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PHYLUM CNIDARIA, CLASS HYDROZOA

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INTRODUCTION

Hydrozoans are well represented in the regional fauna. Hydromedusae (order Hydroida) are abundant in the local spring and summer plankton; however, the alternate benthic solitary or colonial hydroid stages of their diphasic life cycles are less conspicuous and are not as well known. Some hydroid species do not release free-swimming medusae. The common local hydrozoans also include a few calcareous hydrocorals (order Stylasterina), one trachymedusa and a few narcomedusae (order Trachylina), and a few species of the planktonic colonies of mixed polypoids and medusoids known as siphonophores (order Siphonophora).

Marine hydrozoans include free-spawning and brooding species with eggs of a broad range of sizes. In most species, the embryo develops into a non-feeding larval stage, the planula, that soon settles and gives rise to one or more polyps. In some species, the embryo develops to a tentacular motile stage called an actinula that settles and gives rise to one or more polyps. In some hydroids and in stylasterines, the planulae are demersal creeping stages that soon settle. In the trachylines, a tentacular motile larval stage gives rise directly to a medusa and there is no sessile phase in the life cycle. In the siphonophores, the planula gives rise to both polypoid and medusoid individuals that form a highly integrated pelagic colony.

General introductions to Hydrozoa and their development are given by Hyman (1940), Mergner (1971), Campbell (1974a,b), and Tardent (1978). Studies of diphasic life cycles, regeneration and asexual reproduction are also included in reviews or symposia proceedings edited by W.J. Rees (1966), Tokioka & Nishimura (1973), Mackie (1976) and Tardent & Tardent (1980). Asexual reproduction is not discussed in this chapter but is included in reviews cited above.

REPRODUCTION AND DEVELOPMENT

Marine hydrozoans exhibit such diversity in sexual reproduction and development that it is difficult to summarize any basic pattern. A generalized pattern for marine species of the order Hydroida is described below, and variations found in local species are described in the section on Selected Local Species. Development in a few local species of the orders Stylasterina, Trachylina and

Siphonophora are discussed in the section on Selected Local Species. Trachyline development bears some similarities to that of ctenophores (Freeman 1983).

In the order Hydroida, the polyp phase, or **hydroid**, may be solitary or colonial. In most species, sexes are separate and colonies are either male or female. Gonads develop in structures called **gonophores**. In colonies, the gonophores are produced by certain individuals called gonozoids or, if highly modified in structure, blastostyles. In some species, gametes develop directly on the blastostyle, called in this case a spadix; spadix and covering theca are called a sporosac. In some species, a blastostyle and its gonophores are enclosed in a theca; the whole structure is then called a gonangium. Gonangia may occur in groups enclosed in leaf-like structures; the whole complex is called a corbula.

In species of Hydroida with diphasic life cycles, gonophores develop into bell-like, gelatinous individuals that are released as free-swimming **hydromedusae**. As these feed and grow in the plankton, they develop gonads on the underside of the bell below the radial canals or around the manubrium. In some species, hydromedusae asexually bud more hydromedusae before becoming sexually reproductive. Sperm are shed freely into the sea. Eggs are typically transparent, relatively small, and freely spawned. In a few species, female medusae produce large yolky eggs that are retained for fertilization and development to larval stages.

In some marine hydroids, gonophores develop into reduced medusae that are free for only very brief spawning periods or are retained on the polyp in various reduced forms called sessile medusoids, gonomedusae, or meconidia. Sessile male gonophores release sperm freely, but sessile female gonophores often retain eggs for fertilization and development to various stages. Such eggs are typically large and opaque with yolk.

Oogenesis has been described in a few marine hydrozoans (see Hargitt 1917; Honegger 1980; Beams & Kessel 1983; Tardent 1985). Meiosis is completed during ovulation or spawning and before fertilization; polar bodies may be lost after spawning as the jelly coat on the eggs hydrates (Ballard 1942). The eggs of most hydrozoans lack extracellular envelopes.

Spermatogenesis and the flagellate sperm of some marine hydrozoans have been described (e.g. Szollosi 1964; Roosen-Runge & Szollosi 1965; Hanisch 1970; Summers 1970, 1972; Lunger 1971; Afzelius 1971; Miller 1983).

Release of medusae, ovulation, completion of meiosis in oocytes, and synchronous spawning are all triggered by changes in light (Perkins 1902; Uchida 1927; Rugh 1929; Ballard 1942; Roosen-Runge 1962; Miller 1979; Honegger *et al.* 1980; Mills 1983). A conditioning period of varying length is required, possibly to allow production and release of a low molecular weight substance (Ikegami *et al.* 1978; Yoshida *et al.* 1980).

Sperm show species-specific chemotaxis to female reproductive structures and eggs (Miller 1978, 1979, 1980, 1983; O'Rand 1972, 1974; O'Rand & Miller 1974). In a species with internal fertilization, an interaction between female gonangial epithelium and entering sperm confers the capacity for

fertilization upon the sperm (O'Rand 1972, 1974; O'Rand & Miller 1974). It has been shown for some species that sperm fuse to the egg at the site of polar body formation (Freeman & Miller 1982); that first cleavage is initiated at this same site (Miller 1980; Freeman & Miller 1982); and that this site corresponds to the future posterior (oral) end of the larva (Freeman 1981a).

In small eggs with little yolk, cleavage is holoblastic and unilateral, the furrow forming from one side and dividing each cell in a "heart-shaped" cleavage (see Dan & Dan 1947; Rappaport & Conrad 1963; Schroeder 1968). The first two cleavages are equal or nearly equal. Later cleavage may be loosely organized and irregular in appearance. In large yolky eggs, cleavage may be holoblastic, but it is also common that nuclear divisions occur and daughter nuclei become distributed in the cortical cytoplasm before cytoplasmic divisions begin. Early cleavage is usually irregular in appearance (see Cowden 1965; Martin & Archer 1986). The resultant blastula may be hollow or solid. Early development through gastrulation is usually regulative.

Gastrulation occurs by ingression of cells, by primary delamination (a single layer of blastomeres cleaving into inner and outer layers of cells), by secondary delamination (a mass of blastomeres gradually differentiating into an outer cell layer and an inner cell mass), or by a combination of such processes, but not by distinct invagination (Hyman 1940). The gastrula then elongates and forms an ovoid or club-shaped larval stage, the **planula**. The planula has ciliated ectodermal cells, acellular mesoglea, interstitial cells, epithelio-muscle cells, nematoblasts, nematocytes, sensory cells and gland cells (Bodo & Bouillon 1968; Martin & Thomas 1977, 1981; Martin *et al.* 1983; Weiss *et al.* 1985; Martin & Archer 1986).

Hydrozoan planulae are non-feeding and usually settle within a few days. Some planulae secrete mucus threads that are throught to either enhance dispersal (Hughes 1977) or restrict it (Wasserthal & Wasserthal 1973). Planulae may settle in response to specific cues from substratum, current flow, or biological associations (see Kakinuma 1960; Nishihira 1965, 1968a,b; Campbell 1968a; Müller 1973a,b; Donaldson 1974). The settling planula attaches by its anterior end, and usually first transforms into a mass of cells from which a polyp develops (see Müller *et al.* 1976; Martin *et al.* 1983). Some species have a motile juvenile stage with tentacles, called an actinula, that can creep along the bottom until it eventually attaches and becomes a polyp (e.g. *Hybodocon* and *Tubularia* spp.).

