2

Cnidaria (Coelenterata)

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The cnidarians (coelenterates), encompassing hydroids, sea anemones, corals, and jellyfish, are a large (ca 5,500 species), highly diverse group. They are ubiquitous, occurring at all latitudes and depths. The phylum is divided into four classes, all found in the waters of the Pacific Northwest. This chapter is restricted to the two classes with a dominant polyp form, the Hydrozoa (Table 1) and Anthozoa (Table 2), and excludes the Scyphozoa, Siphonophora, and Cubozoa, which have a dominant medusoid form. Keys to the local Scyphozoa and Siphonophora can be found in Kozloff (1996), and Wrobel and Mills (1998) present a beautiful pictorial guide to these groups.

Reproduction and Development

The relatively simple cnidarian structural organization contrasts with the complexity of their life cycles (Fig. 1). The ability to form colonies or clones through asexual reproduction and the life cycle mode known as "alteration of generations" are the two fundamental aspects of the cnidarian life cycle that contribute to the group's great diversity (Campbell, 1974; Brusca and Brusca, 1990). The life cycle of many cnidarians alternates between sexual and asexual reproducing forms. Although not all cnidarians display this type of life cycle, those that do not are thought to have derived from taxa that did. The free-swimming medusoid is the sexually reproducing stage. It is generated through asexual budding of the polyp form. Most polyp and some medusae forms are capable of reproducing themselves by budding, and when budding is not followed by complete separation of the new cloned individuals colonies are formed (e.g., *Anthopleura elegantissima*). In some groups, either the medusoid or the polyp stage may be missing; for example, the medusoid stage is absent or vestigial in the anthozoans. The majority of the following information on both hydrozoan and anthozoan reproduction is from Strathmann (1987) and Campbell (1974).

The hydroids (order Hydoida) and hydrocorals (order Stylasterina), class Hydrozoa, reproduce asexually (through fission and budding) and sexually. There is such diversity in hydrozoan sexual reproduction and development that it is difficult to generalize. In most species the sexes are separate.

