

D. De Vito · S. Piraino · J. Schmich
J. Bouillon · F. Boero

Evidence of reverse development in Leptomedusae (Cnidaria, Hydrozoa): the case of *Laodicea undulata* (Forbes and Goodsir 1851)

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Abstract Laboratory rearing and reconstruction of *Laodicea undulata* (Hydrozoa) life cycle led to the discovery for the first time in Leptomedusae of the potential for ontogeny reversal, i.e. the medusa stage can asexually transform back into the polyp stage. In turn, each rejuvenated polyp stage can newly activate the standard developmental programme towards colony morphogenesis and budding of secondary medusae. These can be considered as clonemates of the initial medusa batch, since they originate by asexual processes. In combination with the ordinary medusa budding process, the potential for reverse development might represent a tool to increase jellyfish population growth rate during the favourable season, but eventually it does not avoid jellyfish to die. Comparably to polyembryony, reverse development leads to offspring multiplication from a single fertilization event, with a wider dispersal of each single genotype; eventually, it favours the enhancement of the overall genetic diversity at small spatial scale. The life cycle of *L. undulata* from the Mediterranean Sea is re-described, linking previously uncoupled descriptions of either the polyp or the early medusa stages. Taxonomic considerations of the genus *Laodicea* and a comparison among the known Mediterranean species are also provided.

Introduction

Cnidaria exhibit a unique feature among the animal kingdom: the potential for reverting the common ontogenetic direction, which leads a fertilized egg to become

an adult organism. Many cnidarians, indeed, can revert the life cycles with substantial morph rejuvenation (see Piraino et al. 2004 for a review of cases).

Reverse development in Cnidaria is known since Hadzi (1909) first described back-transformation of scyphozoan ephyrae to scyphistoma polyps under unfavourable environmental conditions. In Hydrozoa, a few species are known to undergo reverse transformation when early medusa buds are artificially detached from budding polyps (see references in Piraino et al. 2004). The complete differentiation of medusa structures was long considered to become a major barrier to morph reversal, since most species could not transform back to the corresponding polyp stages after liberation of medusae from the polyp colonies. Nonetheless, Piraino et al. (1996) described a thorough ontogeny reversal from adult, sexually competent medusae back to the polyp stage in the Mediterranean anthomedusa *Turritopsis dohrnii* (not *T. nutricula*; see Schuchert 2004 for a revision of the genus).

Here we report the discovery of full potential for reverse development or morph reversal in another hydrozoan species, *Laodicea undulata* (Forbes and Goodsir 1851). In addition, laboratory reconstruction of the life cycle allowed to link previous uncoupled descriptions of either the hydroid (Hincks 1868; Russell 1936) or the medusa stage (Forbes and Goodsir 1851; Russell 1953), providing new information on early medusa stages. A synopsis on the Mediterranean species of *Laodicea* is also provided.

Materials and methods

Sampling has been carried out from July to November 2000 at several localities around the Salento peninsula, Italy (Torre del Serpe, Otranto, South Adriatic Sea; and Torre Inserraglio, Nardò, Ionian Sea) at sub-surface depth levels (from -3 to -15 m). SCUBA divers were scraping off the rocky substrate together with the overgrowing benthic organisms (e.g. seaweeds, sponges,

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D. De Vito · S. Piraino (✉) · J. Schmich · J. Bouillon · F. Boero
Dipartimento di Scienze e Tecnologie Biologiche ed Ambientali,
Università di Lecce, via per Monteroni, 73100 Lecce, Italy
E-mail: stefano.piraino@unile.it
Tel.: +39-0832-298616
Fax: +39-0832-298616

anthozoans, bryozoans). Samples were brought back to the laboratory, where all living hydroid colonies were identified under the stereomicroscope and separately transferred to small trays (200–1,000 ml volume) containing 0.45- μm filtered seawater ($S=38$ ppm). The animals were kept at a RT=24°C, with a 12:12 h light–dark cycle. Water movement and oxygen saturation were achieved by gentle air bubbling. Medusae were also reared on trays placed on a rocking platform, mimicking fine water movement. Hydroid colonies and liberated medusae were fed twice a week with *Brachionus* sp. rotifers and *Artemia salina* nauplii. Two hours after each feeding session, animals were placed into freshly filtered natural seawater. Cnidocyst measurements were made at light microscope at 1,000 \times magnification. Ranges of values of length and width were obtained from replicate measurements of 20 different capsules of each type.