In colonial hydroids, asexual proliferation from the primary polyp produces a colony. Colony growth and form vary with external factors such as temperature, current flow, and food supply. Studies of colony formation (e.g. Crowell 1957; Fulton 1963; Campbell 1968b; Davis 1971; Braverman 1974; Hughes 1980, 1987; McFadden *et al.* 1984) unfortunately include few local species.

METHODS

Identification. Keys to local hydromedusae and siphonophores are given by Mills (1987b,c) and Arai and Brinckmann-Voss (1980). Genera and some species of hydroids may be identified from keys provided by Mills & Miller (1987) or Rees & Hand (1975). Unfortunately, field specimens of hydroids may exhibit great variability in size, color, number of tentacles or annulations, and colony form. Descriptions and synonomies of medusae from various world regions are given by Kramp (1961). Hydroids and hydromedusae of some local species are included in monographs and compendia (Allman 1871-72; Nutting 1900, 1904, 1915; Fraser 1937; Naumov 1960).

Collection and maintenance. Hydromedusae are abundant locally April-October. Seasonal abundances of species near Friday Harbor are given by Mills (1981) and spring and summer abundances of species in the Strait of Georgia are given by Arai & Mason (1982). In calm water, some medusae can be identified on sight by distinctive patterns of gonads, radial canals and tentacles, or swimming movements. At night, a light immersed near the surface shows medusae clearly. Collect mature specimens in long-handled dippers. Keep them completely immersed and subject them to as little water agitation as possible during transfer to containers and aquaria. Ripe testes have a more homogeneous appearance than ovaries and are usually pale or white. Oocytes in ovaries are usually visible under low power magnification.

Medusae may be kept in large aquaria with gently stirred or aerated sea water. They are easily swept toward the outflow and will block the opening, so the outflow pipe should be placed in a large screened compartment or under a false bottom. Small medusae may be kept in clean beakers of sea water renewed daily. If they appear to be damaged by continual contact with the bottom, they may be placed in capped jars one-quarter filled with sea water and set afloat in a large tank (see Rees & Russell 1937). Medusae as a group take prey of considerable variety, including fish larvae, ctenophores, small planktonic crustaceans, eggs of various invertebrates, and other medusae, but each species will have preferences. Species that eat other medusae (see Arai & Jacobs 1980 for a partial listing) may be a problem in collection buckets and in cultures. Intraspecific cannibalism may also occur under crowded conditions. Medusae can sometimes be held in spawning condition for several days if kept in constant light or darkness (Miller 1979).

Hydroid colonies often look like fuzzy coatings on rocks, shells, or algae. If polyps are examined with a hand lens or dissecting microscope, maturing reproductive structures may indicate the sex of the colony. Colonies of different sexes may be closely associated. Remove organisms, such as nudibranchs, that might damage the polyps. Most marine hydroids require clean aerated sea water and rather brisk water flow. Specimens may be fastened with thread or pins to pieces of styrofoam and suspended in flowing or stirred sea water or kept in a planktonkreisel (see p. 17). Some species tolerate recirculated or artificial sea water (Braverman 1969; Worthman 1974).

Polyps may be fed natural zooplankton or *Artemia* nauplii. Polyps fed *Artemia* sp. nauplii may become slightly pink. Polyps can also be fed individually with crushed prey or tiny pieces of fish or bivalve tissue. Baked, dried, and finely ground mussel has also been used successfully as food for polyps; refrigerate the powder for storage (G. Jarms pers. comm.). In flow-through aquaria, water flow should be stopped for a brief feeding period when food is added then restored to full flow to remove the uneaten food. In recirculating systems, hydroids should be transferred into a fresh suspension of food in sea water for an hour once or twice a day, then gently rinsed off and returned to the aquarium. A camel hair brush can be used to gently sweep polyps clean of debris and uneaten food. The common tide-pool copepod, *Tigriopus* sp., has been added to cultures to keep hydroids clean (West & Renshaw 1970). Keeping cultures in the dark keeps zooplankton prey more evenly distributed and reduces algal growth. Well-fed colonies undergo regular cycles of growth and regression in the laboratory (Crowell 1953; Brock 1974; Hughes 1987), but field observations indicate that this may be an effect of space limitation (Hughes 1987).

Some hydroid colonies may be propagated in culture. Slip a cut stem from a colony under a thread tied around a glass slide and place the slide in a bowl of standing sea water or in a rack set so that sea water flows over the polyps. Provide food twice daily. New stolons should appear in a few days, followed in time by appearance of hydranths and eventually gonangia (Crowell 1957; Werner 1968a). Use of microfiltered sea water or antibiotics may increase survival. Racks can be suspended in the sea from floats or docks if cultures do not do well in the laboratory.

Collecting newly released medusae. Place mature hydroids in jars of clean sea water or in mesh-sided boxes immersed in flowing sea water. Medusae may be released, sometimes in response to changes in light, for several days. Newly released medusae can be kept in beakers of filtered sea water (Rees 1978). Most are too small to eat *Artemia* nauplii, but can be fed small zooplankton, macerated *Artemia* nauplii or a thin suspension of cooked chicken egg yolk in sea water (West & Renshaw 1970). Successive generations of hydroids and small medusae have been reared in planktonkreisels (Roosen-Runge 1970).

Collecting gametes. To obtain unfertilized eggs from hydroids with sessile gonophores and internal fertilization, females should be isolated for at least a week. Mature gonangia may be removed and placed in microfiltered sea water to observe maturation of oocytes, spawning, or release of medusae, sometimes occurring in response to light changes (Ballard 1942; Miller 1979).

Most species of hydromedusae spawn either at dawn or dusk in the field. Miller (1979) and Mills (1983) give laboratory spawning times of many of the local species. Hydromedusae collected after mid-day may spawn a short time after transfer to a darkened aquarium. Animals collected at night may spawn shortly after transfer into a lighted laboratory. Medusae collected in the

evening and kept in the dark overnight will usually spawn 30-60 minutes after exposure to light in the morning. Place them in microfiltered sea water to spawn, carefully separating males and females if unfertilized eggs are to be collected. Recently fertilized eggs may be obtained by simply allowing males and females to spawn together. After 30-60 minutes, the medusae may be removed from the spawning tank and the eggs collected by pipette. The eggs of most free-spawning medusae sink in still water. Medusae of several local species spawn repeatedly for 3-5 days after collection.

Sperm for controlled *in vitro* inseminations can be obtained from hydromedusae by macerating excised testis in cold filtered sea water (Roosen-Runge 1962). Sperm can be obtained from hydroids by gently compressing excised male gonangia in a small dish of microfiltered sea water or on an albumin-covered slide. A mass of inactive sperm and some active sperm may emerge. Sperm suspensions can be stored briefly.

Sperm may become active within 20-30 minutes after dilution in sea water, especially when near females or eggs (Miller 1979). In species with internal fertilization, sperm may not be active until some interaction with female structures confers the final capacity for insemination (see O'Rand 1972, 1974; O'Rand & Miller 1974). *Sarsia tubulosa* sperm are motile for several hours after dilution at ambient sea water temperatures, but chemotactic response to egg extract declines after 2 hours (Miller & Staub 1982). *Phialidium* sp. sperm lose ability to fertilize 2-2.5 hours after dilution in sea water (Roosen-Runge 1962).