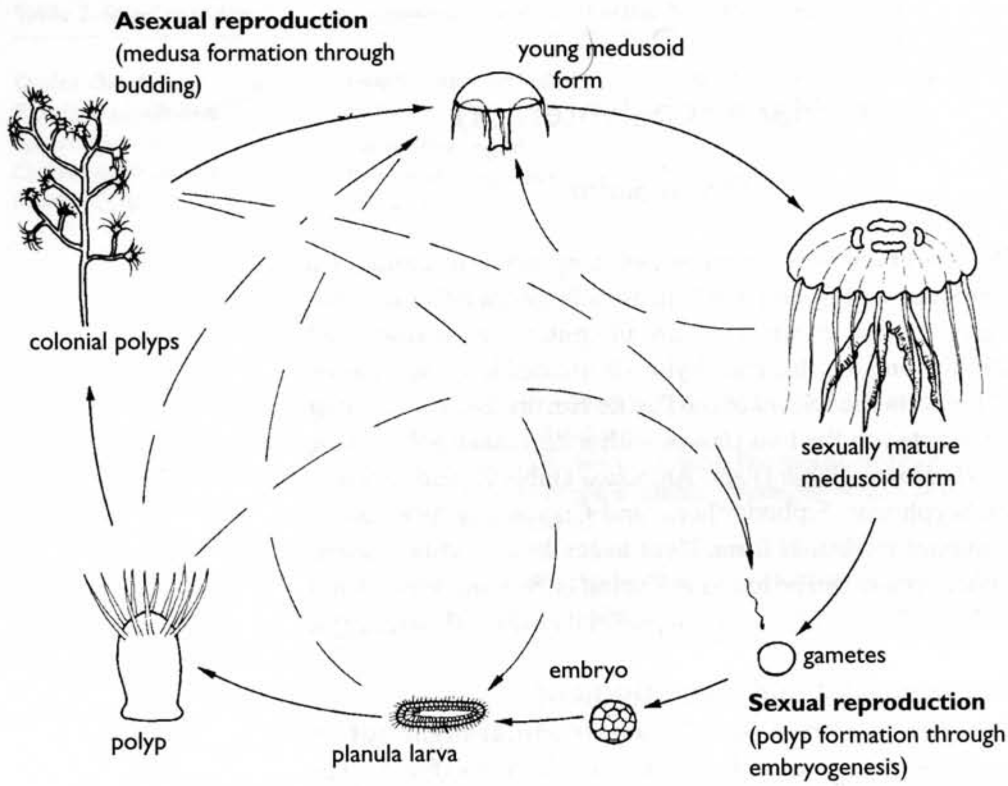

Fig. 1. Basic cnidarian life cycle showing alteration between sexual and asexual "generations." Alternative cycles found in some taxa are indicated by broken lines. (From Campbell, 1974)

Gonads form in specialized structures known as gonophores. In species with diphasic life cycles, gonophores develop into hydromedusae (free-swimming, bell-shaped medusae) that then develop gonads as they feed in the plankton. In some species the medusoid form is lacking and the mudusa is retained on the polyp in various reduced forms. Alternately, the reduced medusa is free in the water column for only a brief period of spawning. Either fertilization in Hydromedusae is internal or the gametes are shed freely in the water column. The propagules develop into planulae, which settle to the bottom and establish a new colony. Wrobel and Mills (1998) and Kozloff (1996) provide an excellent guide to the medusea of common local hydrozoans.

The corals, anemones, sea pens, and solitary cup corals, class Anthozoa, reproduce asexually (through fission, budding, or pedal laceration) and sexually. Some anthozoan species (not reported locally) asexually produce propagules morphologically similar to sexually produced planulae (Black and Johnson, 1979; Carter and Thorp, 1979; Strathmann, 1987). Sexual reproduction and development is more uniform in anthozoans than in hydrozoans. Most species are believed to produce separate sexes, but gonads may be diffuse and scattered throughout the mesoglea and, hence, difficult to detect. Cases of hermaphroditism in species that usually have separate sexes have been documented (Jennison, 1979). Some species (e.g., *Epiactis prolifera* and *Aulactinia incubans*) are simultaneous or sequential hermaphrodites. Although most anthozoans shed large, yolky eggs, some species brood. External brooders retain their eggs or embryos on the parental column, and internal brooders retain their eggs within the enteron in the column or in the tentacles. Internal brooding can continue to the planula (e.g., *Balanophyllia elegans* and *Cribrinopsis fernaldi*) or tentaculate stage (e.g., *Aulactinia incubans*, *Epiactis fernaldi*, and *E. ritteri*). Internal brooders release their young through the mouth or pores in the tentacle tips.