Results

Polyp stage

Small campanuliniid of *Cuspidella* type, creeping colonies (Fig. 1a) were often found on the underneath side of *Peyssonnelia* spp. rhodophytes, from –3 to –15 m depth. Small cylindrical, straight hydrothecae (600–750 μm height; Fig. 1b–d) arise directly from stolons without definite peduncle, sometimes with a basal slight constriction (Fig. 1c, d); some thecae may have a few growth rings. A multi-valve operculum with 12–16 triangular flaps originates from the upper hydrothecal margin, demarcated by a crease line (Fig. 1c, d). The hydranth is long, extending twice the length of the hydrotheca (Fig. 1b); with 8–14 amphicoronate, narrow tentacles encircling a tall, conical hypostome (Fig. 1b). The cnidome is composed by isorhizae of two sizes: large holotrichous isorhizae (14–16 μm length; 5–6 μm width)

and small basitrichous isorhizae (8–10 μm length; 3–4 μm width).

Colonies with gonothecae were reared in the laboratory until the liberation of the medusae. The gonotheca is similar to hydrotheca in shape, but about twice as long, with a tapered basal constriction and multi-valve operculum (Fig. 1e, f), without visible growth rings. It includes 3–5 medusa buds at differing stages. Late stages are held externally (Fig. 1g–i) for 12–24 h before final release (Fig. 1i).

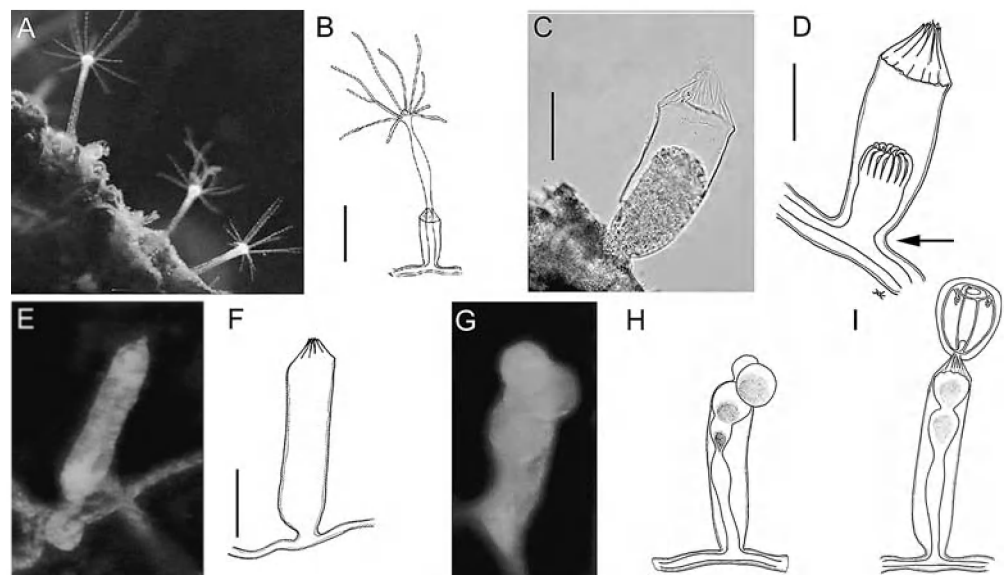
Medusa stage

Liberation of medusae was observed in the laboratory from polyp colonies collected from August to early November.

