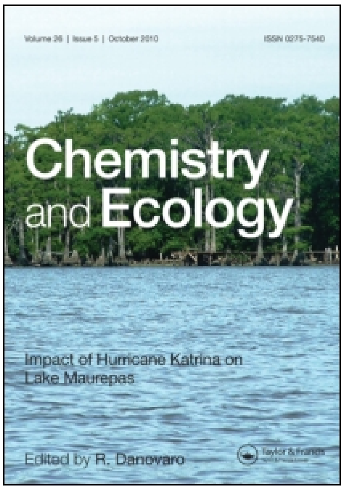

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The problem of seasonality of benthic hydroids in temperate waters

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A wealth of data are available on the seasonal variation of plankton communities, but few studies take into consideration the circannual cycles of benthic organisms. In fact, the macrobenthos is generally considered as composed by slow-growing organisms showing variations mainly in relation to substrate competition. On the contrary, hydroids are an important group of macrobenthos that, in temperate but also in tropical waters, undergo sharp seasonal cycles. For example, on the Portofino Promontory (Ligurian Sea), about half of the recorded species thrive in winter and 30% in the summer, the rest being constant in presence. Here, we revise the available data about the environmental factors switching the passage from quiescent to active phases. The available data suggest that a mosaic of physical factors, biotic interactions, and internal clues triggers the hydroid cyclic behaviour.

Keywords: Temporal variations; Seasonality; Hydrozoans; Cyclase

1. Introduction

Temporal variations, over both long- and short-term cycles, are well documented in the plankton. Plankton communities show circadian migrations along the water column; circannual variations of the diversity/abundance of different planktonic groups are recorded in both temperate and cold waters. In these temporal cycles, the availability of resting stages together with the presence of favourable environmental conditions play a crucial role in the production of unpredictable events, like blooms of gelatinous zooplankton [1].

In the benthos, seasonality is much less studied than in the plankton, and the available data have been recently reviewed by Coma *et al.* [2]. These authors remarked that, in the Mediterranean costal waters, there is a set of species that become dormant in the summer and

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another set of species that enter dormancy in the winter, with the alternation of two types of floras and faunas.

Although seasonal phases of more or less intense metabolism, feeding, growth, and reproduction were recorded in many benthic filter feeders [2], the organisms continue to occupy a substrate portion throughout the whole year. For example, a long-term study on a sponge community in a coralligenous habitat of the Portofino Promontory (Ligurian Sea) demonstrated that the same specimens may be present in a selected area for several years sometimes with negligible variations in size [3]. A similar, but less obvious, pattern has been observed by Boero *et al.* [4] for the hydroid *Eudendrium glomeratum* (see below).

Hydroids are probably, together with colonial ascidians [5] and calcispongiae [6], the most important filter-feeders group that is subjected to wide seasonal variations [7]. Moreover, many species have a life cycle comprising both a benthic polyp and a free-swimming medusa, showing alternative life styles in different habitats. This produces complex temporal patterns in the life histories of species with different phases: a quiescent phase (resting hydrorhiza), the active benthic polyp, the planktonic medusa, and the swimming/creeping planula larva [8].

2. Seasonality in hydroids

Numerous hydroid species, especially in temperate waters, are not constantly present, so that the species composition of the hydrozoan community changes along the annual cycle. Some species can become dominant for more or less long periods, forming facies (see [9, 10] for reviews).

Several hydroids undergo a seasonal regression as part of their life cycle. Most of the hydranth and coenosarc withdraws into the stolons, leaving empty perisarc portions that break away [11]. Boero and Fresi [12] studied the distribution in both space and time of a hydroid community on a vertical rocky cliff on the Portofino Promontory (Ligurian Sea, Italy), showing an evident seasonality: about 45% of the recorded species was present in the winter, 30% were present in the summer, and 25% were observed all around the year (figure 1); also, reproductive periods were sharply seasonal. The presence of seasonal cycles was also

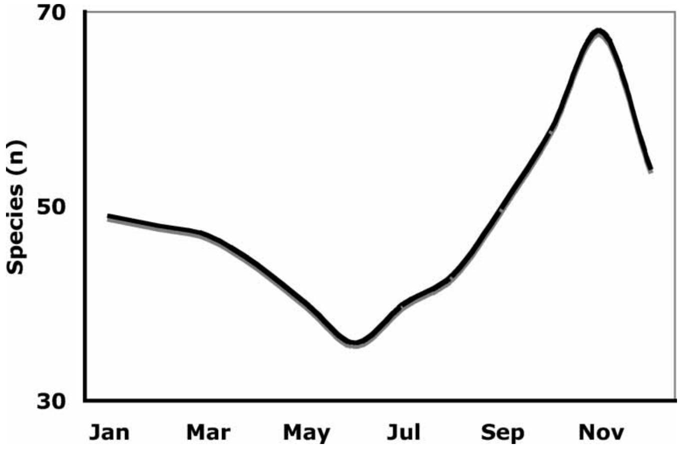

Figure 1. Annual trend of the number of hydroid species along a line transect (0–20 m) on the Portofino rocky cliff (data from [12]).

recorded by Calder [13] for the hydroids in the eastern United States, where he collected winter species, summer species, and species active throughout the year. A similar pattern was recorded for the intertidal and sublittoral hydroid community from the Mar del Plata [14, 15].