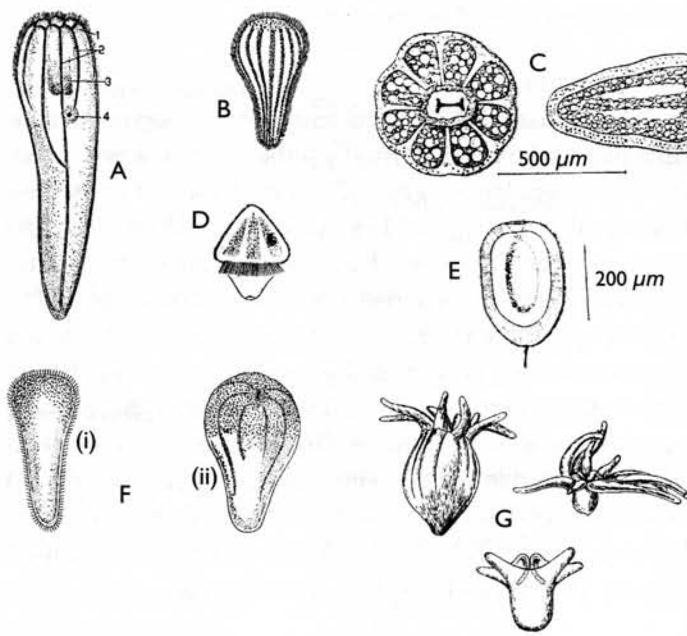

Fig. 2. Cnidarian larvae. (A) Planula of the sea pansy, *Renilla* sp. (order Pennatulacea). (B) Planula of the anemone *Lebrunia* (order Actiniaria). (C) Brooded planula of the anemone ***Urticina*** *filina* (*Tealia filina*, order Actiniaria). (D) Planula from the order Zoanthidea (note that only one species from this order, *Epizoanthus scotinus*, is found in Pacific Northwest waters). (E) Planktotrophic planula of the anemone ***Metridium senile*** (Order Actiniaria). (F) Early- (i) and late- (ii) stage planulae of the stone coral, *Siderastraea* sp. (order Scleractinia). (G) Actinula larvae from burrowing anemones in the order Ceriantharia (note that only one species from this order, *Pachycerianthus fimbriatus*, is found in Pacific Northwest waters). Genera and species with local representatives are bold. (A, B, D, F, G from Hyman, 1940; C, E from Thorson, 1946)

Identification of Local Taxa

A limited number of characteristics can be used to describe cnidarian larvae. There are two basic larval types, the planula and the actinula (Fig. 2). Further distinction among larval types is more challenging. Planulae can be characterized by size, color, ciliary pattern, and presence or absence of an apical tuft. They can be further differentiated into feeding and non-feeding forms, with the non-feeding or lecithitrophic forms typically being larger than their feeding counterparts. Little information is available on distinguishing characteristics of actinula larvae.

Lacking morphological information on cnidarian larvae, this chapter does not attempt to serve as a species identification key but instead compiles useful diagnostic information. The best way to identify a larval type is to either collect gametes from adults or raise larvae to metamorphosis and a recognizable adult stage. Strathmann (1987) describes methods for collecting gametes and rearing larvae.

Class Hydrozoa

In most hydrozoans (Table 1) the embryos develop into a non-feeding planula larvae that usually settles to the bottom within a few days. Planulae are generally club-shaped or ovoid and uniformly ciliated (Fig. 3). They possesses both nematoblasts and nematocytes. They never have an apical ciliary tuft nor do they develop septa, characteristics of some anthozoan planulae. Hydrozoan planulae are free swimming, but in some hydroids and hydrocorals (stylasterines) they may be demersal, drifting near the bottom or creeping along it until metamorphosis. Some types of planulae secret mucus threads that may alter their dispersal (Strathmann, 1987). Some species (e.g., *Hybodocon* and *Tubularia* species) have a post-settlement motile juvenile stage called an actinula. This stage creeps along the bottom until it eventually attaches and develops into a polyp.

Fig. 3. Longitudinal section of a representative hydrozoan planula, *Gonothyraea* (from Brusca and Brusca, 1990, Fig. 39)

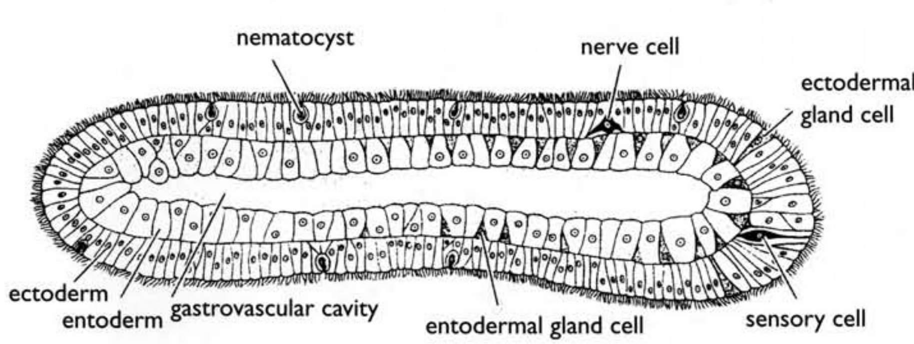

Table 1. Species in the class Hydrozoa from the Pacific Northwest (from Kozloff, 1996)

Order Hydroida
Suborder Athecata (Anthomedusae)
Family Corymorphidae
Corymorpha sp.