The smallest medusa specimens (bell diameter \approx 700–800 μm) were liberated in autumn, small bell-shaped umbrella (diameter \leq 1 mm) with four tentacular bulbs, but only two tentacles, and no ocelli (Fig. 2a, b). After 10–11 days, they developed two additional tentacles and 1–2 spiral cirri on each inter-tentacular quadrant along the bell margin. In August, newly born medusae had already four marginal tentacles (Fig. 2c, d), four simple radial canals (Fig. 2e, arrow indicates a cordylus in formation), a small cylindrical manubrium (Fig. 2f), four tentacular bulbs each with two basal spurs and one adaxial ocellus (Fig. 2c, d, h). Spiral cirri (1–2) can be present between every two tentacles (Fig. 2c). The apex of cirri terminates with a large nematophore knob bearing a clump of 9–10 large holotrichous isorhiza cnidocysts (23–25 μm length; 5–6 μm width) (Fig. 2i, k). The development of cordyli, a distinctive feature of the family Laodiceidae, started only after the formation of cirri (Fig. 2i).

Almost all specimens died within 2 weeks from liberation, without sign of gonad development.

Fig. 1 The polyp stage of *Laodicea undulata*. **a, b** Extended polyps showing a single amphicoronate ring of tentacles; **c, d** typical campanuliniid hydrotheca, with a multi-valve operculum and a slight basal constriction (**d**, arrow); **e, f** elongated gonothecae of *L. undulata* with multi-valve operculum; **g–i** developing medusa buds. Late medusa buds are held outside the gonotheca (**h, i**). Scale bars: **b**, 600 μm ; **c, d** 250 μm ; **f**, 500 μm (**g–i**, same magnification as **f**)



