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On the origins and evolution of hydromedusan life cycles (Cnidaria, Hydrozoa)

ABSTRACT

The planula, the hydroid and the medusa are the main developmental stages of hydromedusan life cycles. The planula is the free-living larva deriving from embryonic development, the hydroid is interpreted as a larval stage, whereas the sexually reproducing medusa represents the adult form. Several types of life cycle diverge from this succession of stages via suppression or modification of the various morphs. A general trend is towards the suppression of the medusa stage and the onset of sexuality in the hydroid stage which, therefore, becomes the adult by a progenetic process. The ecological, morphological and physiological implications of the diversification of hydromedusan life cycle patterns are discussed. Heterochrony is considered as a major agent in hydromedusan evolution.

Key words: Cnidaria, Hydrozoa, Life cycles, Plankton, Benthos, Ecology, Evolution, Sex, Heterochrony.

Introduction

Hydromedusan life cycles can be schematized by the succession of three main stages: planula, hydroid, and medusa. Such cycles are generally proposed as an example of «alternance of generations», or «metagenesis», in the Metazoa. These terms are, however, unfortunate because they have a different meaning in plants, where the alternating of generations is not just that of sexual and asexual stages, but also of haploid and diploid stages (see Bouillon, 1981).

Research on Cnidaria was, and in some cases still is, traditionally focused either on the polypoid or on the medusoid stage. In the Hydrozoa this led to separate classifications for hydroids and medusae and to the formation of specialists of just one of the TWO main stages (planulae being almost totally ignored in taxonomical studies). Such division of labour and experience, often with scant communication between the two approaches, caused also a fierce debate on what stage (polyp or medusa) is to be considered the ancestral stage for Cnidaria and Hydrozoa (see Bouillon, 1981; Stepanjants, 1988). At present the most widely accepted theory envisages a common tetramerous polypoid ancestor for all Cnidaria, with the early separation of two distinct lines regarded as subphyla: the Anthozozoa with the polypoid stage only, and the Medusozoa, comprising Scyphozoa, Cubozoa and Hydrozoa, in which the medusa (when present) is the sexually competent adult (see Werner, 1973; Petersen, 1979). From such a premise (the ancestral stage of the Cnidaria was polypoid) some authors (e.g., Cornelius, 1990) hypothesized that a polyp stage was the direct ancestor of all

Cnidarian classes, and thus also of Hydrozoa. However, no matter what was the form of the ancestral cnidarian, the Hydrozoa could have originated from other cnidarians (scyphozoans, cubozoans or other unknown forms) which already had a medusa stage and even lacked a polyp. Scyphozoa and Cubozoa, in fact, show a major development of the medusa stage, and in many species the polyp stage is totally absent or inconspicuous.

The stages of the hydromedusan life cycle

In most Hydrozoa, embryonic development originates a lecithotrophic planula larva. In some subclasses of hydromedusae retained as primitive (the hypogentic Narcomedusae and the Trachymedusae), the planula larva originates directly a medusa stage, but in all the other hydromedusae (the Narcomedusae with indirect development, Anthomedusae, Leptomedusae, Limnomedusae) the planula invariably originates a polyp which can form colonies via asexual reproduction (see Bouillon, 1985, for taxonomic definitions). The polyp produces medusae which are liberated and become sexually mature. The cycle is closed by the production of zygotes (which will develop into planulae) as a result of sexual reproduction. The medusa, being the sexually reproductive stage, represents the adult form by definition. The planula represents a larval form deriving from gastrulation processes, but it is more problematic to define the polyp stage with the available zoological terms.

A possible answer could be suggested by recent studies on the life cycles of such animals. Bouillon *et al.* (1991) found that in Papua-New Guinea the leptomedusa *Laodicea indica* has a cycle with both hydroid and medusa stages in the wet season (when the water is rich in nutrients and turbid), whereas in the dry season (when the water is poor in nutrients and clear) the hydroid stage is abolished and each planula larva immediately originates a medusa from an independent sessile gonotheca, not connected to a hydroid colony (Fig. 1).

