g., Figs. 3, 4); mouth and anus present; transparent, some surface pigmentation may be present; no internal calcareous skeleton or ossicles 5
1b. No feeding structures or mouth; opaque 2

2a. Color usually orange, may vary from yellow to dark red 3
2b. Color light tan or pale olive-green; with modified brachiolar arms; with groups of podia on juvenile rudiment in advanced larvae .... *Solaster dawsoni* or *Solaster stimpsoni*

3a. With modified brachiolar arms (e.g., Figs. 5A, 5C) 4
3b. No brachiolar arms; color usually orange (may vary from light yellow to dark red); 1-day old larvae ovoid, evenly ciliated; older larvae with circumferential groove, forming anterior and posterior regions; 5 bulges around circumference on posterior region; 5 clusters of podia (1 terminal podium, 2 pairs adjacent podia) within circumferential groove, each centered under bulge on posterior region (Fig. 5B) .... *Pteraster tesselatus*

4a. 3 brachiolar arms (one median anterolateral, 2 ventrolateral, Fig. 5C); advanced larvae with disk of developing juvenile (1.2–1.3 mm diam.) at posterior end; no podia form prior to settlement; color orange .... *Mediaster aequalis*
4b. 4 brachiolar arms (2 anterodorsal, 2 ventrolateral) and single stalked adhesive disc between paired brachiolar arms (Fig. 5A); advanced larvae with juvenile disk on left side and 5 groups of podia on oral (left) surface of juvenile disk; color orange .... *Henricia* sp.

5a. Bipinnaria larger than same stage in other groups (>2.6 mm long); no brachiolaria stage; elongate median dorsal and ventral process (region anterior to oral hood one-half total body length) (Fig. 3) .... *Luidia foliatata*
5b. Bipinnaria not as above, or with feeding brachiolaria stage; long, transparent feeding and locomotory arms in brachiolaria stage, with band of cilia along preoral arms and surrounding mouth, and separate band along all other arms (e.g., Fig. 4); some pigmentation may be present (pale green, gold, orange red), usually on distal ends of arms; advanced larvae with juvenile disk on left side at posterior end (pigmented same color as arms) and brachiolar arms and adhesive disk at anterior end; calcareous ossicles and early juvenile spines may be present on juvenile disk in advanced larvae .... valvatid or forcipulate brachiolariae (*Asterina miniata, Dermasterias imbricata, Evasterias troschelii Orthasterias koehleri, Pisaster brevispinus, P. giganteus, P. ochraceus, Pycnopodia helianthoides, Stylasterias forreri*)[1]

[1] Distal ends of arms and juvenile disk are pigmented pale gold in *P. ochraceus* and orange-red in *P. helianthoide;* other species may have similar pigmentation. Coloration in *A. miniata* may be variable (S. Rumrill, pers. comm.).

Class Holothuroidea

The nearshore sea cucumbers are represented by nine species within three orders (Table 1). Three of these species, all within the genus *Parastichopus*, have a pelagic feeding stage (auricularia larva) that develops into a non-feeding doliolaria larva before metamorphosis. Two of these species, *P. leukothele* and *P. parvimensis*, are generally found in deeper water on the continental shelf, but because the feeding larva of these species may be pelagic for one to two months their larvae may occur nearshore. The dendrochirotid *Cucumaria pseudocurata* is a brooder, and thus larvae of this species are not found in the plankton. All other species produce pelagic, non-feeding, doliolaria larvae that metamorphose to benthic juveniles in six to thirteen days. Holothuroid reproduction and development are reviewed in Hyman (1955) and Giese et al. (1991). Descriptions of larval forms of northeast Pacific holothuroids have been made by Mortenson (1921), Johnson and Johnson (1950), Young and Chia (1982), McEuen and Chia (1985), Cameron (1985), and McEuen (1986).