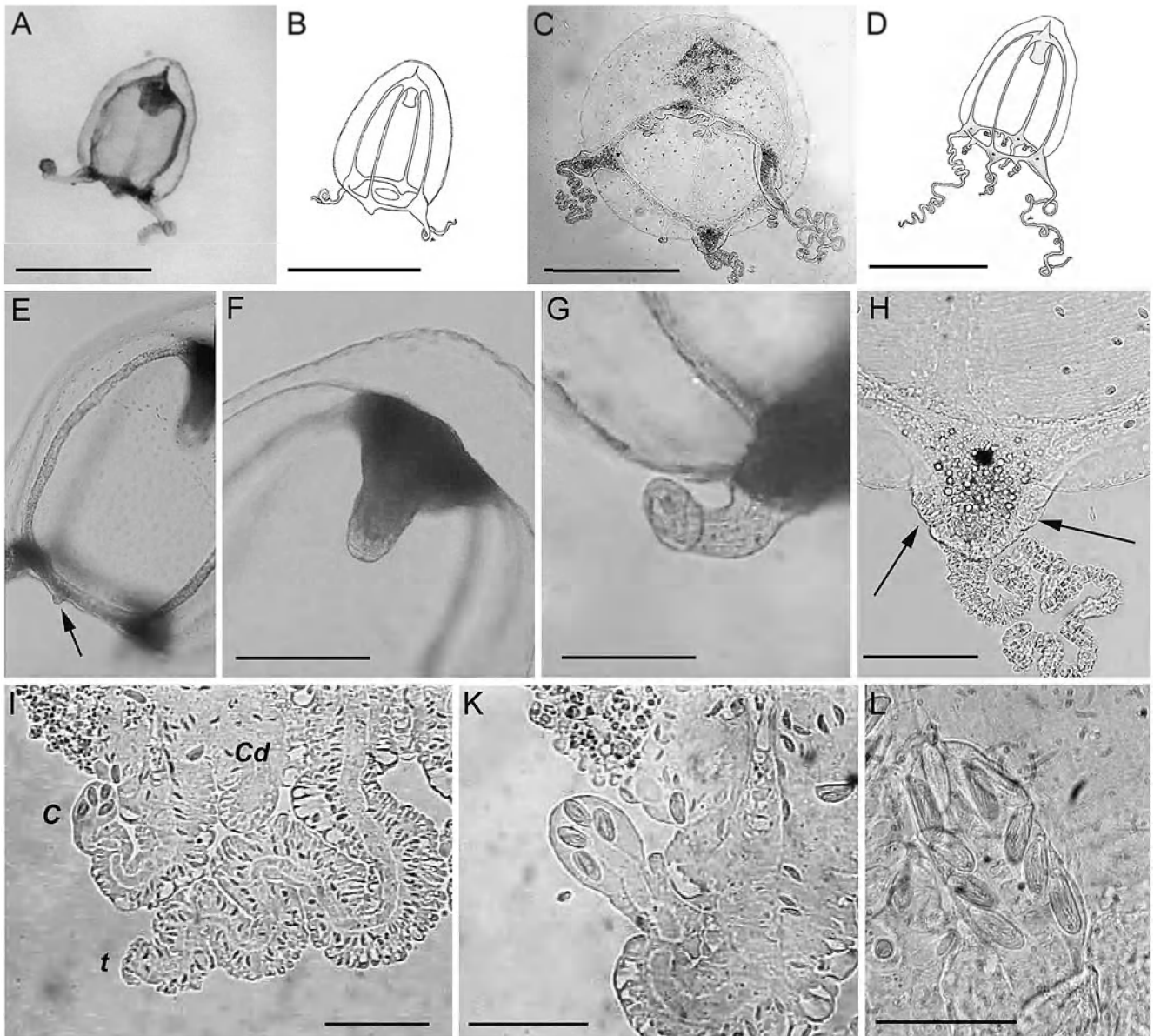


Fig. 2 Medusae of *L. undulata*: at liberation in autumn (a, b) or in summer (c, d). Abbreviations in i: C cyrrhus, Cd cordylus, t tentacle. See text for details on structures. Scale bars: a–d, 1 mm; f–h, 250 μm; i, 150 μm; k, 75 μm; l, 50 μm

The potential for reverse development

Twelve out of 13 *L. undulata* medusa specimens underwent a generalized deterioration (starting from the ectodermal cells) 10–14 days after liberation and died. Surprisingly, a small, two-tentacled specimen did not degenerate. Instead, its mesoglea thinned and tentacles shortened. It soon became unable to swim and settled down to the bottom of the culture vessel. The morphology of the umbrella was lost completely within few hours, and it transformed into a cyst-like rounded mass of cells (Fig. 3a). A chitinous perisarc lined up the remnant and three buds appeared (Fig. 3b). Shortly after, these buds developed into hydrorhizal stolons,

which elongated on the glass surface within 24–36 h from the initiation of the transformation (Fig. 3c). Three days later, the first polyp bud appeared on one stolon (Fig. 3d), followed by additional polyp budding (Fig. 3e–g) in the next days. One week later, six feeding polyps were fully developed (Fig. 3h). Within a month, a new gonotheca with three medusa buds was formed. Three new “reformed” medusae were liberated within 3 days. Before liberation, they remained attached as developing buds (with two tentacles, folded inwards the umbrellar cavity) on the outside of the gonotheca (Fig. 3e) for 12–24 h. The fate (and the potential for reverse development) of these reformed medusae was not followed.