Medusae are typically seasonal organisms and should spend the adverse season with some sort of resting stages. The presence of resting stages in the Hydrozoa, and in all other marine invertebrates, is still poorly studied but seems to be more common than previously thought (see Bouillon, 1975, for a list of hydromedusae with a resting stage in the life cycle). The alternated cycle of *Laodicea indica* suggests that the hydroid could have originated by developmental conversion at the planula stage, with the formation of a benthic morph which, being able to undergo asexual reproduction, produced a great number of adults (medusae) from a single larva (planula). In this framework, the polyp stage represents a second larval morph in the cycle of hydromedusae. Instead of metamorphosing directly into a medusa (as in the Cubozoa) or strobilating many medusae (as in the Scyphozoa), the hydroid larva produces medusae by budding, retaining its anatomical features and having a long independent life, usually lasting much more than that of adults.

Also other groups, such as trematodes (Rees, 1966), have life cycles with several larval stages which undergo asexual reproduction before giving rise to sexually mature adults. The cycles of such animals are usually not regarded as metagenetic. As already pointed out by Bouillon (1981) and Kaufman (1988), the

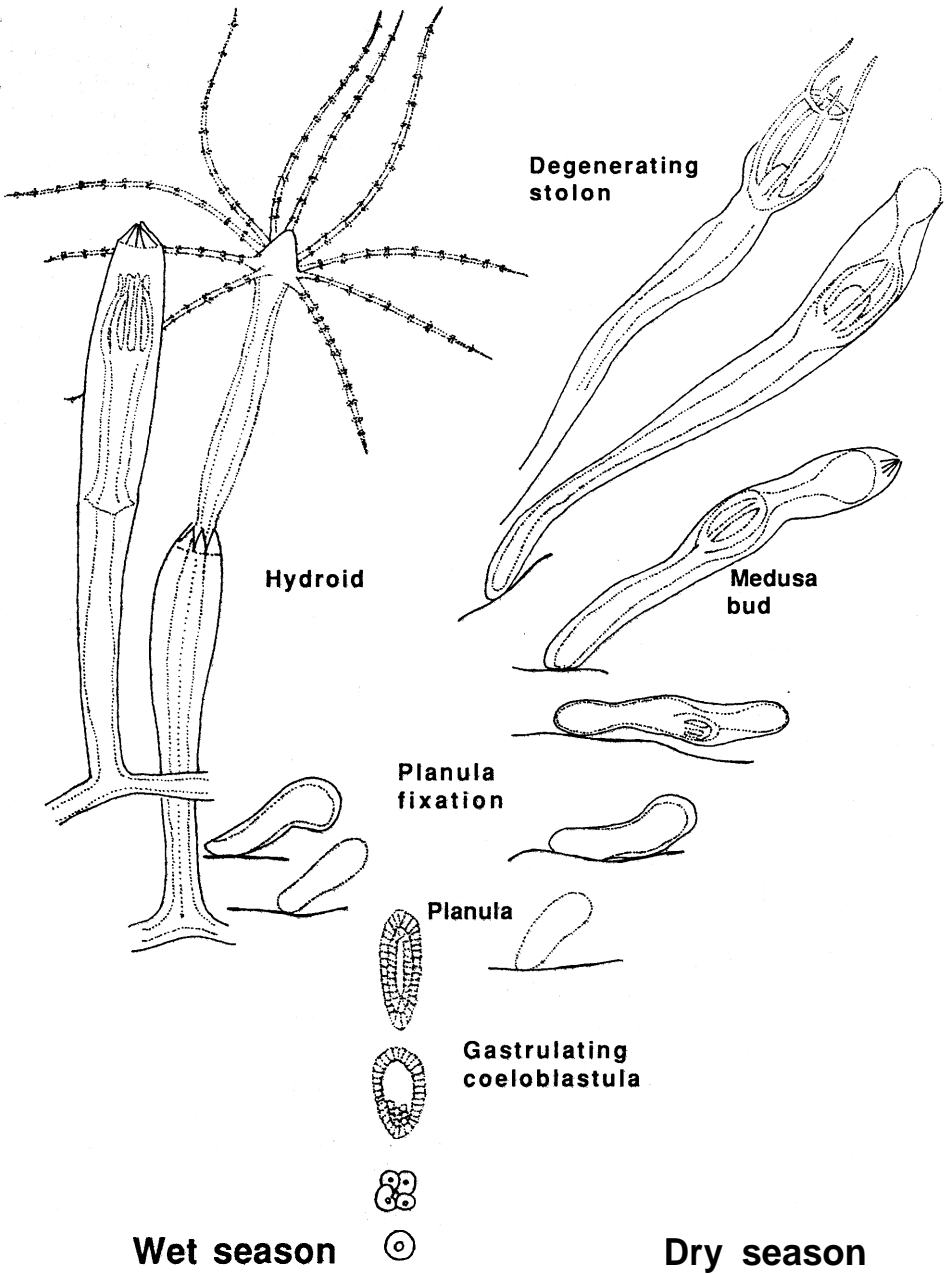


Fig. 1 - Life cycle patterns in *Laodicea indica* from the Bismarck Sea. During the wet season planula development produces a hydroid colony which eventually will produce medusae; during the dry season the planula produces a gonotheca which will degenerate after producing a single medusa. After Bouillon *et al.* (1991).

cycle of hydromedusae could be reasonably considered as analogous to that of other meroplanktonic invertebrates with indirect development, being understood as a continuous process going from the egg to the adult sexual generation: the medusa. This cycle is ecologically peculiar because the planktonic adult, via sexual reproduction, originates a planktonic larva (the planula) which gives rise to another larval stage (the hydroid) which is almost invariably sessile.