Family Euphysidae
Euphysa ruthae
Euphysa spp.

Family Tubulariidae
Hybocodon prolifer
Tubularia crocea
Tubularia harrimani
Tubularia indivisa
Tubularia marina
undescribed species

Family Corynidae
Coryne sp.
Sarsia japonica
Sarsia spp.

Family Boreohydridae
undescribed species

Family Cladonematidae
Cladonema californicum

Family Rhysiddae
Rhysia sp.

Family Clavidae
Cordylophora caspia
Hataia parva
Rhizogeton sp.

Family Hydractiniidae
Hydractinia aggregata
Hydractinia laevispina
Hydractinia milleri
Hydractinia sp.
undescribed species

Family Rathkeidae
Rathkea octopunctata

Family Bougainvilliidae
Bimeria spp.
Bougainvillia spp.
Garveia annulata
Garveia groenlandica

Family Pandeidae
Leucckartiara spp.
Neoturris spp.
Perigonimus spp.

Family Halimedusidae
Halmedusa typus

Family Calycopsidae
Bythotiara huntsmani

Family Trichydridae
Trichydra pudica

Family Eudendriidae
Eudendrium spp.

Family Protohydridae
Protohydra ?leuckarti

Suborder Thecata (Leptomedusae)
Family Tiarannidae
Stegopoma spp.

Family Laodiceidae
Staurophora spp.
Ptychogena spp.

Family Mitrocomidae
Foersteria spp.
Mitrocoma spp.
Mitrocomella spp.
Tiaropsidium spp.
Tiaropsis spp.

Family Haleciidae
Halecium spp.
Hydrodendron spp.

Family Campanulariidae
Campanularia spp.
Clytia spp.
Gonothyraea spp.
Obelia bidentata
Obelia dichotoma
Obelia geniculata
Orthopyxis spp.
Rhizocaulus verticillatus

Family Campanulinidae
Calycella spp.

Family Bonneviellidae
Bonneviella spp.

Family Lafoeidae
Cryptolaria spp.
Filellum spp.
Grammaria spp.
Hebella spp.
Lafoea spp.
Zygophylax spp.

Family Sertulariidae
Abietinaria spp.
Diphasia spp.
Dynamena spp.
Hydrallmania spp.
Sertularella spp.
Sertularia spp.
Symplectoscyphus spp.
Thuiaria spp.

Family Plumulariidae
Plumularia spp.

Family Aglaopheniidae
Algaophenia spp.
Cladocarpus spp.
Thecocarpus spp.

Family Eirenidae
Eutonina indicans

Family Aequoreidae
Aequorea victoria

Suborder Limnomedusae
Family Olindiasidae
Gonionemus vertens
Monobrachium parasiticum

Family Proboscidactylidae
Proboscidactyla flavicirrata

Order Stylasterina (Hydrocorals)
Family Stylasteridae
Allopora petrograpta
Allopora porphyra
Allopora venusta
Allopora verrilli
Errinopora pourtalesii

Suborder Physonectae
Family Agalmidae
Cordagalma cordiformis
Nanomia cara

Family Physophoridae
Physophora hydrostatica

Suborder Calycophorae
Family Diphyidae
Chelophyes appendiculata
Dimophyes arctica
Lensia baryi
Lensia conoidea
Muggiaea atlantica

Family Prayidae
Desmophyes annectens
Praya dubia
Praya reticulata

Family Sphaeronectidae
Sphaeronectes gracilis

Class Anthozoa

Most anthozoans (Table 2) produce planula larvae. The local exception is the species *Pachycerianthus fimbriatus* (family Cerianthidae), which produces an actinula larva (Fig. 2G). Planulae can be divided into three types: feeding, non-feeding with pelagic development, and non-feeding with demersal or benthic development.