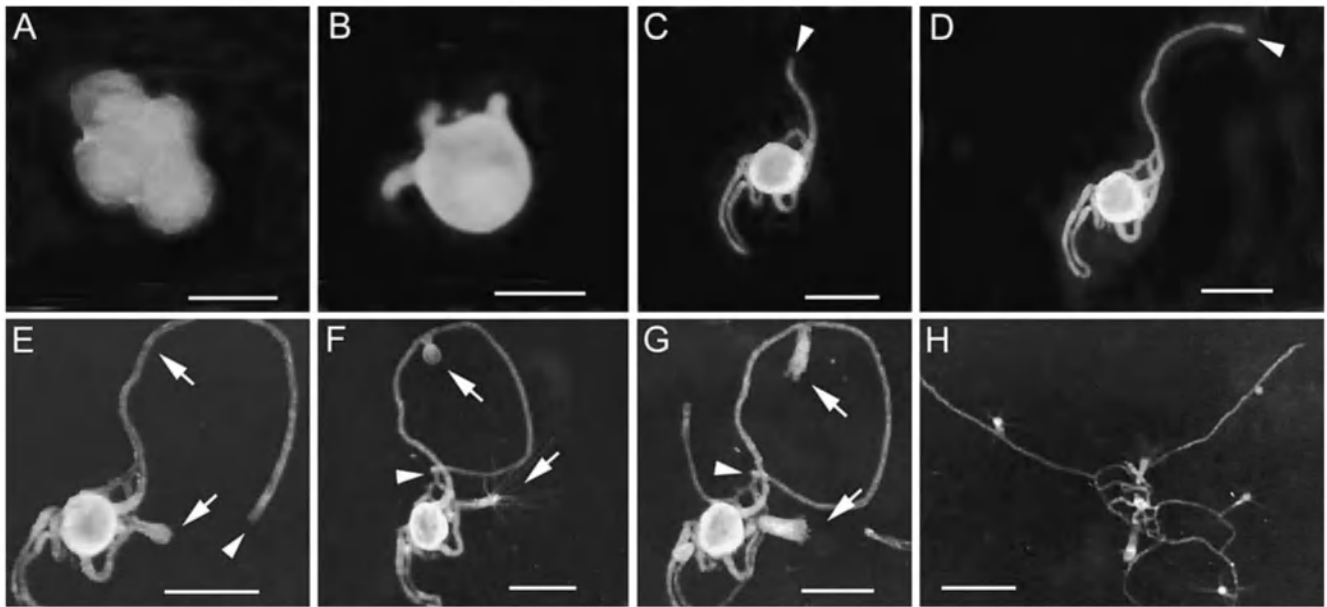


Fig. 3 The reverse development of *L. undulata*. The transforming medusa soon acquires a cyst-like morphology (**a, b**); hydrorhizal polyp stolons appear after 24–36 h (**c, d**). *White triangles* point the

tip of growing stolons, *white arrows* indicate polyp buds (**d–g**). Within a week, a colony with six polyps is formed (**h**). *Scale bars*: **a, b**, 500 μ m; **c–g**, 1 mm; **h**, 2 mm

Discussion

Systematics

Laodicea undulata colonies can be common within the sub-littoral hydroid assemblages along the Salento peninsula, but the small-sized hydrothecae are not easily seen since they usually live in cryptic habitats (e.g. the underneath sides of *Peyssonnelia* spp. algae). With reference to the hydranth morphology, *L. undulata* belongs to the Leptomedusae, order Conica, whose hydranths share a conical or rounded-conical hypostome. A detailed description of polyp and adult medusa stages of *L. undulata* is given by Cornelius (1995).

The early development of *L. undulata* (Forbes and Goodsir 1851) has been described by Metschnikoff (1886, as *Laodicea cruciata*) and leads to the formation of a short-lived planula larva. Russell (1936) gave the first description of *L. undulata* polyps and colony morphology. His specimens developed from planula larvae kept in the laboratory. The presence of an operculum with four or more valves and sessile hydrothecae link this species to a more generalized “campanulinid-type” taxon, grouping together several unrelated medusa-based families with “*Cuspidella*-like” colonies (Campanulinidae, in part; Cirrholovenellidae; Dipleurosomatidae; Laodiceidae; Mitrocomidae; Tiaropsidae) (Bouillon and Boero 2000). This is one of the best cases of inconsistency of the evolutionary rate between polyp and medusa morphology. As a consequence, identification at specific level of *Cuspidella*-like hydroid colonies needs observation of characters of the medusa stage.

The lack of periradial pouches in all medusa specimens reared so far led to ascribe them to the genus *Laodicea*. In the framework of a revision of the world hydrozoan fauna (Bouillon et al., in preparation), 12 species of *Laodicea* have been recently listed. Only three of them, namely *L. fijiana*, *L. ocellata* and *L. undulata*, have been recorded from the Mediterranean Sea (Bouillon et al. 2004). The features of their medusa stage have been compared here (Table 1). *L. undulata* is by far the most common *Laodicea* species in the Mediterranean Sea, and possibly is the only valid species. In fact, the real occurrence of *L. fijiana* (Agassiz and Mayer 1899) in the Mediterranean Sea is questioned, and doubts about the validity of *L. ocellata* (Babnik 1948) are still unsolved.