Edwards (1973) interpreted such cycle patterns as adaptations to seasonal environments: the acquisition of a long-lived stage allowing the survival of the species during periods unfavourable for the medusa. The hydroid colony, in fact, can produce new polyps for a long time and can also become a resting stage, as quiescent hydrorhiza, when the environmental conditions are not favourable (Calder, 1990; Petersen, 1990).

The hydroid stage could thus have evolved from the activation, via asexual reproduction, of a resting stage which became able to acquire resources from the environment, and to retain them in an organized form also after the production of sexual morphs. Such multiplication of the hydroid stage resulted in the production of a great number of medusae from a single fertilized egg. Furthermore, species with short-lived adults, most frequently dying after spawning, can become pluriannual with the asexually reproducing stage (Fig. 2). The adaptive value of this «new» type of life cycle and, above all, of the presence of a hydroid stage led to reduction and even suppression of the adult stage, the medusa, by progenetic processes (Kubota, 1984; Boero & Sarà, 1987; Boero & Bouillon, 1987; Boero & Bouillon, 1989). The hydroid, in these contracted cycles, is not a larval or postlarval stage but becomes the adult by acceleration in the onset of sexual reproduction.

Thus the adult role can be played by the medusa or by the hydroid according to the degree of contraction of the life cycle due to paedomorphic processes.

The variations of life cycle patterns in hydromedusae have been schematized by Boero & Bouillon (in press) as follows (Fig. 3):

- 1 - Medusa - Planula - Medusa.
- 2 - Medusa - Planula - Benthic hydroid - Medusa.
- 3 - Liberable eumedusoid of swimming gonophore - Planula - Benthic hydroid - Liberable eumedusoid or swimming gonophore.
- 4 - Benthic hydroid - Planula - Benthic hydroid.
- 5 - Medusa - Planula - Planktonic hydroid - Medusa.