Insemination. For free-spawning species, add a fresh sperm suspension to unfertilized eggs in filtered sea water. After a few minutes, fertilized eggs may be collected by pipette and transferred to culture dishes. Excised eggs of some hydroids, such as *Gonothyrea* sp., can be inseminated *in vitro*. In *Campanulina flexuosa*, epithelial-covered egg clusters squeezed from gonophores can be inseminated *in vitro* (O'Rand 1972) either from sperm present in the gonophore or from sperm obtained by macerating testicular tissue. The epithelial covering of the egg cluster appears to play a role in activating the sperm (O'Rand 1974; O'Rand & Miller 1974).

Cultures. Early developmental stages can be kept in spot plates or standing bowls of microfiltered sea water with or without antibiotics. At 8-12°C, planulae of many species form within one or two days. Siphonophore embryos kept in sea water made viscous with polyethylene oxide (10 mg per ml) develop normally despite the restriction of movement (Freeman 1983).

Some planulae settle preferentially on microbial filmed surfaces prepared by incubating glass, fiberglass, or slate plates in sea water. Some epiphytic species settle on specific algae or in the presence of aequeous algal extracts (Kakinuma 1960; Nishihira 1967a,b, 1968a,b). Synchronous settlement and metamorphosis has been induced in *Hydractinia* species (see Müller 1973a,b; Müller *et al.* 1977; Berking 1984) and *Phialidium gregarium* (see Freeman 1981b), by exposure to a 9:1 mixture of filtered sea water and CsCl solution

(9.76 g CsCl in 100 ml distilled water). After 3 hours the treated planulae should be washed several times with sea water to remove CsCl that would otherwise interfere with development (Müller *et al.* 1977, modified by Freeman 1981b). If possible, leave cultures undisturbed during settlement and metamorphosis.

Newly settled polyps are delicate and should be kept free of debris. If they are on the bottoms of culture dishes, the water should be changed daily, or the dishes should be placed on edge in gently flowing sea water so that the current moves over the polyps. Glass slides on which polyps have settled can be placed on edge in holders so that the current moves over the face of each slide. *Artemia* sp. nauplii are too large and active to be used as food for most newly settled polyps. Small copepod nauplii or pieces of *Artemia* sp. nauplii may be used as food for new polyps (Rees & Russell 1937; Werner 1968a).

SPECIAL TECHNIQUES

Isolation or fusion of embryo parts. Embryos can be cut apart using glass knives in agar coated dishes (see p. 31); fragments skewered on a glass needle and left in contact for 1-2 hours may fuse (Freeman 1981a).

Vital staining. Immersion in 0.01% Nile blue sulfate or 0.1% neutral red (sea water dilutions of 1% stock solutions in distilled water) is not toxic to *Phialidium gregarium* embryos. Surfaces of embryos can be micromarked by the Novikoff technique (Freeman 1981a) (see pp. 31-32).

Dissociation and reaggregation of blastomeres. Freeman (1981b) dissociated 10 hour old embryos of *Phialidium gregarium* by placing them in calcium and magnesium free medium (27 g sodium chloride, 1 g sodium sulfate, 0.8 g potassium chloride, and 0.18 g sodium bicarbonate in 1 liter of distilled water) containing 1 mM EDTA, for 15 minutes, then transferring them to normal sea water and repeatedly passing them through a pipette with a bore diameter 3-4 times larger than the blastomeres. About half the embryos dissociated into single cells. The cells reaggregated when centrifuged in small plastic tubes for two hours at about 500 x g, at 11-12°C.

Centrifugation of eggs. Centrifugation redistributes the pronucleus and other cytoplasmic contents. To vary the direction of centrifugal movement, the eggs must be marked and immobilized in gelatin during centrifugation (see Freeman & Miller 1982; Freeman 1983).

SELECTED LOCAL SPECIES

Most of the synonomies of hydromedusae given in this section are from Arai and Brinckmann-Voss (1980); seasonal abundances in Friday Harbor are from Mills (1981 and unpubl.). Information on hydroids is mostly from Haderlie *et al.* (1980), and Naumov (1960). The local species below have been selected

because they have been reared through a complete life cycle or because they have a conspicuous or unusual medusa or polyp.

Order Hydroida, Suborder Anthomedusae/Athecata

Bougainvillia principis (Steenstrup) (= *B. multitentaculata*). Bougainvilliidae. Hydroid unknown locally, but see Edwards (1966). Medusae occur April-June in Friday Harbor. Mature medusae may be collected in May and kept in captivity until July. Four interradial gonads surround the mouth. Eggs are about 160 µm in diameter (estimated from figures by Szollosi 1969). Each egg has a 30-50 µm thick jelly coat containing cnidocytes; the cnidocytes become evenly distributed among the ectodermal cells of the gastrula and planula, but development remains normal if the cnidocytes are triggered with acetic acid or trypsin, or removed from the egg (Szollosi 1969). The planulae of this species settle gregariously (Mills unpubl.). Development of hydroids and medusae of related species has been described (Russell 1953; Berrill 1964; Uchida & Nagao 1960b; Nagao 1964; Edwards 1966).

Eudendrium californicum Torrey. Eudendriidae. Large bushy hydroid colonies are found on rocky open coasts from British Columbia to Monterey Bay. Colonies are male or female. Sessile medusoids develop near the bases of the gastrozoids. Large orange eggs are retained for fertilization and development to planulae. Development of the blastostyles and spermatogenesis of *E. racemosum* has been described by Hanisch (1970), and sperm morphology of this species has also been described by Summers (1972). Syncytial early cleavage and development of *E. racemosum* have been described by Mergner (1971). Several species in this genus release yolky planulae that secrete mucous threads tethering them to the mother colony (Wasserthal & Wasserthal 1973). Similar threads are produced by planulae of *Nemertesia antennina* (Plumulariidae) (Hughes 1977).

Euphysa ruthae Norenburg & Morse. Euphysidae. Small solitary polyps live in coarse sublittoral and littoral sand in high current areas. They are collected by sieving slurries of sand through 63 µm mesh. Up to six buds form in two alternate whorls above the aboral tentacles on the polyp where gonophores would be expected. These buds had a gonophore-like appearance on newly collected polyps but after some time in the laboratory they developed into actinuloid structures with reversed polarity (Norenburg & Morse 1983).

Euphysa japonica (Maas) and *Euphysa tentaculata* Linko. Hydroids are solitary under laboratory conditions (V. Schmid pers. comm.). Mature medusae bearing gonads on the manubrium occur April-October, especially May-June. Medusae spawn within 30 minutes in light after 8-10 hours of darkness; evening spawnings also occur (Miller 1979). Eggs of *E. japonica* are 250 µm in diameter, yolky and opaque; sperm are larger than in species of *Sarsia* (R. Miller pers. comm.).

Garveia annulata Nutting. Bougainvilliidae. Robust bright orange hydroid colonies occur on sponge and coralline algae. Colonies are either male or female. Globose sessile medusoids develop on the thick main stalks.

Hybocodon prolifer L. Agassiz. Tubulariidae. Large pink hydroids with unbranched stems are solitary or occur in small groups (Uchida & Nagao 1960a). Medusae are budded between the whorls of the hydranth tentacles. Hydroids with medusa buds have been dredged from San Juan Channel in early May, and medusae are seen in Friday Harbor for a short period during March-May (Mills 1981 and unpubl.). Medusae may bud additional medusae from each tentacle bulb before becoming sexually reproductive. Gonads develop around the stomach. During oogenesis, small oocytes or nurse cells are absorbed or engulfed by pseudopodial processes of the oocytes, and only one or two large eggs are produced by each female (Hargitt 1917). Mature males spawn after an hour in light following 8-10 hours of darkness (Miller 1979). Eggs are fertilized in place on the medusa and embryos are retained until they develop to actinulae.