Feeding planulae (Fig. 4A–D) develop from small (100–250 µm diam.) yolky eggs that are spawned into the water column (Strathmann, 1987). The planulae are ovoid and taper toward the anterior (aboral) end (Gemmill, 1920; Widersten, 1968, 1973; Chia and Koss, 1979). They swim actively, and at least the ones that have been studied are photopositive. A long apical tuft of cilia is swept side to side as the larvae swim. Later in development, mesentaries form and protrude into a spacious gastrocoel. In these more developed planulae, the mesentaries are quite obvious (Figs. 2B, 4B). Feeding methods of planulae are diverse. Some species filter particles out of the water directly (e.g., *Metridium* spp.; Fig. 2E), other species produce strands of mucus that are ingested and any adherent particles consumed (e.g., *Anthopleura xanthogrammica* and *Caryophyllia smithi*), and some species are endoparasites, feeding on particles in the gastrovascular cavities of hydromedusae (e.g., *Peachia quinquecapitata*).

Non-feeding planulae with pelagic development (Figs. 2C, 4E) develop from free-spawned, large yolky eggs (500–850 µm diam.) (Strathmann, 1987). These planulae commonly take the form of a ciliated ovoid that tapers toward the posterior (oral) end (Widersten, 1968; Stricker, 1985). The planulae lack apical tuft and apical organ. Larvae may be pelagic for a week or more. Later-stage planulae develop mesentaries.

Non-feeding planulae with demersal or benthic development (Fig. 4F–H) develop from large, yolky eggs (500–800 µm diam.) that are shed with a mucus coat. They are retained near the adult (Strathmann, 1987). These ciliated, lecithotrophic planulae lack both the apical tuft and apical organ (Nyholm, 1949; Widersten, 1968). Older larvae develop mesentaries. Larvae of this type (e.g., *Ptilosarcus gurneyi* and *Halcampa decemtentaculata*) are free swimming for approximately a week. They generally remain near the bottom or creep across the bottom.

Order Pennatulacea, *Ptilosarcus gurneyi*. Eggs are pink-orange in color, initially fusiform, and then rounding to 500–600 µm diameter. Eggs in the lab are at least initially bouyant (Chia and Crawford, 1973). Larvae are lecithotrophic and develop-

Table 2. Species in the class Anthozoa from the Pacific Northwest (from Kozloff, 1996)

Class Anthozoa
Subclass Alcyonaria (Ococorallia)
Order Alcyonacea
Suborder Stolonifera
Family Clavulariidae
Clavularia moresbii
Clavularia spp.
?Sarcodictyon sp.

Suborder Alcyoniina
Family Alcyoniddae
?Alcyonium spp.

Family Nephtheidae
Gersemia rubiformis

Suborder Holaxonia
Family Acanthogorgiidae
Calcigorgia spiculifera

Family Plexauridae
Swiftia kofoidi
Swiftia simplex
Swiftia spauldingi
Swiftia torreyi

Family Chrysogorgiidae
Radiceps sp.

Family Isididae
Acanella sp.

Family Primnoidae
Callogorgia kinoshitae
Parastennella sp.
Primnoa willeyi

Suborder Scleraxonia
Family Anthothelidae
Anthothela pacifica

Family Paragrogiidae
Paragorgia pacifica

Order Pennatulacea
Suborder Sessiliflorae
Family Kophobelemnidae
Kophobelemnon affine
Kophobelemnon biflorum
Kophobelemnon hispidum

Family Anthoptilidae
Anthoptilum grandiflorum

Family Funiculinidae
Funiculina parkeri

Family Protoptilidae
Helicoptilum rigidum

Family Scleroptilidae
Scleroptilum sp.