In some cases, for instance that of some tubulariids, the planula stage is not liberated, but develops inside the gonophores, becoming a juvenile hydroid, the actinula.

The presence of a long-lived planktonic stage is often considered important for dispersal and, therefore, for the attainment of a wide distribution, but this is not confirmed by studies on similar organisms with different life cycle patterns. Boero & Bouillon (in press) could not detect differences in the world distribution of Mediterranean hydromedusan species with sharply differing cycles. Equal numbers of endemic Mediterranean species have or have not a medusa stage; furthermore, many species deprived of the medusa stage are cosmopolitan and many species with medusa have a restricted distribution.

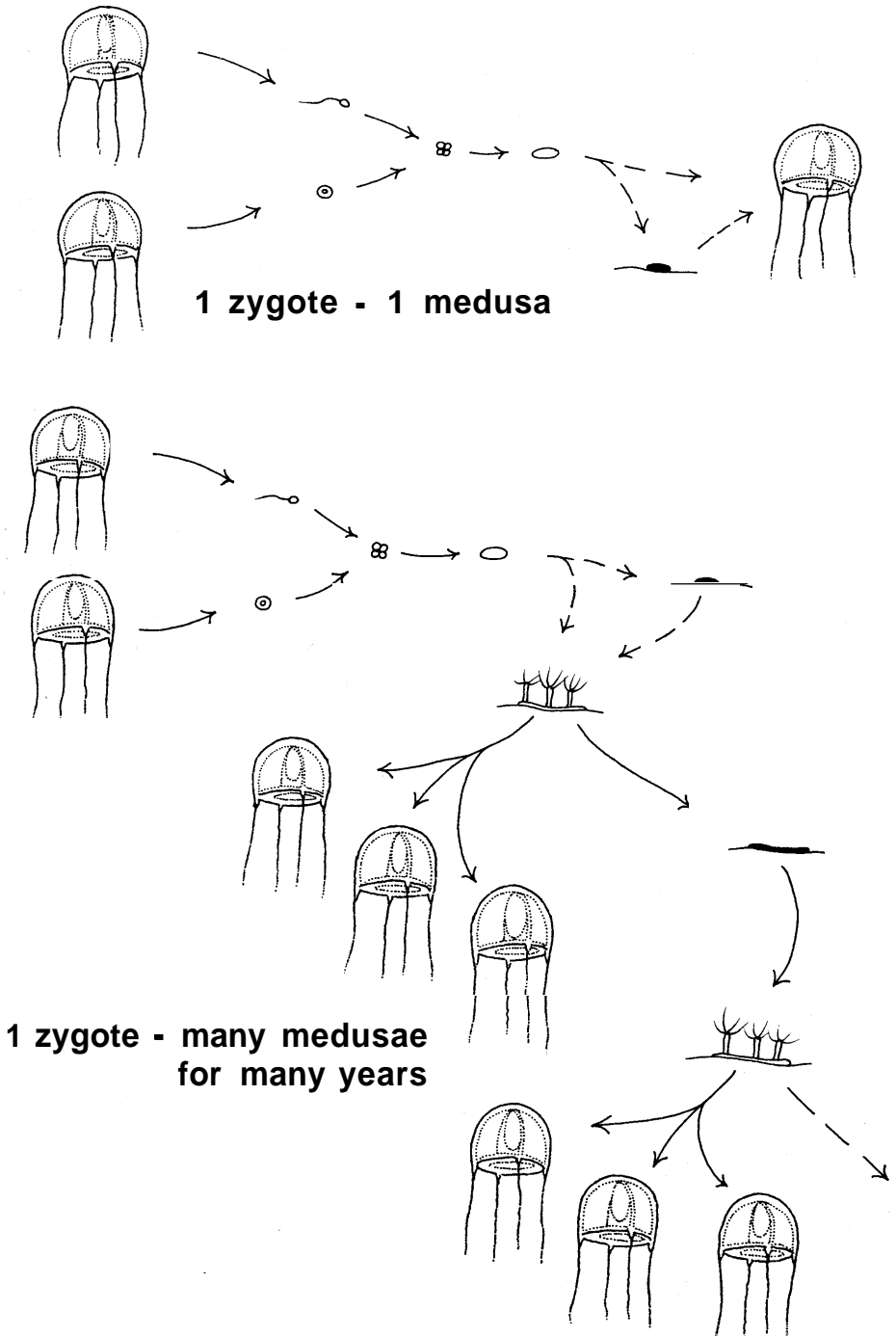


Fig. 2 - Above: life cycle pattern of hydromedusae with no hydroid stage. Below: life cycle pattern of hydromedusae with hydroid stage.

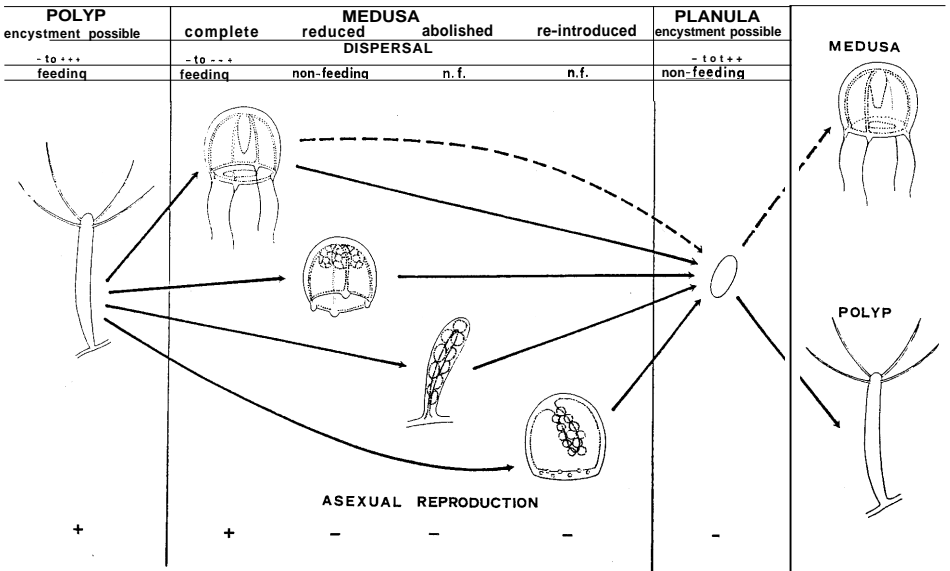


Fig. 3 - Life patterns of hydromedusae, with dispersal possibilities (from - to + + +), presence (+) or absence (-) of asexual reproduction, and trophic role of the various stages. Broken arrows: direct development, with no hydroid stage; solid arrows: indirect development, with hydroid stage (After Boero & Bouillon, in press).

Possible causes for medusa reduction

Hydromedusae probably show the widest variety of life cycle patterns among marine invertebrates. The degree of expression of the medusa stage is the main source of variation. Most hydromedusan species have a suppressed medusa stage and the hydroid is the sexually reproductive adult. A possible explanation for the reduction of the planktonic adult, as already mentioned, could be searched for in the different ecological roles respectively played by hydroids and medusae (Table I).

TABLE I - Main ecological and functional differences between hydroid and medusa stages.

Feature	Medusa	Hydroid
Life span	Short	Long
Environment	Planktonic	Benthic
Trophic position	Near apex of food chains	Many intermediate positions
Feeding type	Carnivore	Carnivore (DOM, symbiosis, photosynthesis)
Niche differentiation	Low	High
Interspecific competition	High	Low
Morphological diversification	Low	High

