

Aequorea victoria

Crystal Jelly

Phylum: Cnidaria
Class: Hydrozoa, Hydroidolina
Order: Leptomedusae
Family: Aequoreidae

Taxonomy: Originally described as *Mesonema victoria* (Murbach and Shearer, 1902), current synonyms and previous names for *Aequorea victoria* include *Aequorea aequorea*, *A. forskalea*, and *Campanulina membranosa* (a name proposed for the polyp form by Strong 1925) (Mills et al. 2007; Schuchert 2015). The taxonomy of Aequoreidae is currently in flux and awaiting further molecular research (Mills et al. 2007).

Description

General Morphology: *Aequorea victoria* has two forms. Its sexual morphology is a gelatinous hydromedusa. It has a wide bell, many tentacles, and radial canals that run from the mouth to the bell margin, where they are connected by a ring canal. Suspended from the inside of the bell by a peduncle is the manubrium, or mouth. A velum rings the inside of the bell margin (Fig. 1). Its asexual morphology is a small polyp. Each polyp has a stem (hydrocaulus), and most have a sheathed (thecate) hydranth with a mouth (manubrium), stomach, tentacles, and an operculum (Fig. 4). Rather than having hydranths, some polyps have gonophores (Fig. 5).

Medusa:

Size: *Aequorea victoria* is much wider than tall and can get up to 12 cm in diameter (Kozloff 1987), but only 4 cm in height (Arai and Brinckmann-Voss 1980).

Color: Adult specimens are transparent aqua blue with whitish radial canals, while juveniles have a green sub-umbrella, opalescent gray or milky gonads, and occasionally have brown tentacle bulbs (Arai and Brinckmann-Voss 1980). Mature specimens also fluoresce and luminesce, with their luminescence concentrated around the bell margin (Kozloff 1983).

Body:

Bell: The bell is large and relatively flat, and contracts when swimming. It is thick, gelatinous, and rigid, with a ring canal around the margin and radial canals running from the mouth to the margin (Fig. 1). It has a short, thick peduncle (Arai and Brinckmann-Voss 1980).

Radial Canals: *Aequorea victoria* individuals can have over 100 symmetrical, unbranched radial canals. In mature specimens all radial canals reach the bell margin (Mills et al. 2007, Kozloff 1987) (Figs. 1, 2). Excretory pores open at the canal bases near the tentacles (Hyman 1940).

Ring Canals: The ring canal surrounds the bell margin.

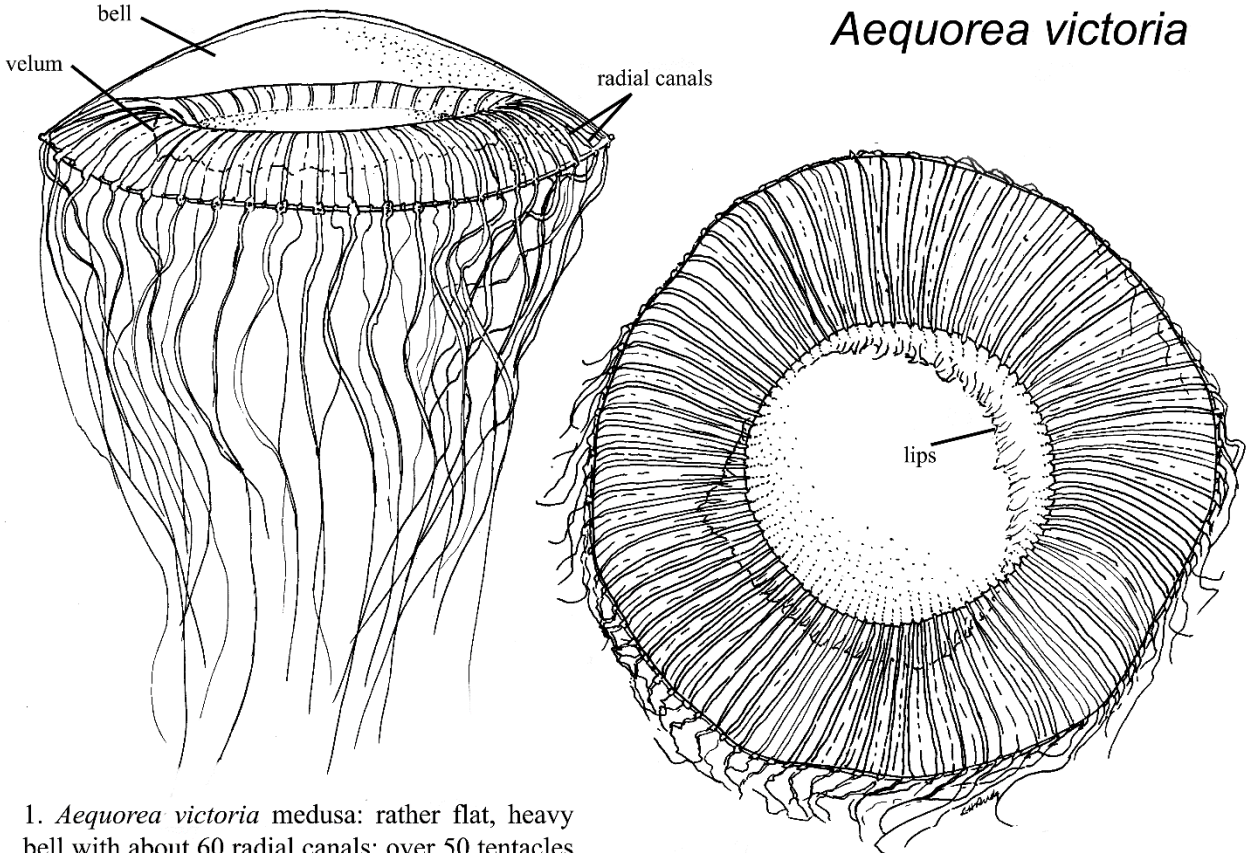
Mouth: The mouth is part of the tubular manubrium, which is large and surrounded by numerous frilled lips (Fig. 2).