Family Umbellulidae
Umbellula lindahli

Suborder Subselliflorae
Family Virgulariidae
Balticina californica
Balticina septentrionalis
Stylatula elongata
Virgularia spp.

Family Pennatulidae
Pennatula phosphorea
Ptilosarcus gurneyi

Subclass Ceriantipatharia
Order Ceriantharia
Suborder Spirularina
Family Cerianthidae
Pachycerianthus fimbriatus

Order Antipatharia
Suborder Antipathina
Family Antipathidae
Antipathes sp.

Subclass Zoantharia
Order Scleractinia (Madreporaria)
Suborder Caryophylliina
Family Caryophylliidae
Caryophyllia alaskensis
Cyathoceras quaylei
Desmophyllum cristagalli
Paracyathus stearnsi
Lophelia californica
Solenosmilia variabilis

Suborder Dendrophylliina
Family Dendrophylliidae
Balanophyllia elegans

Order Actiniaria
Suborder Nynantheae
Family Edwardsiidae
Edwardsia sipunculoides
Nematostella vectensis

Family Halcampoididae
Halcampoides purpurea

Family Haloclavidae
Bicidium aequoreae
Peachia quinquecapitata

Family Halcampidae
Halcampa crypta
Halcampa decemtentaculata

Family Actiniidae
Anthopleura artemisia
Anthopleura elegantissima
Anthopleura xanthogrammica
Aulactinia incubans
Cribrinopsis fernaldi
Cribrinopsis williamsi
Urticina columbiana
Urticina coriacea
Urticia crassicornis
Urticia lofotensis
Urticia piscivora
Urticia sp.

Family Liponematidae
Liponema brevicornis

Family Actinostolidae
Paractinostola faeculenta
Stomphia coccinea
Stomphia didemon
Stomphia sp.

Family Hormathiidae
Stephanauge annularis

Family Metridiidae
Metridium senile
Metridium sp.

Family Haliplanellidae
Haliplanella lineata

Order Corallimorpharia
Family Corallimorphidae
Corallimorphus sp.
Corynactis californica

Order Zoanthidea
Family Epizoanthidae
Epizoanthus scotinus

ment is demersal. Developing larvae appear similar to those of *Renilla* (see Fig. 2A). At 18 days, planula are pear-shaped and uniformly ciliated. They swim with the narrow anterior end forward (Chia and Crawford, 1977). Therer is no apical organ. The posterior end consists of eight tentacular buds surrounding the pharynx. The cilia around the pharynx are longer then those on the remainder of the body. Planula settle on sand covered with organic film.

Order Ceriantharia, *Pachycerianthus fimbriatus.* The burrowing anemone, *P. fimbriatus,* is the only local repres-entative of this order. The development of Ceriantharia species from other regions has been described by Nyholm (1943). The larvae are planktontrophic and carnivorous. They are the only local taxa that produce a pelagic actinula larva.

Order Zoanthinaria, *Epizoanthus scotinus.* This is the only local representative of this order. Their larvae have not been described. The planula of a zoanthinarian in Fig. 2D is, compared to other Cnidaria larvae, unique in appearance. If the local zoanthinarian has a similar-shaped planula, then one should be able to differentiate it from other local planulae.

Order Scleractinia, *Balanophyllia elegans.* This cup-coral broods it large red-orange embryos internally until the planula stage. The non-feeding planula are demersal, large (3–5 mm long by 1–2 mm wide), completely covered with short (ca. 20 µm) flagella, and colored crimson red (Fadlallah and Pearse, 1982). If suspended in the water column the planulae return quickly to the bottom, where they adhere and resume crawling.