Hydractinia spp. Hydractiniidae. Several colonial species are found locally on shells and rocks, on shells occupied by hermit crabs, on spider crab legs, and on tubes of sabellid polychaetes. Polymorphic polyps are closely spaced on a basal mat of stolons. Gonophores are sessile. The number of eggs produced per female gonophore varies with species. One local species found on hermit crab shells has four eggs (180 μm in diameter) per gonophore and spawns upon changes in light; another local species with one egg per gonophore appears to fertilize internally and brood; males of both these species shed sperm in response to light following darkness (R. Miller pers. comm.). Studies of Atlantic *Hydractinia echinata* have shown that colonies, isolated gonozoids, or excised gonophores will spawn, and that isolated oocytes will mature, upon exposure to light following a period of darkness, but not in constant light or darkness (Ballard 1942); that sperm become active in the presence of eggs (Miller 1973); and that planulae settle on shells of hermit crabs or on microbial filmed surfaces and transfer to shells of moving hermit crabs (Müller *et al.* 1976). Cell lineage and electrical coupling of blastomeres have been demonstrated by microinjection of Lucifer Yellow CH, a brightly fluorescent non-toxic dye, into zygotes or blastomeres (Pfannenstiel 1986).

Polyorchis penicillatus (Eschscholtz). Polyorchidae. Regional variations are discussed by Rees & Larson (1980). A polyp and newly released medusa attributed to this species by Brinckmann-Voss (1977) are those of a species of *Sarsia* (Mills unpubl.). Medusae are abundant summer and fall in some Washington and B.C. coastal harbors and shallow bays, retreating to deeper water to overwinter (S. Arkett pers comm.); they can be found year-round in shallow harbors in central California. These medusae often occur in association with *Zostera* sp., but rarely co-occur with *Gonionemus vertens* (Mills 1981). In captivity, medusae require flowing or frequently changed

water. They eat copepods, amphipods, polychaetes and their larvae, nauplii, veligers, cyprids, zoeae, rotifers, ostracods, and cumaceans (Arkett 1984). Up to 45 gonads are pendant from each radial canal. Medusae spawn within an hour after dark following 10-12 hours in light, and sometimes when the water in the culture is changed (Miller 1979; Mills 1983). Transparent eggs are 100 µm in diameter (R. Miller pers. comm.). Planulae do not readily settle on glass or mud in culture, and the polyp remains unknown in spite of extensive attempts to culture it (Mills unpubl.). This is also true of *P. karafutoensis* in Japan (Nagao 1963, 1970).

Sarsia spp. Corynidae. Pinkish athecate hydroid colonies occur on rocks, shell, barnacles, sponge, tires, and algae. Colors vary, probably with diet (Edwards 1978; Brinckmann-Voss 1985). Club-shaped hydranths bear whorls of capitate (knobbed) tentacles and may also bear inconspicuous filiform tentacles. Gonophores form below the capitate tentacles. Kakinuma (1966a) and Edwards (1978) describe budding of *S. tubulosa* medusae from hydroids in culture at 5-10°C maintained on a diet of *Artemia* sp. nauplii. Medusae may be released or retained (see Edwards 1978, 1983). Newly released medusae are about 1 mm in bell height and diameter. Gonad develops around the long manubrium. In local *Sarsia* spp., medusae reach maturity after a month or more in culture at 10°C. Female medusae spawn 1-3 hours after exposure to light following overnight darkness; males spawn about 15 minues before the females (Miller 1982).

In Friday Harbor, *Sarsia* spp. medusae can be collected from February to September, but sexually mature specimens are not usually found until late April (Mills 1981 and unpubl.). Hydroids are common on the Friday Harbor Laboratories float tires and associated fauna in some years.

There are at least 7 species of *Sarsia* in the Friday Harbor area (Arai & Brinckmann-Voss, 1980; Miller 1982; Brinckmann-Voss 1985; Mills 1987b; see also Edwards 1978, 1983). These are *S. tubulosa, S. princeps, S. apicula, S. viridis, S. japonica,* the orange *Sarsia* sp. of Arai & Brinckmann-Voss (1980), and *Sarsia* species "L" of Miller (1982). Miller (1982) distinguished the following three species within the "*S. tubulosa* complex" at Friday Harbor, based on spawning times, egg size, specificity of sperm chemotaxis and rates of hybridization (hybridization experiments with these 3 species showed 90% normal cleavages in homotypic crosses and usually only about 10% normal cleavages in heterotypic crosses, although some heterotypic crosses yielded up to 90% normal cleavages.):

S. tubulosa. Average egg diameter is 92 µm. Females spawn 2-3 hours after exposure to light following overnight darkness.

S. princeps. Average egg diameter is 107 µm.

Sarsia species "L". Average egg diameter is 129 µm. Spawning occurs 1-2 hours after exposure to light.

Stomotoca atra A. Agassiz. Pandeidae. The atentaculate hydroids (= *Hydrichthys*) of the related species *S. pterophylla* have been identified from leptocephalid fish larvae (Larson 1982). No similar hydroids have yet been found in the Friday Harbor region; it is unlikely that the *Perigonimus* sp. hydroids mentioned by Strong (1925) are *S. atra*. In British Columbia coastal waters and Puget Sound the medusae occur April-September and are common May-July (Arai & Brinckmann-Voss 1980). In Friday Harbor, medusae are abundant May-November; a late summer increase may indicate production of a second generation of medusae (Mills 1981). Medusae spawn within 30 minutes of exposure to light following 8-10 hours of darkness (Miller 1979). Eggs are about 100 μm diameter and somewhat opaque. At 12-14°C, early cleavages occur hourly. Planulae settle in culture dishes with a heavy organic film and may develop stolons, but polyps have not been successfully cultured (V. Schmidt pers. comm.).

Tubularia spp. Tubulariidae. Large colonial or solitary polyps produce tentaculate young that develop directly into polyps. Medusae are not formed. Hydranths autotomize in unfavorable conditions and should be kept in fast flowing, clean sea water below 15°C. The polyps have been used extensively in studies of regeneration (see reviews by Webster 1971 and Tardent 1978).

Hermaphrodites can occur (Berrill 1961), but each colony is usually of a single sex. Groups of stalked gonophores are borne between the whorls of the hydranth tentacles. Male gonophores are rounded bodies without tentacles; Benoit (1925) describes their internal structure. Afzelius (1971) describes fine structure of spermatozoa. Males release sperm 5-20 minutes after they are placed in light. Female gonophores are rounded bodies with two or four small tentacles; Van de Vyver (1968) describes their internal structure. It is reported that during oogenesis the growing oocyte absorbs cytoplasm from adjacent nutritive "oocytes" (Fennhoff 1978). Fertilization is internal. Sperm are attracted to the female gonophore and enter by the vestigial bell opening; sperm chemotaxis is apparently non-specific within the genus (Miller 1973). The large embryos are brooded in the gonophores to tentaculate actinulae; embryos brooded by a given female may be at different stages of development (Miller 1976).