L. fijiana was described from the Pacific, but it was recorded only once (Schmidt 1973) in the Mediterranean, as a single specimen collected offshore the Egyptian coast. In this specimen, the only valuable difference from *L. undulata* was the absence of cirri, but in fixed specimens of *L. undulata* cirri can usually disappear due to strong fixation. Moreover, there are no records of *L. fijiana* in the well-studied Indian Ocean. Thus, there are still few arguments to consider *L. fijiana* as a valid example of Lessepsian migrant in the Mediterranean Sea.

Besides mere citations, there is no other re-description of *L. ocellata* (i.e. with several big ocelli) after the first record (Babnik 1948). Contrarily to Kramp’s wrong interpretation (1959), cordyli (a distinctive feature for Laodiceidae) were present in Babnik’s original description and drawings of *L. ocellata*. However, it is not known how many specimens Babnik observed, if and

Table 1 Comparison of the main features among *Laodicea* medusae known from the Mediterranean Sea

	<i>L. undulata</i> (Forbes and Goodsir 1851)	<i>L. fijiana</i> (Agassiz and Mayer 1899)	<i>L. ocellata</i> (Babnik 1948)
Bell shape	Hemispheric or flat	Spherical	Spherical
Width	Up to 50 mm	6 mm	2–3.5 mm
Velum	Broad	Narrow	Narrow
Mouth lips	Wrinkled	Not wrinkled	Not wrinkled
Marginal tentacles/bulbs	200–300 or more, with slight bulbs and basal spurs	About 70, without basal spurs	7–14, without basal spurs. 10–18 intertentacular (non-tentacled) bulbs
Marginal cirri	Spiral, 1–2 between adjacent tentacles. Sometimes absent	Absent	Twice the number of tentacles
Cordylia	Usually one between adjacent tentacles, without nematocysts	Very few (up to eight)	Usually one between adjacent tentacles, without nematocysts
Ocelli	Small, adaxial on some tentacle bulbs, variable in number	Small, adaxial on some tentacle bulbs, variable in number	Big, black ocelli at all tentacular and intertentacular bulbs
Gonads	Friiled and developing in cylindrical pouches from the manubrium downwards, along almost the entire length of radial canals	On complex, lateral diverticula (pouches) along the proximal half of radial canals	Club shaped along half or 2/3 of radial canals. Proximally narrow, distally enlarging, not hanging in the subumbrellar cavity
Seasonality	Spring–summer (maximum abundance in late summer)	November (one record, Eastern Mediterranean Sea)	Spring–summer

where the type specimens were deposited. If new observations will confirm the original description (and, consequently, the validity of the species), then the size and frequency of ocelli might be regarded as an additional discriminatory tool between adult specimens of *L. ocellata* and *L. undulata* (see Table 1).

From the above considerations and the comparison of stage-specific medusa features (Table 1), our specimens can be referred to *L. undulata* (Forbes and Goodsir 1851), because of (a) the presence of basal spurs lateral to the tentacular bulbs (Fig. 2c), (b) the small size of adaxial ocelli (Fig. 2h) and (c) the occurrence of spiral cirri (Fig. 2i).

Russell (1936) reproduced the original descriptions (with drawings) of polyps, gonotheca and newly liberated medusa of *L. undulata* made in 1906 by M.J. Delap (cited in Browne 1907), but never published before. Delap's description of newly liberated medusa fits to the two-tentacle medusa we observed in November (Fig. 2b). Her description confirms our present observation that the two-tentacle stage may not have sense organs. Instead, we observed ocelli in the four-tentacle stage. The presence of ocelli is a typical feature of fully grown *L. undulata* medusae, but their number is a variable character. Russell (1953) reported that they can be very few, compared to tentacle numbers, or they can be on nearly every alternate marginal tentacle. Development of ocelli can be delayed during medusa development and, therefore, this feature is not helpful when attempting identification of early medusa stages of *L. undulata*.

