

BULLETIN OF MARINE SCIENCE, 30(2): 522-526, 1980

DIRECT FISSION: AN UNDESCRIBED REPRODUCTIVE METHOD IN HYDROMEDUSAE

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Although sexual reproduction is the primary means by which Hydromedusae reproduce, a few species are known to reproduce asexually (Mayer, 1910; Russell, 1953). Two methods of asexual reproduction have been described (Russell, 1953). The first involves the direct budding of young medusae from either the adult medusa's gonad (Mayer, 1910) or from marginal tentacular bulbs (Hyman, 1940). The second method is a longitudinal division process known as schizogony (Russell, 1953). Schizogony proceeds via the formation of multiple stomachs (polygastry) followed by longitudinal splitting into two daughter medusae. We report here for the first time, *direct fission*—an undescribed method of asexual reproduction in the Hydromedusa, *Aequorea macrodactyla* (Bigelow).

During June–August, 1977, *in situ* observations of the leptomedusan jellyfish, *A. macrodactyla*, were made using SCUBA (Hamner, 1975). Observations, photographs, and collections were taken at depths of 5–20 m while diving in the Gulf of California 3 km east of Puerto Escondido, Baja California, Mexico.

Most Hydromedusae, including *A. macrodactyla* (Fig. 1A), alternate between a planktonic medusoid generation and a benthic hydroid. The medusae reproduce sexually by means of eggs and sperm to produce planula larvae. After a short time in the plankton, the planula larvae settle, metamorphose, and develop into hydroids. The hydroids complete the life cycle by asexually budding free-swimming juvenile medusae (Hyman, 1940).

This study shows that *A. macrodactyla* also reproduces asexually by a method we term direct fission (Fig. 1A–E). Direct fission does not resemble budding and, unlike schizogony, is not dependent upon the formation of multiple stomachs. *In situ* observations and photographic examinations of 27 individual medusae during some stage of direct fission have enabled us to describe this reproductive method (Fig. 1). The initiation of direct fission begins with the inward invagination of the medusa's umbrellar margin (Fig. 1B). This marginal invagination draws opposing margins together toward the center of the medusa (Fig. 1C–E). Partial severing and separation of the umbrellar margin, exumbrellar surface, velum, ring canal, and stomach wall tissue occurs as a result of invagination (Fig. 1C and D). Synchronous and asynchronous swimming contractions observed in bilobed medusae may aid in the mechanical separation of invaginated marginal tissues. We observed asynchronous swimming contractions only after direct fission was well progressed. Invagination is completed once opposing marginal structures contact one another toward the center of the medusa. Severed tissues of the opposing lateral margins begin to heal at this time (Fig. 1D and E). Close examination of photographic records indicate final separation occurs along the aboral exumbrellar surface (Fig. 1E). Direct fission does not appear to prohibit *A. macrodactyla* from feeding. Marginal and oral tentacles were extended during the fission sequence. Dividing animals were often observed with ctenophore and crustacean prey at various stages of capture and digestion.

The entire direct fission process could not be observed *in situ* through time. Determinations of natural rates of direct fission were therefore impossible. Estimates of the duration of direct fission may be possible only by observing dividing individuals through time under culture conditions, which have yet to be accom-