Tentacles: The tentacles are hollow, unbranched, and numerous (up to 150, often about as many as radial canals) (Arai and Brinckmann-Voss 1980, Mills et al. 2007). They occur on a single whorl on the ring canal (Mills et al. 2007). Not all of the tentacles are the same length and they can be very long when extended (Kozloff 1987). They have stinging cells (nematocysts) used in prey capture and defense. According to Purcell (1989) these nematocysts are isorhiza and microbasic mastigophore, but there is variation in cnidoblast naming schemes between researchers.

Velum: The velum is a flap of tissue, barely visible inside the bell rim, which is used for swimming (Fig. 1) (Hyman 1940).

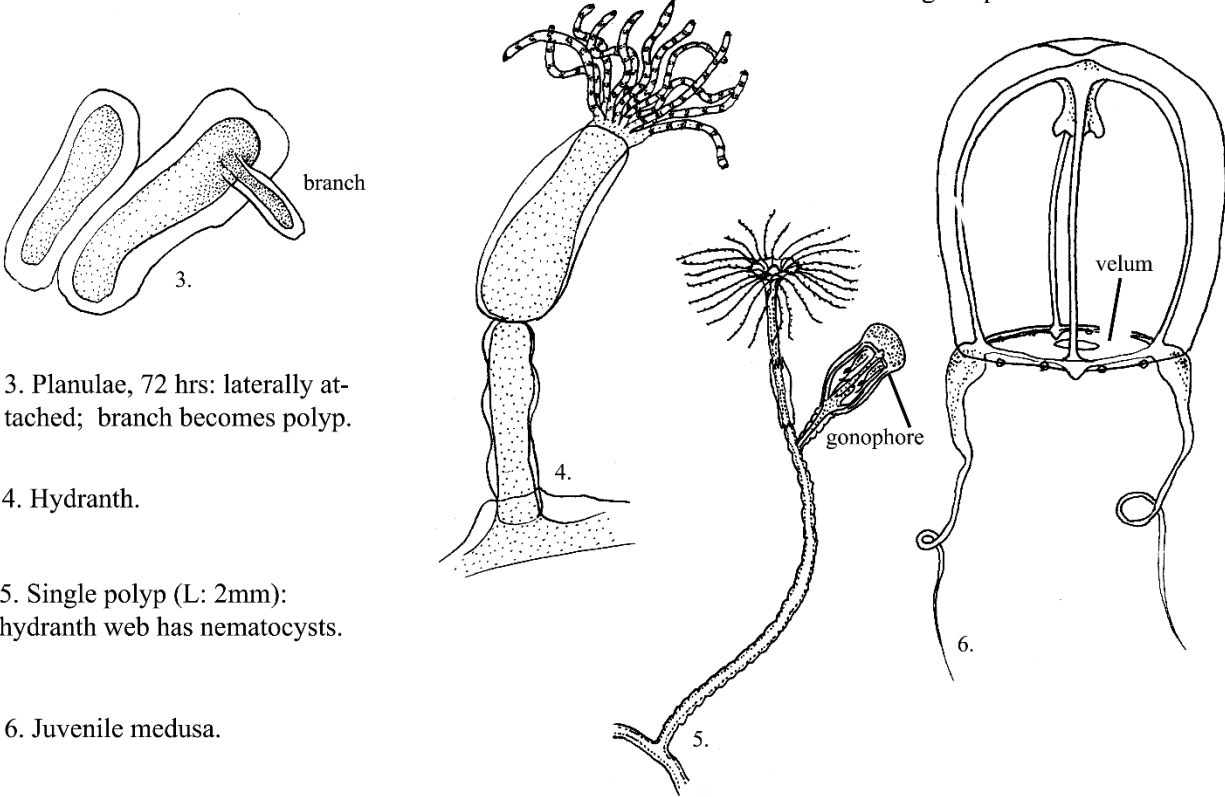
Gonads: Gonads in *A. victoria* are not finger-like as in many other hydromedusae. They develop once the bell diameter reaches 25 mm (Mills and Strathmann 1987), and are suspended from and span nearly the entire length of the radial canals (Fig. 1) (Mills et al. 2007, Kozloff 1987).