The appearance of four-tentacled versus two-tentacled medusae can be read in several ways. First, it might be interpreted as an example of phenotypical plasticity, a well-known event within the Hydrozoa group. It can be described as the ability for a species to produce differing sexual morphs according to the ecological situation. In the warm season, *Clytia* spp. colonies may liberate long-lived medusae, with slow growth rates, but reaching large final sizes, with higher tentacle numbers; in autumn, the same species can produce short-lived, smaller medusae with already mature gonads (Kramp 1927; Russell 1938; Boero and Sarà 1987). Other species, like *Orthopyxis integra*, are known to liberate swimming eumedusoids or to keep them within the gonothecae as cryptomedusoids (Agassiz 1860; Stefani 1959; Brinckmann-Voss 1970). This phenomenon was named allogony by Giard (1898). Berrill (1953) showed the influence of temperature on the fate of developing buds of *Sarsia tubulosa*. Medusa buds on polyps can develop, according to the water temperature, either in normal free medusae (with normal tentacles) or in sessile eumedusoids (with rudimentary tentacles, lacking mouth and ocelli). At low temperatures (6–8°C), medusa buds of *S. tubulosa* can even transform back into polyp buds (Werner 1963).

As a second hypothesis, it is possible that fewer quantities of available food may result in a slower development of medusa buds and ultimately, to small-

sized and less resistant planktonic stages. For instance, this is the case for *Eugymnanthea inquilina* medusoids liberated from symbiotic hydroids, living within the mantle cavity of bivalves. While hydroid colonies in mussels can exploit large feeding currents and allocate enough resources to fully develop gonads on medusoids, the feeding habit (and clearance rate) of infaunal bivalve species seems not to be a comparable resource input, leading to a smaller and sterile medusoids production of their inhabiting hydroids (Piraino et al. 1994).

Third, late stages of *L. undulata* medusa buds are normally held outside the gonothecae (Fig. 1h, i). This might facilitate the detachment of early stages and the release of two-tentacled medusae can be due to a premature detachment mechanically induced by strong water movement.

Fourth, the differences between summer and autumn medusae may be due to liberation from colonies belonging to different species. Indeed, *Cuspidella*-like hydrozoans are very similar in colony morphology (or almost identical) and mature medusae, whose morphology would allow more precise identification, were not obtained here. Nevertheless, the progressive development of cirri and cordyli is a distinctive feature of the family Laodiceidae (see Results) whereas the apparent lack of perradial pouches in the oldest medusae allows to identify the specimens as belonging to the genus *Laodicea* (see above).

Reverse development (RD)

Laboratory rearing of *L. undulata* medusae led to the discovery of their potential for life cycle reversal. Within the whole animal kingdom, this is the second species known to undergo rejuvenation from the liberated medusa back into the polyp stage. The same potential is known already in the anthomedusa *T. dohrnii* (as *T. nutricula*, Bavestrello et al. 1992; Piraino et al. 1996). Other medusozoans (reviewed by Piraino et al. 2004) have a lower potential for reverse development (e.g. *Chrysaora hysoscella*, whose early ephyrae can transform back into the scyphistoma stage), but none of them involves the reversion of the jellyfish stage to the polyp stage. The reverse development recorded in *Turritopsis* and *Laodicea* is to date exceptional, since it must involve the rearrangement of highly differentiated structures and cell types. Another hydrozoan, *Hydractinia (Podocoryne) carnea* has a powerful potential for reverse development, but it seems to be restricted only at the stage of young medusa buds (Frey 1968; Schmid 1972). Dissociation–reaggregation experiments may alter the potential for Reverse development (RD) in *H. carnea*: reaggregated cells from liberated medusae can occasionally produce very small hydrorhizal stolons (up to 1 mm), but polyps are never reformed (Frey 1968).

Starving is one of the conditions of stress affecting medusa growth. The medusa can react to the unfavourable conditions starting reverse transformation into

the polyp stage: a complete reduction of all medusa-specific organs and tissues, followed by the differentiation of new, polyp-specific cell types and the formation of the polyp bauplan (Schmid 1992; Boero et al. 1998). This process must be considered as a true metamorphosis, but in the opposite direction of larval metamorphosis. At the molecular level, this is reflected into a definite, stage-specific pattern of gene expression, as it is demonstrated in *H. carnea* (Spring et al. 2000; Yanze et al. 2001).