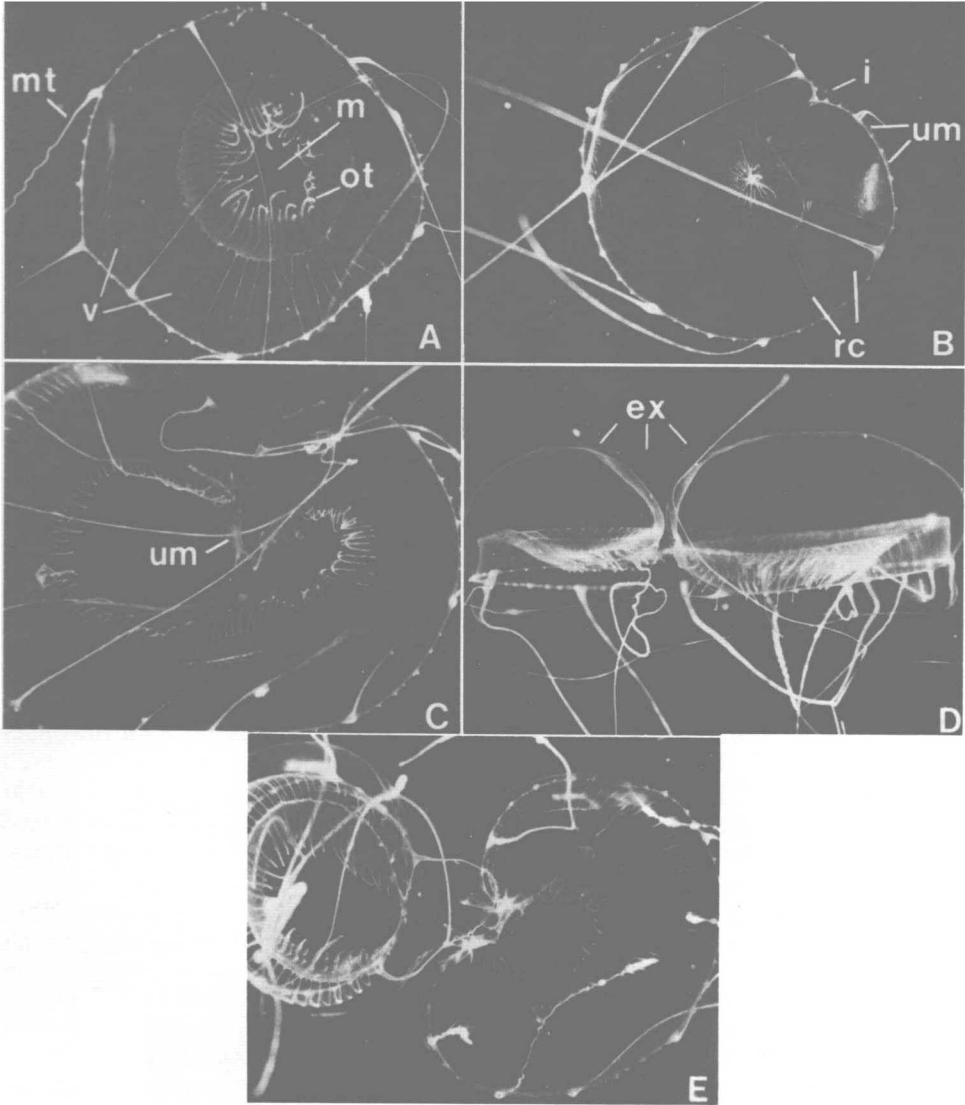


Figure 1. Direct fission sequence depicting various stages of division in several individual *Aequorea macrodactyla* medusae. (A) Oral view showing a non-dividing medusa with marginal fishing tentacles (mt) deployed. Bell diameter equals 2.6 cm. (B) Initiation of invagination (i). Bell diameter equals 2.9 cm. (C, D, and E) Progression of direct fission: Oral (C) and marginal (D) views illustrate the severing of umbrellar margin (um) and the separation of exumbrellar halves. Bell diameter for both (C) and (D) equals 4.8 cm across long axis. (E) Exumbrellar surface beginning to pull apart producing free-swimming daughter medusae. Healing is nearly complete in the smaller daughter medusa on the left. Bell diameters for the small (left) and large daughter medusae are 2.5 and 3.2 cm, respectively. Additional abbreviations: (mt), mouth; (ot), oral tentacle; (rc), radial canals; (v), velum; (ex), exumbrellar surface.

plished for *A. macrodactyla*. The frequency of direct fission was often quite high, with up to 100% of the observed population at some stage of division during any particular research dive. Population densities ranged from 1–5 animals per 10 m³. It is not surprising that this reproductive method has not been previously de-

scribed. Standard net sampling methods would undoubtedly damage these fragile gelatinous zooplankters (Hamner et al., 1975) and likely destroy any evidence of the medusa's reproductive condition. With the development of specialized SCUBA techniques (Hamner, 1975) it is now possible to directly observe this and other oceanic biological phenomena. We suggest that direct fission may well be a common asexual reproductive method.