Embryogenesis has been described in *T. radiata* by Nagao (1960, 1965) and in *T. crocea* by Fennhoff (1978, 1980). Nuclear divisions in the large zygote (ca. 0.5 mm diameter) produce nuclei that migrate to peripheral positions before cleavage furrows form. At 11-13°C, furrows appear about 3 hours after fertilization, and somewhat irregular cleavage divisions follow about hourly. An inner endodermal mass and an outer ectoderm form by delamination. Interstitial cells arise in the endoderm then move between endo- and ectoderm. The embryo elongates, a small gastric cavity forms, a mouth opens, and tentacles develop. The aboral end elongates, and a mobile actinula emerges after about 4-5 days. In *T. larynx*, actinulae emerge in slightly greater numbers at night; they crawl about, using their aboral tentacle tips, then after 6-46 hours attach by their aboral ends, more settling on surfaces

with microbial films than on clean glass (Pyefinch & Downing 1949). In the field, most settle near parent colonies. Similar development in several species is summarized by Kume & Dan (1968).

T. crocea (L. Agassiz). Tangled colonies of large pink polyps grow on pilings and floats in protected waters, usually with a temperature above 18°C. Polyps may be kept at 14°C in flowing water or in large volumes of recirculating water renewed weekly. Oogenesis and early development are described by Fennhoff (1978, 1980). In Elkhorn Slough, California, actinulae are released August-October and February-March, August-November in the less favorable places (Cooper 1980). Release of actinulae and their settlement and growth are described by Mackie (1966).

T. marina (Torrey). Large pink polyps, up to 5 cm long, are solitary or occur in well-spaced groups on exposed rocky shores or pilings and floats in fast flowing current (Haderlie *et al.* 1980). In Friday Harbor, this is the most common *Tubularia* species. Female gonophores, without radial canals or ring canal but with 3-4 long tentacles (Mills & Miller 1987), bear developing actinulae April-August, most commonly May-June (R. Miller pers. comm.). In Monterey Bay, developing actinulae are found February-July (Haderlie *et al.* 1980). Actinulae are readily released in the laboratory.

T. indivisa (Linnaeus). This very large species, up to 30 mm long, is occasionally dredged near Friday Harbor. Actinulae are released in April (R. Miller 1982 and unpubl.) and August (Tardent 1980). Hydroid regeneration is slower and is limited to distal regions in this giant species (Tardent 1980).

Order Hydroida, Suborder Leptomedusae/Thecata

Aequorea victoria (Murbach & Shearer). Aequoriidae. This species has also been called *A. forskalea* and *A. aequorea* in the Puget Sound region (see Arai & Brinckmann-Voss 1980). Small specimens are common March-October in Friday Harbor (Mills 1981). Gonads appear when bell diameters reach 25 mm (Fraser 1916; Arai 1980). Mature medusae, 50 mm or more in diameter, bear gonads along most of the length of the radial canals (Mills unpubl.). Although medusae of some *Aequorea* spp. undergo fission (Stretch & King 1980; Mills 1987), this does not occur in *A. victoria*. Medusae spawn mid-morning in nature (Mills 1983) or within 3 hours in light following 8-10 hours in darkness, and similarly in dark following light (Miller 1979). Sperm become active after 20-30 minutes in sea water and remain so for 2-3 hours (R. Miller pers. comm.). Transparent eggs are 100 μm in diameter; germinal vesicle breakdown and polar body formation occur soon after spawning (Strong 1925). Cleavage begins 50-60 minutes after fertilization (R. Miller pers. comm.; Strong 1925). Planulae form within 24 hours and settle within 3-12 days in culture (Fernald unpubl.). Formation of hydroid colonies (as *Campanulina membranosa*) is described by Strong (1925). Planulae settle

onto their sides and develop a perisarc. Within a day, hydrocaulus, tentacle buds and hydrotheca form. A hydranth with 12 proximally webbed tentacles develops within six days. Additional hydranths rise singly from unbranched stolons. A similar life cycle of a species from Japan has been described by Kakinuma (1966b).

Aglaophenia spp. Aglaopheniidae. Colonial hydroids. Gonangia are enclosed in corbulae with unfused leaflets in males, fused leaflets in females (Allman 1871-72). The male spadix has symmetrical spermatogenous tissue; the female spadix bears one large egg off center (Torrey & Martin 1906). Embryos develop to planulae within the female sporosacs.

A. latirostris Nutting. Common. Low intertidal to 35 m on rocks and larger algae along sheltered rocky shores. Large orange planulae are released from corbulae upon exposure to light after a period of dark (Fraser 1937).

A. struthionides (Murray). On rocky exposed shores, low intertidal to 160 m. Corbulae of this species are illustrated by Torrey & Martin (1906).

Eutonina indicans (Romanes). Eirenidae. Polyps occur on various substrata (Rees 1978). Medusae occur year-round, commonly April-June, in Bodega Bay (Rees 1978); March-October (Foerster 1923), commonly April-June, in the Strait of Georgia (Arai & Brinckmann-Voss 1980); and abundantly April-June of some years in Friday Harbor with occasional specimens to November (Mills 1981). Medusae spawn within 30 minutes in light following 8-10 hours of darkness (Miller 1979). Eggs are 170-180 μm in diameter (R. Miller pers. comm.). Atlantic and Pacific specimens have been reared through the life cycle (Russell 1953; Werner 1968b; Rees 1978). Polyps and medusae are hardy in culture, and can be reared in standing or recirculating sea water renewed every 2 months (R. Miller pers. comm.). New polyps and new medusae can eat whole *Artemia* sp. nauplii. At 11-14.5°C, fertilization to settlement takes about 3 days, and settlement to first release of medusae about 40 days (Rees 1978). First release of medusae may possibly be stimulated by crowding in culture. Medusae grow rapidly at first; they have been kept 105 days in culture (Rees 1978). At 11-14°C at Friday Harbor, medusae take 1-1.5 months to reach sexual maturity (R. Miller pers. comm.).

Gonothyrea sp. (possibly = *Gonothyrea loveni*). Campanulariidae. Laboratory colonies may be fed *Artemia* sp. nauplii. Miller (1970) describes reproductive structures and methods for obtaining fertilization *in vitro*. Reduced medusoids emerge from gonangia but are retained by attachment stalks. In *G. loveni* the mature male medusoid has a large white sperm mass with an outer layer of active sperm. If gonangia with newly emerged male medusoids are detached, sperm may be released for up to 30 minutes. The female medusoid is larger than the male and has larger tentacles; these lack nematocysts but have a jelly-like coating to which sperm adhere, afterwards passing into the female

and through a thin membrane enclosing the eggs. Oocytes contain a prominent germinal vesicle until just before the female medusoid emerges. Oocytes obtained by tearing the membrane inside the female medusoid may be artificially inseminated just after germinal vesicle breakdown. Up to eight fertilized eggs (about 140-170 µm in diameter, judging from a figure by Miller 1970) are retained in the female medusoid for development to planulae. This requires 4 days at 14°C (Allman 1872; Miller 1970). Development has been described by Wulfert (1902).

Mitrocoma cellularia (A. Agassiz) (= *Halistaura cellularia*). Mitrocomidae. Medusae occur locally May-December, most abundantly June-August (Mills 1981). They mature at a bell diameter of 40-50 mm; gonads extend almost the full length of the four radial canals. Spawning occurs at dawn in nature or within 30 minutes in light following 8-10 hours in dark in the laboratory (Miller 1979; Mills 1983). Development was observed and described by Sund (1954) at Friday Harbor. Eggs are about 150 µm in diameter. At ambient sea water temperatures, first cleavage occurs 15-30 minutes after fertilization. A ciliated planula forms after 15 hours. Planulae will settle on glass. Early stages should be kept below 17°C (Fernald unpubl.).