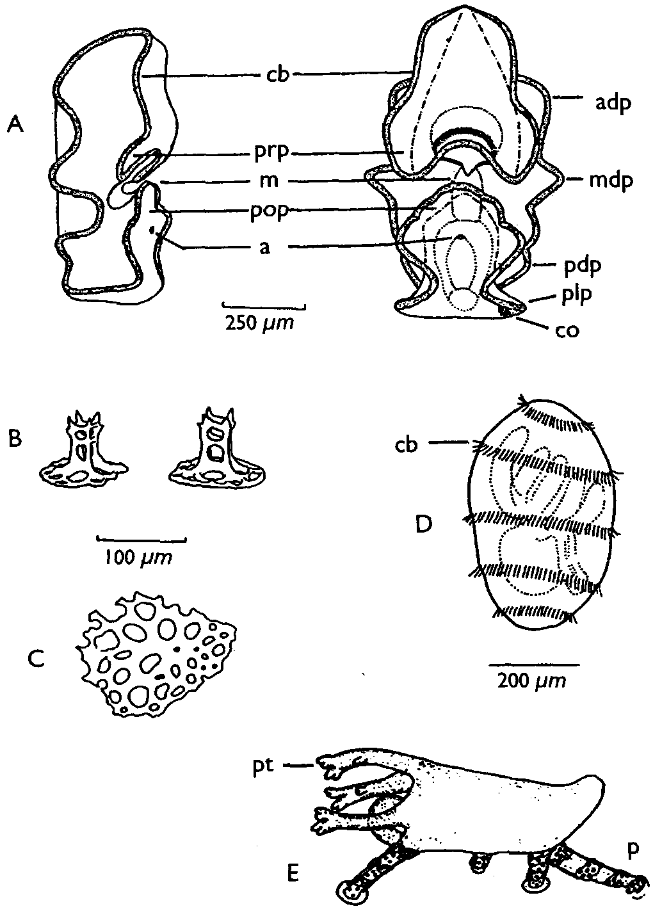

Fig. 6. Larval forms of holothuroids. (A) Auricularia stage of *Parastichopus californicus*, lateral view on left, ventral view on right. (B) Fenestrated table ossicles from pentacula stage larva of *Parastichopus* sp. (C) General form of flat ossicles from pentacula stage larvae. (D) Doliolaria stage of *Parastichopus californicus*. (E) General form of early pentacula stage larva. Abbreviations: anus (a), anterodorsal process (adp), ciliated band (cb), calcareous ossicle (co), mouth (m), median dorsal process (mdp), podium (p), posterodorsal process (pdp), posterolateral process (plp), postoral process (pop), preoral process (prp), primary feeding tentacles (pt). (A adapted from Strathmann, 1971; B adapted from Lambert, 1986; D adapted from Strathmann, 1987; E adapted from Johnson, 1931)

Pelagic planktotrophic development within the northeast Pacific holothuroids is restricted to the genus *Parastichopus*. The early larva, the auricularia, develops a looped band of cilia for both feeding and swimming (Fig. 6A). Further growth produces arms and lobes over which the single, continuous band is looped. This single band of cilia distinguishes the auricularia larva from the similar early bipinnaria stage larva of asteroids, which develops two separate ciliated bands. A second trait useful for distinguishing auricularia is the presence of a calcareous ossicle in the left posterolateral lobe. Further, the anterior colomic cavities of the auricularia do not enlarge and extend forward on both sides of the esophagus as they do in asteroids. Larvae are transparent with occasional tinting along the ciliary band. In preparation for metamorphosis, the larva of *Parastichopus* develops into a simplified, barrel shape, the doliolaria larva (Fig. 6D). The ciliary band rearranges into five transverse rings of cilia. Five primary tentacles develop and push through the oral indentation. Protrusion of the tentacles marks the onset of the pentacula stage (Fig. 6E). The tentacles are used to attach to the substrate during settlement, when the benthic juvenile stage begins. Calcareous ossicles begin to form during the pentacula stage and cover the larval surface at metamorphosis. These ossicles can be used to distinguish between some species.

In other groups of holothuroids, pelagic lecithrotrophic development begins with large yolky eggs (267–627 µm diam.), usually brightly pigmented, extruded singly or bound in strings or pellets that disperse soon after release. Larger eggs are positively buoyant, whereas smaller eggs are neutral or slightly negative. Larvae develop as non-feeding doliolaria,