Order Scleractinia, *Caryophyllia alaskensis.* The development of this species has not been described, but that of a closely related species *(C. smithi)* has (Tranter et al., 1982). Eggs are fertilized externally. Ova are either brown or cream in color, spherical or slightly oval in shape, and 130–150 µm diameter. Planktotrophic planulae develop 48 hours after fertilization, at which time feeding commences. An apical tuft (30–60 µm long) is present during the first six weeks of development. After eight to ten weeks, lab-reared planulae are 800–1,000 µm in length.

Order Actiniaria, *Anthopleura elegantissima.* Eggs are freely spawned, brown, spherical, and ranging in size from 120 to 250 µm. The yolk in the eggs is evenly dispersed and contains no symbiotic algae. Three-week-old planulae are oval to cylindrical and uniformly ciliated (Chia and Koss, 1979). They are 170–190 µm long with an apical tuft 70 µm long. They swim

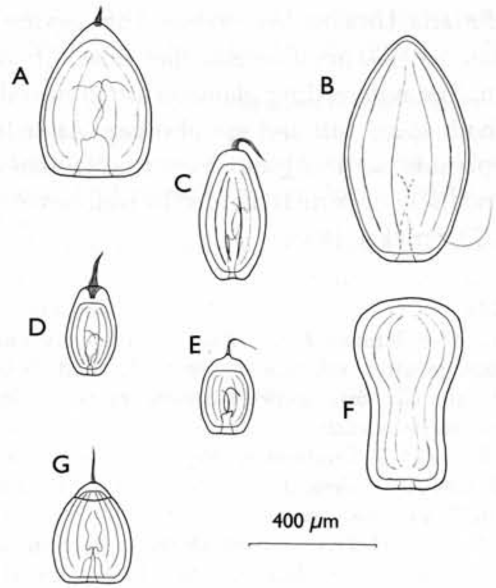

Fig. 4. Anthozoan planulae. (A–D) Planktotrophic planulae with pelagic development. (E) Lecithotrophic planula with pelagic development. (F–H) Lecithotrophic planulae with demersal development. Faint lines with the planulae represent the internal mesentaries. (modified from Widersten, 1973)

actively with the apical tuft forward. The cilia of the apical tuft sweep the water as a unit. The planulae are feeding.

Order Actiniaria, *Anthopleura xanthogrammica*. Eggs are 175–225 µm diameter, spherical, and purple in color. The planulae are feeding and similar in appearance to those of *A. elegantissima*. The planulae are initially ca 150 µm long and 100 µm diameter. After several days of development the planulae are about 250 µm long and 150 µm in diameter. Within a week after fertilization the planulae posses numerous nematocysts. Primary septa and contractile elements begin to appear in the first and second week after fertilization (Siebert, 1974).

Order Actiniaria, *Halcampa decemtentaculata*. The eggs are yellowish gray-green, 310–330 µm diameter, and surrounded by a clear mucilaginous jelly coat. A planula emerges from the jelly coat after the third day. Planulae are 440 by 330 µm and are not active swimmers. They settle within 28 days.

Order Actiniaria, *Metridium* **sp.** The eggs are pink and 120–195 µm diameter. Early planulae are 180–190 µm long, excluding the apical tuft. A blastoporal indentation is present on the postereor end. The planulae are strong swimmers, positively phototactic, and planktotrophic. By five to seven days the planulae have grown to 225 µm long, with a 200 µm long apical tuft (Fig. 2E). By the eighth or ninth day the planulae are 320 µm long and 165 µm in diameter at the posterior end. The enteron is brownish and pointed at the anterior end. The enteron can be protruded as a button or collar with thin cilia.

Order Actiniaria, *Urticina ?crassicornis*. The eggs are yellow to greenish tan, 500–700 µm diameter; they float with the animal pole down. The non-feeding planulae are uniformly ciliated and lack both apical tuft and apical organ. After 18 days or fewer the planulae settle. At settlement the planulae are ca 600 µm long and the endoderm is divided by well-developed septa (see Fig. 2C3; Stricker, 1985).

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