Aequorea victoria



1. *Aequorea victoria* medusa: rather flat, heavy bell with about 60 radial canals; over 50 tentacles on ring canal; wide mouth; gonads along radial canals.

2. Medusa: dorsal view; mouth with fringed lips.



3. Planulae, 72 hrs: laterally attached; branch becomes polyp.

4. Hydranth.

5. Single polyp (L: 2mm): hydranth web has nematocysts.

6. Juvenile medusa.

Sensory: *Aequorea victoria* lacks eyespots but has statocysts, which are used for balance and orientation in the water column (Kozloff 1983).

Polyp: Rare (Mills 2001).

Size: Very small (0.5-1 mm) (Figs. 3–5) and composed of simple or slightly branched colonies with rarely more than two polyps (Strong 1925).

Color:

Body:

Pedicel: The polyp is pedicellate (Kozloff 1987; Mills et al. 2007), with hydrocaulus (stem) up to 2.5 mm in length, and is ringed rather than spirally grooved (Mills et al. 2007).

Hydranth: Each polyp has about twenty tentacles, a mouth, and an intertentacular web armed with nematocysts. The colonies are stolonial (connected by horizontal shoots at the base of each hydrocaulus) (Mills et al. 2007). The hydranth is covered by a theca (hydrothecae) that is deeper than it is wide and is able to hold the entire hydranth when contracted (Mills et al. 2007; Kozloff 1987) and the hydrothecae are radially symmetrical and do not have true marginal cups (Mills et al. 2007). Instead, they have longitudinal striations with straight walls (Mills et al. 2007; Kozloff 1987), and the opercular valves are continuations of the hydrothecal margin (Mills et al. 2007; Kozloff 1987).

Gonangium: Some branches of a colony have gonophores (Fig. 5) that reproduce by releasing free, spherical medusae (Mills et al. 2007; Kozloff 1987).

Cnidae: The intertentacular web contains nematocysts (Mills et al. 2007).

Possible Misidentifications

The family Aequoreidae includes leptomedusae with numerous radial canals, gonads attached to the radial canals, a broad short stomach, but lacking marginal or lateral cirri (Arai and Brinckmann-Voss 1980). There is only one other *Aequorea* species locally: *A. coerulescens*. It is larger than *A. victoria* and having a bell that is up to 25 cm in width with three to six times as many tentacles as radial canals. It is also less common and lives

further offshore than *A. victoria* (Mills et al. 2007).

Aequorea victoria medusae are very large among hydrozoans, and this species is the only Leptomedusa with more than 24 radial canals (most have only four) (Rees and Hand 1975). The Scyphozoa, or true jellyfish, are large, have fringed mouth lobes, scalloped margins, no velum, and a complex pattern of radial canals (Rees and Hand 1975). Some scyphozoans also have prominent, pendant oral arms. Very young *A. victoria*, up to 4 mm in diameter, can look similar to *Polyorchis penicillatus* in shape (Fig. 6); additionally, the young *A. victoria* lack the many radial canals that they will develop as they mature, and so seem more similar to the *P. penicillatus* with its four radial canals (Russell 1953).

Ecological Information

Range: Type localities are Victoria Harbor, British Columbia and Puget Sound, Washington (Murbach and Shearer 1902). Found in temperate waters in both northern and southern hemispheres. Well known in Puget Sound and British Columbia.

Local Distribution: Oregon distribution includes most bays and nearshore waters.

Habitat: Medusae are found in plankton and harbors (e.g., Charleston boat basin). The attached, or polyp, forms have been found intertidally (Mills et al. 2007).