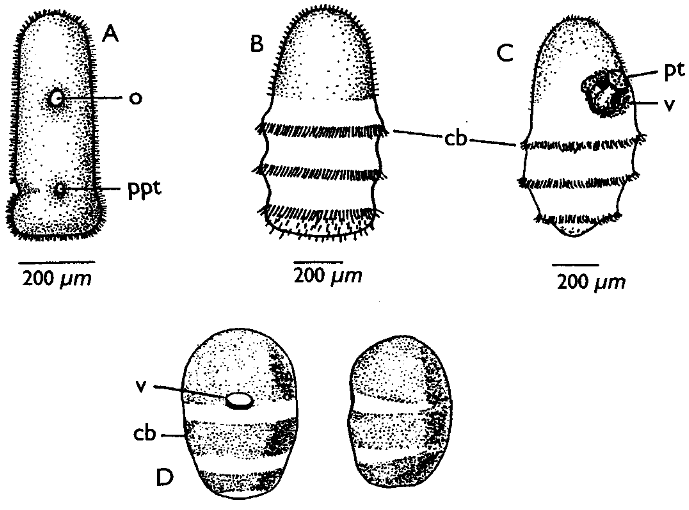

Fig. 7. Doliolaria stage larval forms of holothuroids. (A) *Eupentacta quinquesemita*, ventral view. (B) *Psolus chitonoides*. (C) *Cucumaria* sp., advanced stage, ventral view. (D) *Paracaudina chilensis*, ventral view on left, left side view on right. Abbreviations: ciliated band (cb), oral indentation (o), podial pit (ppt), primary tentacle (pt), vestibule (v). (A, B adapted from Strathmann, 1987; D adapted from Inaba, 1930)

usually retaining the color of the egg (Fig. 7). Early doliolaria are evenly ciliated, but older larvae develop two or three transverse rings of cilia. These rings first form as epidermal ridges along the posterior two-thirds of the body, and cilia between the ridges are eventually lost. The preoral lobe, which is the pigmented yolk reservoir anterior to the oral indentation, retains its uniform ciliation. As part of metamophosis, larvae develop and extend five primary podia through the oral indentation, marking onset of the pentacula stage. After settlement in the dendrochirotids, two podia also develop from the podial pits posterior to the oral indentation.

Key to holothuroid larvae

1a. Transparent larva (auricularia) with single, continuous band of cilia along arms and lobes; calcareous ossicle present in left posterolateral lobe (Fig. 6A) .... *Parastichopus* spp.
1b. Opaque, pigmented, barrel-shaped larva (doliolaria) (Fig. 6D) 2

2a. 5 transverse ciliary bands present (Fig. 6D); yellow-tan pigmentation; late pentacula stage covered with fenestrated "table" ossicles (Fig. 6B), which protrude from body surface .... *Parastichopus* spp.
2b. Evenly ciliated or 2–3 ciliary bands present 3

3a. No ciliary bands (evenly ciliated); pigmentation of preoral lobe light green, posterior body semitranslucent white; pentacula semiopaque white or light tan; late pentacula with small ossicles perforated with fine pores (Fig. 7A) .... *Eupentacta quinquesemita*
3b. 2–3 ciliary bands 4

4a. Doliolaria and pentacula red-orange, with yellow-orange posterior lobe in older larvae; 3 ciliated bands by 7 days of age (Fig. 7B) .... *Psolus chitonoides*
4b. Pigmentation not red-orange 5

5a. 2 ciliary bands present (1 in early doliolaria); pigmentation brown-red in doliolaria and pentacula (Fig. 7D) .... *Paracaudina chilensis*
5b. 3 ciliary bands present, pigmentation of preoral lobe olive green, light green posterior; late pentacula with large ossicles perforated with large pores (Fig. 7C) .... *Cucumaria* sp.

Class Ophiuroidea

Ophiuroids display a wide variety of reproductive strategies: (1) pelagic development with planktotrophic larvae; (2) pelagic, demersal, or benthic development with lecithotrophic larvae; (3) external brooding; (4) ovoviviparous or viviparous bursal brooding; and (5) asexual development. The seven species of ophiuroids found in nearshore waters off Oregon display at least three of these strategies (Table 1). Four of these species have pelagic, planktotrophic larvae. One species (*Amphipholis squamata*) is an ovoviviparous brooder. The lecithotrophic larvae of the basket star, *Gorgonocephalus eucnemis,* have not been fully described, but development is probably by external brooding or as a benthic or demersal larva on or in soft corals. Pelagic development has been inferred from egg size for larvae of *Amphiodia occidentalis* (Rumrill, 1982), but further work has shown this species to have lecithotrophic larvae that probably develop by external brooding or as benthic or demersal larvae (R. Emlet, pers. comm.). Development is similar among species with small eggs and planktotrophic larvae. Patterns of development are modified in species with lecithotrophic larvae and in species with internal development.

Species with planktotrophic development have small eggs (70–200 μm diam.) that are free-spawned, with external fertilization. Larvae develop into an ophiopluteus with a pelagic period of 20–90 days. Cleavage is radial, holoblastic, and equal. Larvae hatch as a ciliated coeloblastula. Primary mesenchyme cells migrate inward at the vegetal pole, and gastrulation takes place as an invagination of the flattened vegetal plate. The larval mouth forms where the invaginating archenteron fuses with a stomodeal depression in the body wall. The archenteron also gives rise to the larval gut, with the anus at the site of the blastopore. Groups of primary mesenchyme cells on either side of the larval archenteron secrete a pair of triradiate or tetraradiate calcareous spicules. The skeletal rods that support the larval body and arms develop from these spicules.