Awareness of direct fission as a reproductive method leads to a better understanding of the causes of taxonomic and distributional problems long associated with *Aequorea* (Russell, 1953; Kramp, 1961). Taxonomic descriptions of 14 species of *Aequorea* (Kramp, 1961) are based primarily upon morphometric analysis of the animal's overall size, including the relative number of various anatomical structures (Russell, 1953; Kramp, 1961). Depending on the symmetry of fission, direct fission ultimately reduces the size and/or number of the daughter medusa's anatomical structures by 15–85% of that of the adult's. According to Mayer (1910), *A. macrodactyla* should have between 60–150 radial canals. Of six adults examined, all possessed radial canals within this described range, but their progeny, produced by direct fission, possessed 18–130 radial canals. Of these 12 progeny, 7 possessed fewer than 60 radial canals. Direct fission is therefore responsible for some of the morphological variations observed within this genus. We propose that numerical measurements of morphological characters are not useful in taxonomic analyses among the many described species of *Aequorea*.

It is at present unclear what characters should be used to distinguish *A. macrodactyla* from other *Aequorea* medusae. Kramp (1968) cites the presence of abaxial keels and prominent excretory papillae on tentacle bulbs as being diagnostic characters of *A. macrodactyla*. Russell (personal communication) acknowledges the diagnostic character of these traits but concludes that the specimens identified from this study most closely resemble *A. macrodactyla* even though they lack the abaxial spur (i.e., keel) on tentacle bulbs. Russell (1953) states that the marginal tentacle bases (i.e., bulbs) may be considerably distorted if the medusae are not in a perfect state of preservation. Distortion of animals due to preservation may be another source of taxonomic confusion.

Sexual reproduction is held to be adaptive in unpredictable environments because of the variety of genotypes produced, thereby increasing the chances of some propagule survival under a variety of conditions (Williams, 1975). Physical dispersal mechanisms strongly influence the number of environments encountered by propagules of marine invertebrates which release their gametes into the water column. We support the idea that dispersal may increase the chances of some propagules finding suitable habitats. We suggest that the world-wide distribution of *Aequorea* may have been facilitated by dispersal of progeny produced by both sexual and asexual methods. We suspect that, under variable and unpredictable conditions, sexual reproduction by *A. macrodactyla* may be more advantageous. If favorable habitats are encountered by the planula larvae, the hydroid generation may colonize a new geographic area. It is important to note that dispersal of the medusa's sexually produced propagules is limited in duration to the short time the planulae spend in the plankton. Direct fission may be important as a wholly pelagic form of reproduction since survival of progeny is not temporally or spatially dependent upon the presence of suitable hard substrates.

Warner (1978) argues that asexual reproduction is the most efficient means of propagation in predictable environments. As he suggests, it is not unreasonable to expect organisms, which are capable of both asexual and sexual reproduction to continue reproducing asexually in predictably favorable environments. Progeny produced via direct fission are relatively large and undergo immediate de-

velopment, both of which should reduce the mortality of daughter medusae as compared with that experienced by smaller and slower developing sexual propagules. The survival of directly fissioned daughter medusae may be dependent upon their ability to capture and consume prey. Our observations indicate that these daughter medusae do capture and ingest prey during and after direct fission reproduction. One might therefore expect that these mature daughter medusae are increasing in density as a result of asexual direct fission. Such an increase in density of mature medusae should ultimately result in the production of more widely dispersed sexual propagules when sexual reproduction takes place. Careful demographic studies of dividing populations are necessary to determine if direct fission contributes to significant population growth. We conclude that the discovery of direct fission increases our understanding of the reproductive biology of *A. macrodactyla* and may account for the cosmopolitan distribution of *Aequorea*.

ACKNOWLEDGMENTS

We thank A. L. Alldredge for her continued support and comments; D. Davenport, H. Duncan, D. Morse, B. Robison, R. R. Seapy, R. K. Trench, R. R. Warner, A. M. Wenner, and three anonymous reviewers for their reviews and comments. We wish to express our appreciation to Sir Frederick Russell for his comments and for identifying the specimens. Research was supported by NSF grant #OCE76-23534 to A. L. Alldredge, and by the Marine Science Institute, University of California, Santa Barbara.

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DATE ACCEPTED: December 18, 1979.

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