Salinity: Collected at salinities of 30 and cannot tolerate large fresh water influx (e.g., from storms, MacGinitie and MacGinitie 1949).

Temperature: A cold to temperate species.

Tidal Level: Medusae are pelagic, while polyps are intertidal.

Associates: The small anemone, *Peachia quinquecapitata*, is sometimes parasitic on *A. victoria* individuals (Puget Sound, Washington). *Aequorea victoria* ingests *P. quinquecapitata* larvae, and once inside the hydromedusae, the larvae feed on nutrients in the radial canals and gonads. These parasitic larvae grow and metamorphose into juveniles while still inside *A. victoria*. Ultimately, the juvenile leaves its host mid-water and may

become ectoparasitic on another *A. victoria* host (Mills and Strathmann 1987).

The hydromedusae are also parasitized by larval and juvenile forms of *Hyperia medusarum*. *Aequorea victoria* provides a pelagic host on which hyperiid amphipods can overwinter (Boonstra et al. 2015, Towanda and Thuesen 2006).

Abundance: *Aequorea victoria* is one of the most common large medusae. At the right time of year, it can occur in great numbers locally. It was present in high densities in Puget Sound, Washington, from the early 1960s to the mid-1990s. At that time, thousands were collected by researchers for their aequorin (luminescent protein) and GFP (Green Fluorescent Protein). Since the mid-1990s, *A. victoria* populations have decreased in both number and size, though this trend may be due to environmental change as well as high takes (Friday Harbor) (Mills 2001).

Life-History Information

Reproduction: Hydrozoans provide a good example of alternation of generations. The sessile, polypoid colony is delicate and plant-like. Medusae develop asexually from buds on the colony and become free swimming. All medusae from a single colony are the same sex (diecious). Eggs are transparent and 100µm diameter (Mills and Strathmann 1987) and medusae spawn within several hours of daybreak or sundown (Mills and Strathmann 1987). Embryos become planula larvae, which settle and develop into new polypoids. The first hydranth forms about a week after settlement, and additional hydranths grow from unbranched stolons (Mills and Strathmann 1987).

Larva: Embryos become tiny planula larvae. Planulae are uniformly ciliated and usually oval or club-shaped. These larvae are non-feeding and free-swimming. They are armed with nematocytes, but lack an apical ciliary tuft and septa (see Fig. 3, Sadro 2001). These larvae settle on their sides (Fig. 3) and become new polyps (Figs. 4, 5) (Strong 1925). In culture, the larvae form within 24 hours of fertilization and settle within 3–12 days (Mills and Strathmann 1987).

Juvenile: Juveniles are free, spherical medusae. They have two tentacles and

scattered exumbrellar nematocysts that form a broad ring on the lower half of the bell (Fig. 6) (Mills et al. 2007 and Kozloff 1987). They are not considered mature until they reach about 50 mm in diameter (Mills and Strathmann 1987). Juvenile recruitment occurs in the spring (Larson 1986).

Longevity: Unknown.

Growth Rate: Medusae grow very quickly, especially as compared to anthozoans (MacGinitie and MacGinitie 1949). In laboratory conditions they grow from egg to polyp in less than six days (Strong 1925).

Food: Their diet consists predominately of soft-bodied prey (e.g. ctenophores, medusae, cannery refuse), but they also eat mature crustaceans, crustacean larvae (Purcell 1989), and polychaetes. They are an important predator of fish larvae and eggs (Purcell 1989), but once the fish larvae pass the post-yolksac stage they are better able to escape the medusae and are less commonly preyed upon (Purcell et al. 1987). They also participate in intraguild predation, eating other gelatinous species that compete for zooplankton (Purcell 1991). Their feeding response is mostly tactile (Hyman 1940) (i.e. they use their tentacles to capture prey, Purcell et al. 1987). Additionally, they can sense water-borne chemicals produced by crustacean prey, *Artemia* (Arai 1991), though further research is required to fully understand this behavior.

Predators: *Aequorea victoria* is well protected by nematocysts (stinging cells). Giant sunfish (*Mola mola*) eat them, as do some nudibranchs and the hydromedusae *Stomatoca atra* (Arai and Jacobs 1980) and *Phacellophora camtschatica* (Towanda and Thuesen 2006).

Behavior: The small polypoid stage requires a well-sheltered place in order to attach. The floating medusa is the stage most commonly seen (Figs. 1, 2), but often exhibits high mortality after a storm or a sudden pulse of fresh water (MacGinitie and MacGinitie 1949). *Aequorea victoria* medusae are luminescent when stimulated, and provided the original source for the commonly-used green fluorescent protein (GFP) and the luminescent protein aequorin (Mills et al. 2007).

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