The ophiopluteus larva is distinguished primarily by the long widely spreading posterolateral arms, which develop first. Anterolateral arms develop next, followed by postoral arms that form as a pair of extensions that branch from the junction between the posterolateral and anterolateral arms. The postoral arms are the last to develop, completing the development of the eight-armed ophiopluteus (Fig. 8A). Continuous bands of cilia loop around the arms and larval body of planktotrophic ophioplutei. The cilia are used for swimming and to collect and transport food particles to the mouth.

The juvenile rudiment develops in a mid-ventral position in all planktotrophic ophioplutei, but metamorphosis occurs by two different patterns. In type 1 metamorphosis, the anterolateral, posterdorsal, and postoral arms are gradually resorbed. The rudiment continues to develop while attached

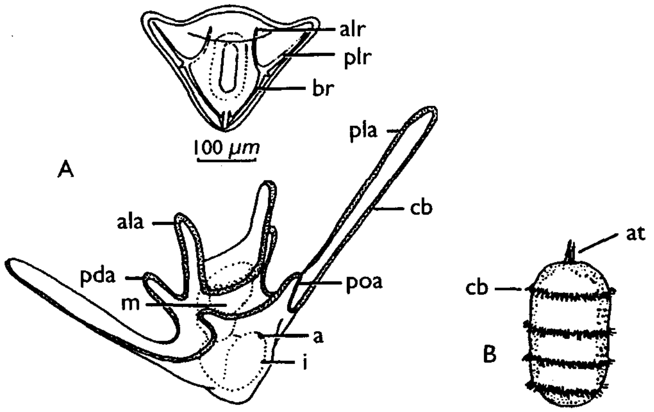

Fig. 8. Larval forms of ophiuroids and crinoids. (A) Ophioplutei of *Ophiopholis aculeata*, two-armed stage (above), ventral view, and eight-armed stage (below), oblique view. (B) Doliolaria of the crinoid *Florometra serratissima*. Abbreviations: anus (a), anterolateral arm (ala), anterolateral rod (alr), apical tuft (ap), body rod (br), ciliated band (cb), intestine (i), mouth (m), posterodorsal arm (pda), posterolateral arm (pla), postoral arm (poa). (A adapted from Strathmann, 1987; B adapted from Emlet, 1999b)

to the long posterolateral arms, which are finally shed just prior to or following settlement. The larvae of *Ophiopholis aculeata* display this type of metamorphosis. In type 2 metamorphosis, all four pairs of arms are resorbed into the rudiment. In both types of metamorphosis, a terminal podium and pairs of podia develop along each radial extension of the hydrocoel. Six branched spicules form on the right side of the larva which will become the central and radial plates on the aboral surface of the juvenile disc. Five spicules also form on the left side of the larva and are rudiments of the terminal plates adjacent to the juvenile arms.

Ophiopholis aculeata is the only species with pelagic planktotrophic larvae found in Pacific Northwest waters that has been thoroughly described (Olsen, 1942, Fig. 7A). Although ophioplutei develop characteristic skeletal traits and pigmentation on the arms and ciliated band which may permit differentiation between species, descriptions of the larvae of local species have not been made. Because larvae may be pelagic for several months, it is also possible that nearshore collections of plankton may include larvae from species found in the deeper waters of the continental slope. Little is known of development modes of these deep-water species.

Class Crinoidea

Only one species of crinoid, the feather star, *Florometra serratissima*, is found in nearshore northeastern Pacific waters. Adults may be found in water ranging from 11 to 1,200 m depth, but this species has been observed to be abundant on rocky reef habitat at depths 50–150 m off Oregon (Oregon Department of Fish and Wildlife, unpub. data). Although early development of *F. serratissima* has been described, nothing is known of the embryology of the dozens of species of crinoids found in deeper waters.

Sexes are separate and fertilization is external. In British Columbia, *F. serratissima* is reported to spawn year-round (Mladenov, 1986). Eggs are pale pink and 207 µm in diameter. Cleavage is radial, holoblastic, and asynchronous. Gastrulation occurs by invagination. Larvae hatch at about one and a half days as actively swimming, evenly ciliated gastrulae with an apical tuft of cilia at the anterior end (Mladenov and Chia, 1983). By four days, larvae have developed four circumferential bands of cilia, a vestibular invagination on the mid-ventral surface, and an adhesive pit on the anteroventral surface (Fig. 8B). Larvae at this stage are termed doliolaria. Settlement occurs at ca five to seven days.

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