Mitrocomella polydiademata (Romanes). Mitrocomidae. Medusae occur locally April-July, abundantly late April-early June (Arai & Brinckmann-Voss 1980; Mills 1981). Edwards (1973) and Martin *et al.* (1983) describe development and metamorphosis. The eggs are ovoid to globular, 130-170 µm in diameter. At 12°C, planulae form in 29 hours. After 3-5 days, they are 200 µm long and have a thickened anterior end. Settling planulae attach by the anterior end but within 12 hours slump onto one side and become mound-shaped. In another 12 hours a perisarc is secreted over this bulbous area. As a filiform stolon grows along the substratum, the perisarc is extended as an enclosing tube. The elongating end rises from the substratum and develops into a hydranth with a single whorl of 8-10 tentacles at first, 12-16 later. Martin *et al.* describe fine structure of the planula and its metamorphosis. Edwards describes a series of medusae from the plankton.

Obelia spp. Campanulariidae. Hydroids colonies are common on floats and docks. Three species are recognized by Cornelius (1975), but recent examination of living European hydroids has invalidated some synonomies. Systematics of most North American *Obelia* remain to be examined. Colonies with ripe gonophores readily release medusae in the laboratory in summer (Mills 1981). Medusae are small, flat and under 0.5 mm in bell diameter when released; they are nearly 5 mm in diameter when full grown (Kozloff 1983). Medusae have 16 tentacles when released (Cornelius 1975), more when mature. A round gonad develops on each of the four radial canals. Medusae spawn within 1 hour in light after 8-10 hours in darkness (Miller 1979). Medusae occur March-September in the Strait of Georgia, mostly April-June (Arai & Brinckmann-Voss 1980). They may be collected in plankton tows.

Orthopyxis compressa (Clark) (possibly = *O. caliculata*). Campanulariidae. Medusae formerly called *Agastra rubra*. Hydroids are common on red algal blades (Arai & Brinckmann-Voss 1980). The hydroids bear large gonangia that appear to the unaided eye as beige protrusions on the stolons between polyps. Each contains one developing medusa; these may sometimes spawn without leaving the gonagium. From April to late October in Friday Harbor, medusae are released just after dark, females first, then males 15-20 minutes later. Reproductive structures, spawning, and fertilization are described by Miller (1978). Medusae lack tentacles and stomach. They normally spawn 10 to 15 minutes after release and die a few hours later. Although constant light suppresses release of medusae and spawning, medusae collected just after release at dusk will spawn in a lighted laboratory. Females have ovaries packed with large yolky eggs, each about 200-220 μm in diameter. The first polar body is usually present when the eggs are spawned, and the second polar body forms about 10 minutes later. Within two minutes after spawning, sperm in the water or entrapped in the egg jelly become active. They move toward the egg surface, aggregating at the site of polar body emission for about 10 minutes. The sperm attraction subsides, presumably after fertilization occurs. First cleavage follows in about 45 minutes. Preferential settlement of *Orthopyxis platycarpa* on *Rhodamela* sp. and other algae is reported from Japan (Nishihira 1965).

Phialidium gregarium (A. Agassiz). Campanulariidae. The hydroid (*Clytia johnstoni* or *Clytia* sp.) is easily reared from planulae settling in culture (Bovard & Osterud 1918; Strong 1925; Roosen-Runge 1970; Worthmann 1974). Locally, medusae occur March-November or December, commonly April-September, and abundantly July-August. Gonads are borne beneath the distal parts of the radial canals.

Spawning occurs at dawn and dusk, usually more heavily at dusk (Roosen-Runge 1962). In the laboratory, spawning occurs within 30 minutes in light following 8-10 hours in darkness, or similarly after a change from light to dark (Miller 1979). Isolated males or excised testes release sperm upon the change in light; the response involves temporary rupture of attachments between the epithelial cells covering the testis, and sperm are released for about 15 minutes (Roosen-Runge & Szollosi 1965). Egg release is similar. Eggs are 165-180 μm in diameter. They remain fertilizable for 3-4 hours. For *in vitro* insemination, add sperm to a final concentration of about 100 per ml. To start batch cultures, place 30-40 medusae in a large bowl. They will produce about 1000 embryos in the two daily spawnings. Remove the adults or transfer the embryos to cultures kept at 10-15°C. Embryos can withstand brief warming to 18°C (Roosen-Runge 1970).

Development has been described by Roosen-Runge (1962, 1970) and Freeman (1981a). The site of fertilization, polarity of the egg and embryo, and developmental potentials of blastomeres have been studied experimentally by Freeman (1981a,b, 1982). Cleavage is somewhat irregular.

At 12°C development follows this schedule (Roosen-Runge 1962):

50 min	First cleavage begins
70-90 min	Two-cells
95 min	Second cleavage begins
110-120 min	Four-cells
150 min	Eight-cells
4 hrs	128-cells
5-10 hrs	Coeloblastula formation
16 hrs	Gastrulation by unipolar ingression begins
24-48 hrs	Planulae form
3-12+ days	Planulae settle

Planulae settle on substrata with microbial films. The settled planula rounds up and then spreads into a disc in about 2 days. Polysaccharides released by ectodermal cells form a chitinous covering (Bonner 1955). A stalk and functional hydranth form after 2-4 more days.

New polyps should be individually fed small copepods or pieces of *Artemia* nauplii for a few days. If fed abundantly, the primary hydranth may regress, followed by the appearance of several larger hydranths from the pedal disk. A stolon forms in the first week, and hydranths develop at 1-3 mm intervals along the stolon. A colony may grow to three inches in diameter in a single summer; branching, annulation and tentacle number vary with conditions (Roosen-Runge 1962, 1970). Colonies can be kept for long periods in large (ca. 200 liter) tanks with recirculating artificial sea water (Worthmann 1974).

At 14-15°C, well-fed colonies produce gonangia in about three weeks. Formation of gonangia and release and growth of medusae are described by Roosen-Runge (1970). Gonangia form on the stolon near, sometimes on, the stem of a hydranth. A smooth gonotheca encloses a blastostyle with 2-7 buds. These buds develop to medusae in 4-5 days. Medusae are released over a 6-10 day period. Newly released medusae are 1.2 to 1.4 mm in diameter, with 4 tentacles, 4 tentacle buds and 8 lithocysts. They can eat *Artemia* sp. nauplii. They may double their diameter within the first two days. Medusae reared in planktonkreisels reach sexual maturity in 4 weeks and remain reproductive for their entire three month life span.

Similar or synonymous species have been reared in California (West & Renshaw 1970), Japan (Kubota 1978), and Europe (Metschnikoff 1886; Bodo & Bouillon 1968; Honegger *et al.* 1980).

Phialidium lomae **Torrey** (= *Clytia attenuata*). Campanulariidae. This species occurs locally, although less commonly than *P. gregarium* (Kramp 1962). It has been reared in culture (Roosen-Runge 1970). Fine structure of testis and gamete release have been described (as that of *P. hemisphaericum*) by Roosen-Runge & Szollosi (1965). The eggs are smaller than those of *P. gregarium* (E. Roosen-Runge pers. comm.; Larson 1986).