Medusae are voracious predators which could be placed near the apex of planktonic food chains, so that their massive predatory activity can even become the main agent of mortality for commercially exploited organisms such as herring (e.g. Purcell & Grover, 1990). The planktonic environment is relatively homogeneous from a spatial point of view, and the available resources are mostly fluctuating so that predators likely compete directly for limited resources. It is reasonable to predict that the maximum number of medusan species in a given environment, cannot be high and that the species heavily interact for the acquisition of trophic resources. The situation is radically different in hard bottom benthic habitats where the polypoid stage of hydromedusae shows the highest diversity and where animals with the average size of hydroids (from a few millimetres to a few centimetres) can specialize for the colonization of an unlimited number of microhabitats. In other words, the fractal dimension (Sugihara & May, 1990) of planktonic environments is much lower than that of hard bottom benthic environments. Hydroids, furthermore, utilize relatively stable and unlimited resources. Several species, for instance, are photosynthetic due to the presence of zooxanthellae, and have a theoretically unlimited energy supply. Epibiosis, commensalism, mutualism and even parasitism are widespread in hydroids and free most of them from the competition for the substratum, the only limited resource in hard bottom benthic environments.

The postulated limits for the coexistence of medusan species might account for a low speciation rate in the planktonic habitat, whilst benthic hydroids could evolve more rapidly because of a wider microhabitat variety. Thus, the presence of a medusa stage in the cycle might represent a constraint for the diversification of the hydroid stage. The species with reduced or suppressed medusa should be favoured, being free from the conditioning of food availability and competition in the pelagic environment.

This hypothesis is further supported by the fact that medusae exhibit a higher morphological homogeneity compared to polyps, as if the medusoid body plan were subjected to such strict morpho-functional constraints to be scarcely modified in the various taxa. On the contrary, modularity and division of labour in the colony, with the evolution of polymorphism, led to an astonishing diversity of body plans in the hydroid stage.

Besides the adaptative and environmental pressures which could explain the ultimate causes for the suppression of the free medusa stage from the hydromedusan life cycle, we have also to take into account some proximate causes (structural and physiological) for this pattern.

The degree of expression of the medusa stage, in fact, is directly linked to the timing of gamete production. The differentiation of sex cells is discontinuous and late in the cycle in species with long-lived medusae. The germ cells appear in medusae only long after their liberation from the hydroid colony. On the contrary, in species with fixed gonophores or with short-lived medusae (e.g., *Podocoryne carnea*) the sexual elements are formed precociously, often before gonophore appearance, and sex cells differentiation is continuous. In these animals, the germ cells differentiate in the ectoderm of the hydroid colony, often far from the zone where gonophores will be produced. They frequently migrate in the endoderm, where they seem to find particularly favourable physiological conditions. Later in

the cycle the germ cells will migrate to the differentiating gonophoral bud, where they will attain the last stage of development (for careful descriptions of such patterns see Weismann, 1883; Goette, 1907; Kuhn, 1910; Brien, 1942, 1962; Mergner, 1957; Glatzer, 1971). In these last cases, free medusae never form and the type of fixed gonophores (styloïd, heteromedusoid, cryptomedusoid, eumedusoid) depends on the level of differentiation of the medusa bud at the time of gonocyte migration and maturation. This suggests that the early appearance of sex cells in the hydroid colony somehow prevents the formation of the free medusan generation: the medusa buds never reach their complete development, never attain their complete genetic expression, remaining part of the colony as fixed gonophores, being reduced to structures with the function of gonads.

Conclusion

The polyp stage was possibly introduced in the cycle of hydrozoans by early alternative activation of resting stages which, via asexual reproduction, might have produced a great number of medusae at the onset of the following favourable season. The presence of both polyps and medusae in the life cycle caused a sharp differentiation in the outcome of evolution in the various species (see Boero & Bouillon, 1987; Boero & Sarà, 1987; Cornelius, 1990; Petersen, 1990, for recent discussions), and the «new» asexual stage often became the sexually mature adult. In the hydromedusae, heterochrony by progenesis is perhaps the main factor which allowed the wide adaptive radiation of the hydroid stage.

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