The plasticity of hydrozoans is paradigmatic and it derives from multiple features. Complex life cycles are characterized by alternation of morphs living in different habitats. This strategy allows persistence of hydrozoan species in time, by tuning the production of larvae, polyps or medusae according to the most favourable timing for each stage. Larvae can encyst as resting stages (Werner 1954). Also polyps can encyst and stay in a reduced, metabolically low-cost morph as creeping stolons (Boero 1984; Boero et al. 1986; Gili and Hughes 1995). From there, new polyps can arise at the onset of each favourable season and re-start feeding activity gathering energy to be invested in medusa budding (Boero et al. 1992). In most cases, spawning is followed by medusa degeneration and death. Usually, from a single fertilization event, an embryo will develop into a planula larva. A primary polyp develops by larval metamorphosis and it is the start for a new colony, from where several medusae will bud off at one time: the outcome of this process is comparable to events of polyembryony (Craig et al. 1997; Boero et al. 2002). True polyembryony in Hydrozoa is a well-known process: several polyps (larvae) bud off from a single planula (e.g. *Oceania armata*, *Mitrocoma annae*). In parasitic Narcomedusae one egg gives an embryonic stage from which hundreds of juvenile medusae will bud. Even though not a polyembryonic event *sensu strictu*, additional offspring cloning in Hydrozoa is common, arising from direct medusa budding from liberated medusae (see Introduction). In *T. dohrnii* and *L. undulata*, the ability of medusae reverting to the polyp stage leads to a comparable amplification of the budding process. From each medusa undergoing reverse ontogeny, potentially a new colony can be originated, which in turn will produce new copies of the original medusa, leading to an exponential increase in the total number of clonemate offspring. To date, this potential has been demonstrated in the laboratory only but the number of available observations (several thousands) in the Mediterranean *T. dohrnii* suggests that the potential can be a common process also under natural condition. Furthermore, reverse development was also observed in Japanese *Turritopsis* medusae (Kubota and Mizutani 2003; Kubota 2005).

It is not known how long next medusa generations will retain the potential for reverse metamorphosis. Ecological advantage seems not relevant since they are not dominant species, as it would be expected from exponentially growing populations of long-lasting

animals. On the other hand, the strategy of buying “multiple tickets of the same number in a lottery” (Craig et al. 1997) may reduce the uncertainty of sexual reproduction in organisms with adult stages in the plankton, like jellyfish, freely spawning in the water column. Eventually, the redundancy of each genotype by medusa budding and medusa reverse development will concur also to enhance the overall genetic diversity at small spatial scale.

As observed, the potential of RD is common to other hydrozoans but few of them are able to fully revert into polyp stages. This suggests that (a) the full potential for back-transformation can be transiently expressed only under extraordinary conditions; or (b) the genetic programme involved in the transformation process can be activated in several species, but only few of them retain the whole signalling cascades needed for the completion of morph reversal. Possibly, a number of species might be able of reverse development to stolon formation but, probably, do not have the competence for the next step, that is polyp formation; or, alternatively they need special conditions that might not be easily encountered under laboratory rearing.

Concluding remarks

Medusozoa are the only known animals that are able to rejuvenate by reversing their life cycle. All these reversal processes as well as the variety of budding and regeneration mechanisms occur through activation of cellular pathways unparalleled in the whole animal kingdom. Therefore, these medusa-based animals appear as ideal systems to investigate molecular mechanisms for life span control and stage-specific cell differentiation and signalling, key issues cutting across areas of evolutionary and developmental biology, ageing and even cancer research.

From an evolutionary point of view, hydrozoans are also clonal animals with the simplest level of tissue organization in the animal kingdom. Nowadays, a growing set of molecular data sharply indicate that cnidarians and bilaterians share highly conserved homologies in basic genetic machineries involved in cell differentiation, body patterning, axis formation and regulation of development. The case of *L. undulata* is another example that the outcome of biodiversity studies (such as simple life cycle reconstruction) can reach targets far beyond any reasonable expectations.

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