Plumularia spp. Plumulariidae. Several species are common along the west coast of North America. Feathery hydroid colonies, about 2 cm tall, occur on protected low intertidal and subtidal rocks and algal holdfasts. In the spring and summer, elongated gonangia form near the bases of branches or on the main stalk. Male gonangia are white with sperm; female gonangia contain bright yellow eggs or embryos. Ciliated planulae can be released by opening gonangia with a needle.

Sertularia spp. and *Sertularella* spp. Sertulariidae. Colonial hydroids. Some species liberate medusae, but most produce sessile gonophores on blastostyles enclosed in gonangia (Allman 1871-72). Allman (1871) and Honegger (1980) describe female gonangia and oogenesis in two species. Eggs are extruded in a gelatinous mass through a terminal pore in the ovoid female gonangium, and a tough cover forms over the mass, producing an ovoid brood chamber, called an acrocyst (Hyman 1940). Local colonies bear acrocysts with pale pink eggs or embryos in spring; their development is undescribed.

Reproduction and development are described for sertulariids from other regions (Nutting 1904; Müller-Calé 1913; Teissier 1923). *Dynamena pumila*, from the coast of France, has large yolky embryos that undergo equal then irregular cleavage and gastrulation by delamination (Teissier 1923). In several species, demersal creeping planulae emerge from the acrocyst and settle on stone, shell (Hancock *et al.* 1956) or blades of algae (Nishihira 1965, 1967a,b).

Order Limnomedusae

Gonionemus vertens A. Agassiz. Olindiasidae. Solitary polyps, less than 1 mm tall, occur on bits of wood, rock or shell in shallow sandy bays. Polyps are reported to produce frustules (Perkins 1902; Joseph 1925), but this has not been observed in local populations. In the San Juan Archipelago, individual polyps produce single medusae; medusae are released mid-April to June, and the first medusae reach maturity at about 20 mm in bell diameter by mid-June (Mills unpubl.). Medusae tend to be on the bottom by day and in the water column by night (Mills 1983). They eat copepods, mysids, isopods, amphipods, and fish larvae (see Arai & Brinckmann-Voss 1980), and can be fed crab meat in captivity (Mackie & Mackie 1963). **Caution:** Medusae from the northeast Pacific Ocean are not toxic, but it is reported that contact with medusae from the northwest Pacific Ocean (near Vladivostok) can cause serious illness (see Arai & Brinckmann-Voss 1980).

Medusae bear sinuous gonads pendant along most of the length of the radial canals; testes are buff to brown, ovaries are orange (Gellermann 1926). Medusae spawn 45-60 min after dusk or placement in darkened aquaria (Murbach 1895, Perkins 1902, Miller 1979) and the spawning process takes less than 15 minutes (Mills 1983). Spawning is suppressed by continuous light, but once underway is not interrupted by light (Rugh 1929). Locally, each female produces 1,000-13,000 eggs per nightly spawning; the relationship of fecundity to bell size varies as summer progresses (Mills unpubl.). Rugh

(1929) reported females averaging 6,642 eggs per spawning and a maximum single spawning of 22,165 eggs.

Eggs are bright yellow to orange and 95-100 μm diameter. They are covered by a sticky jelly coat that will adhere to glass slides and may cause the eggs to stick together. Early cleavages are regular and holoblastic, occuring about every fifty minutes (Murbach 1895; Perkins 1902, Bodo & Builllon 1968). The cells become columnar with nuclei toward the surface of the ciliated stereoblastula; gastrulation occurs by delamination (Perkins 1902). Planulae develop within about 12 hours and settle after 1-3 days; a small solitary polyp with two primary tentacles forms within the first week, but additional tentacles do not form nor does the mouth open for several more weeks (Perkins 1902; Bodo & Bouillon 1968). In Friday Harbor, *G. vertens* embryos sometimes develop into swimming larvae, but may also bypass the swimming stage to develop into polyps (Mills 1983).

***Proboscidactyla flavicirrata* Brandt.** Proboscidactylidae. Hydroids are obligate commensals on sabellid polychaete tubes (Uchida & Okuda 1941; Hand 1954). Locally, orange-pink hydroid colonies with two-tentacled gastrozoids are found on the rims of tubes of *Schizobranchia insignis* and *Potamilla occelata* (Hand 1954; Campbell 1968a,b; Strickland 1971; Donaldson 1974, 1977). Club-shaped gonozooids, each with up to 8 medusa buds, form a ring below the gastrozooids. Worms and hydroids should be kept in well aerated, circulating sea water. Colonies on empty worm tubes resorb their gastrozooids but retain the gonozoids. Hydroids should be fed newly hatched *Artemia* sp. nauplii every 2 days. After 4 weeks of ample feeding in culture, colonies begin to release medusae. These are about 0.9 mm in bell diameter when newly released. The medusae may be kept in beakers of gently aerated sea water and fed every two days with brine shrimp nauplii, but they grow slowly in these cultures, taking 14 weeks to reach a bell diameter of 7 mm. Growth stages of medusae are described by Rees (1979).

In the Strait of Georgia, medusae occur March-November, commonly June-July (Arai & Brinckmann-Voss 1980). In the San Juan Archipelago, medusae occur in small numbers all year, abundantly in May and August-October (Mills 1981). Four inter-radial gonadal masses cover most of the stomach. Medusae spawn within 30 minutes in light after 8-10 hours in darkness (Miller 1979).

Development has been described by Campbell (1968a) and Donaldson (1974). Eggs are 120 μm in diameter. Gastrulation is by ingression. Cilia appear at about 14 hours. Planulae swim and creep. Cnidocils protrude from their surface during day 2. Planulae settle from day 3 on with high specificity on tubes of living *Schizobranchia insignis* and *Pseudopotamilla occelata.* Settling planulae are swept into the ciliated currents of the worm tentacles and attach to the worm, usually on the tentacle pinnules, by discharging special nematocysts. After 1.3-11 minutes, they elongate; after another 3 minutes they can transfer, again using nematocysts, to the rim of the tube where they round up and complete metamorphosis. Gastrodermis and mouth form in 5-6

hours. The primary polyp has a stolonic region and a slender gastrozoid with 1 tentacle. Metamorphosis can be observed by placing a small piece of tube rim with a newly attached planula in a wet mount chamber (see p. 29). The sabellid worm *Eudistylia vancouveri* induces settlement but not metamorphosis (Donaldson 1974).

Order Trachylina

Aglantha digitale (O. F. Müller). Rhopalonematidae. All life stages are pelagic. The planula develops into a planktonic actinuloid stage then directly into a medusa. In the North Atlantic, medusae are common April-July and spawn April-June; development to maturity takes about 2.5 months, and in some years a second generation breeds late July-August (Williams & Conway 1981). In the North Pacific, specimens averaging 5-7 mm in bell height in July grow to 6-9 mm by December, descending to sea depths below 150 m as they grow (Williams & Conway 1981). The gonads are sausage-shaped and depend beneath eight radial canals. Hargitt (1917) describes the anatomy of gonads and gametogenesis.

Medusae occur in deep water of Departure Bay, the Strait of Georgia (Arai & Mason 1983), and Saanich Inlet, B.C., where they show diel migrations, moving upward at night (Arai & Fulton 1973; Mackie & Mills 1983). The local population undergoes either one or two generations per year, depending on conditions in the field (Mills 1982). Medusae appear sporadically year round in Friday Harbor, appearing in moderate numbers May-July of some years (Mills 1981; G. Freeman, pers. comm.). Medusae are fragile. They survive best in the laboratory when kept in wide-mouth green bottles in a darkened 10°C refrigerator (G.O. Mackie pers. comm.). Newly collected specimens held unfed usually spawn out within 24 hours, releasing gametes at various times, but often between 2 and 4 A.M. or 10 A.M. and noon; a single female produces 200-1000 eggs (Freeman 1983). Single embryos, planulae, or actinulae may be cultured in spot plates at 11-12°C; use of microfiltered pasteurized sea water with 100 units per ml of penicillin improves survival rates of experimentally manipulated specimens (Freeman 1983).

Freeman (1983) has described embryos and larvae reared in culture, and has noted similaries in development to that of ctenophores. The egg, average diameter 139 μm, has granular endoplasm surrounded by a less granular ectoplasm. An egg envelope, unusual in a hydrozoan, is closely applied to the egg surface. Polar bodies are formed while oocytes are still in the ovary or just before they are ovulated into a cavity within the gonad. Cleavage is unilateral. The first two cleavages are equal and originate at a common site; the third cleavage is unequal. It produces four macromeres and four micromeres, the latter at the pole opposite to the site of first cleavage initiation. The fourth division produces two tiers of macromeres. Gastrulation occurs by epibolic spread of micromeres over macromeres and a delaminating cleavage of some macromeres. A ciliated planula hatches during day 1. During day 2, two tentacles appear at the oral or posterior end; this end corresponds to the

initiation site of first cleavage. Two more tentacles form and a manubrium appears. The mouth opens during day 3, and by day 4, it is heavily ciliated and surrounded by gland cells. Large, highly vacuolated endodermal cells become separated by a basement membrane from ectodermal cells. Feeding begins on day 4. A pelagic actinula is formed. It moves by means of ciliated tracts on the flexible tentacles.

Eggs have been centrifuged (15 minutes at 10,800 x g in 1:2 sea water and 1 molal sucrose), surface markers traced, and blastomeres separated to study developmental potentials; potential for ectoderm or endoderm is set in the cytoplasm of the uncleaved egg and separates to micromeres and macromeres by the 8-cell stage (Freeman 1983).

Order Stylasterina

This is a group of calcareous encrusting or branching colonial species, sometimes called "hydrocorals". Openings on the surface, called cyclosystems, each contain a feeding gastrozoid surrounded by defensive dactylozoids. Zooids, each on a basal spine, are connected within and between cyclosystems by thin strands of tissue. Species from this region are described by Fisher (1931, 1938) and Naumov (1960). Colonies are found in areas exposed to current or surge, and should be raised slightly off the bottom of aquaria and kept free of debris and silt.

Allopora petrograpta Fisher. Pink to purple encrusting calcareous colonies occur on smooth subtidal rock. Fritchman (1974) has briefly described development. Eggs are produced in ampullae, small cavities arranged around the gastrozoid, usually alternating with the dactylozoids. They remain in the ampullae for fertilization and development. Planulae are released June-August. Ciliated planulae emerge from the ampullae either into the gastropore of the cyclosystem or directly out of the surface of the colony. Planulae are orange and have a white anterior end with large ectodermal gland cells. Although very contractile, they average 1980 μm in length and 318 μm in diameter. They creep downward during the night of release and are always found on the bottom near the mother colony. Most planulae attach within 3-8 hours. Attachment is followed by rapid metamorphosis. At 12-14°C, the settled planula transforms into a disc within 15 to 45 minutes. The disc, 500-1300 μm diameter, temporarily develops concentric folds, then expands until it is only 50-80 μm thick. Fritchman describes subsequent colony formation and secretion of the epidemal skeleton.

Ostarello (1973, 1976) has described oogenesis, superficial cleavage, and gastrulation by delamination in another species, *Allopora californica*, whose development and planulation appear to be similar to those of *A. petrograpta*.

Order Siphonophora

A comparative study of 8 species suggests a basic pattern of development in siphonophores (Carré 1975). The egg cytoplasm is distinctly separated into a finely granular cortical zone, containing most of the cellular organelles, and an endoplasmic region that is vacuolar and yolky. Cleavage up to the 32-cell stage is total and equal. Subsequent cleavage becomes partial and superficial, giving rise to a peripheral cell layer surrounding a central anucleate yolk mass. Endoderm cells form by primary delamination, some of the endoderm cells migrating into the yolk mass while others, originally scattered, spread out and form a continuous layer beneath the ectoderm by the planula stage. Along one side, in the plane of the first cleavage, a larval tentacle forms and and ectodermal delamination produces a medusoid nodule from which the first nectophore (swimming bell) develops. In physonect siphonophores, an ectodermal invagination forms the rudiment of the pneumatophore.

Muggiaea atlantica **Cunningham.** Suborder Calycophora. Pelagic colonies occur year-round in Friday Harbor; the polygastric phase is sometimes abundant in May-June and September-November (Mills 1981 and unpubl.). Colonies, which are hermaphroditic, release small reproductive sub-colonies, called eudoxids. These are found in the local plankton June-November (Mills 1981; Freeman 1983). They spawn after 8-10 hours in light following 8-10 hours of darkness (Miller 1979). Eggs average 319 μm in diameter; they float (Freeman 1983). Polar bodies are associated with an extracellular structure, the cupule, which has been shown to be the site of a sperm attractant (Carré & Sardet 1981), and which is lost soon after fertilization. Sperm structure has been described for *M. kochi* (Carré 1984).

Freeman (1983) has described egg structure, cleavage, gastrulation, and planula formation. Cilia appear at 6-8 hours and a swimming planula is formed by 12-15 hours. At the end of day 1, an invagination in an anterior endodermal thickening on one side forms the rudiment of the nectophore, and just below it the larval tentacle rudiment appears as a bulge. The nectophore grows rapidly and becomes a functional locomotory organ by day 4. The initial part of the gastrovascular canal system, the somatocyst, forms. Cnidobands develop on the tentacle, a gastric cavity appears, and a mouth opens at the posterior end of the larva. Russell (1938) describes formation of the larval and adult nectophores.

Nanomia cara **A. Agassiz.** Suborder Physonecta. Colonies occur all year in Friday Harbor, more commonly in summer (Mills 1981). They are fragile and should be kept isolated. Colonies are hermaphroditic and become reproductive by late May. Gonads are borne by medusoids budded from the stem. Spawning occurs within 6-8 hours of light after 8-10 hours of dark (Miller 1979).

Eggs average 274 μm in diameter (Freeman 1983). Freeman has described development. Cleavage is unilateral. The first two cleavages are equal but their initiation sites are not always the same. The third cleavage occurs at

right angles to the second, producing two tiers of four equal-sized cells. Gastrulation begins after the 64-cell stage and is completed six to seven hours after fertilization. During the next six to twelve hours, the embryo elongates, develops cilia, and begins to swim. The posterior end of the planula corresponds to the site of first cleavage initiation. During day 4 and 5 of development the planula develops enlarged anterior ectodermal cells which invaginate and form the rudiment of the pneumatophore. At the same time, an anterior endodermal thickening begins to grow out as a tentacle. Gas secretion begins in the pneumatophore and red pigment cells appear at the posterior end, the site of mouth formation. A gastric cavity forms and the young stage, called a siphonula, begins feeding by day 7. Cnidobands appear at the base of the tentacle, then on the tentacle.

Development of the Mediterranean species *N. bijuga* has been described by Carré (1969, 1975); it remains regulative to a later stage than *N. cara*.

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