Also, in equatorial habitats, characterized by constant temperature conditions, like the North Sulawesi coral reefs (Indonesia) and the Bismarck Sea (Papua New Guinea), benthic hydroids show a clear seasonality in their annual life cycles (unpublished data). In these cases, seasonality is probably driven by the alternation of a dry and a wet season, affecting nutrient availability and turbidity [16]. Besides being affected by external cues, however, hydroids are also influenced in their activity patterns by endogenous circannual clocks [17].

Some species show apparently unpredictable periods of presence in the environment, completely disappearing during some periods of the year or even for a long period of time. A particular case involves *Paracoryne huvei*, an encrusting species typical of the tidal layer: Bouillon [18] observed, in French waters, that the colonies of *P. huvei* are absent from June to October, when this species is present only as resting cysts. The same species, recorded for the first time in the Ligurian Sea in 1981 [19], disappeared completely in the late 1980s and was then observed only in 1997 and 2004 (unpublished).

Also, the species living in symbiotic association with other organisms show sharp seasonal cycles. The annual cycle of a hydractiniid hydroid living on a gastropod was studied by Herberts [20, 21]. *Hydractinia* (*Podocoryna*) *exigua* is abundant on the shells of the hermit crab *Diogenes pugilator* during the winter and rare during the summer [22] (figure 2). Sometimes, the seasonal cycle of the hydroid affects that of the host as in the case of *Cytaeis* (*Perarella*) *schneideri*, which is very abundant during the winter, strongly affecting, probably by direct predation, the life history of the bryozoan host [23] (figure 3).

The hydroid sexual reproduction may occur throughout the year, but generally each species has a limited typical period of fertility (see [10] for a revision). In the Ligurian Sea, Boero and Fresi [12] recorded, out of a total of 29 studied species, four species fertile in the warm season, seven species fertile between winter and summer and 18 species fertile during the winter. Hughes [24], studying the life cycle of *Tubularia indivisa*, observed that the oldest hydroids became mature during the winter, and the peak of recruitment was from April to June. Also, several species from Mar del Plata have a reproductive period more restricted than the period of presence in the field [14, 15].

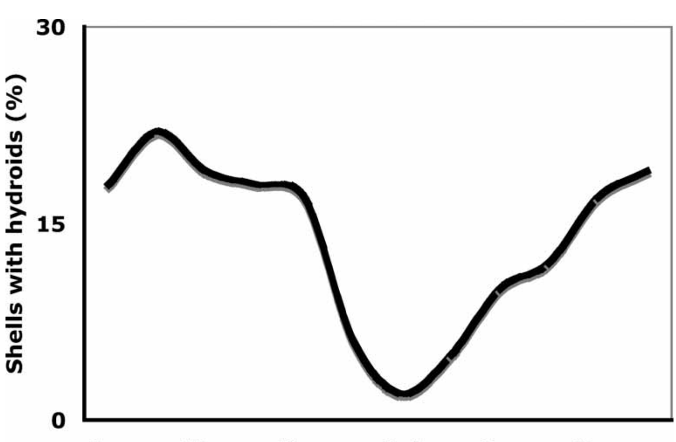

Figure 2. Annual trend of the amount of gastropod shells infested by *Hydractinia* (*Podocoryne*) *exigua* from the Ligurian Sea (modified after [20]).

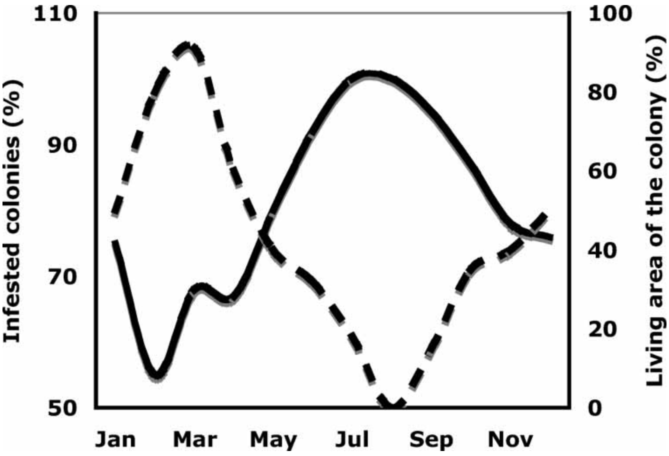

Figure 3. Annual trend of the amount of colonies of the bryozoan *Schizoporella longirostris* infested by the hydroid *Cytaeis* (*Perarella*) *schneideri* (continuous line) and of the living area of the colonies of the bryozoan (dotted line) from the Ligurian Sea (modified after [21]).

3. Cycles of the Mediterranean *Eudendrium*

The annual life cycle was studied in detail for two Mediterranean species of the genus *Eudendrium: E. glomeratum* and *E. racemosum*. Both species are very common in Mediterranean shallow waters and produce large colonies (up to 20 cm in height). They have fixed gonophores on more or less reduced hydranths.

Eudendrium glomeratum is a winter species that appears on rocky cliffs at mid-October. The average height of the colonies increases until January and decreases thereafter until April, when all colonies regress (figure 4). The field evidence that in the following year new colonies arise again, exactly in the same position of those of the previous year, suggests that the summer period is spent as quiescent hydrorhizae [4]. We have observed that the hydrorhizae of *Eudendrium* are able to penetrate deeply inside the substrate, into the erosion tracks produced by boring organisms; in this protected environment, they may spend the adverse seasons (unpublished).

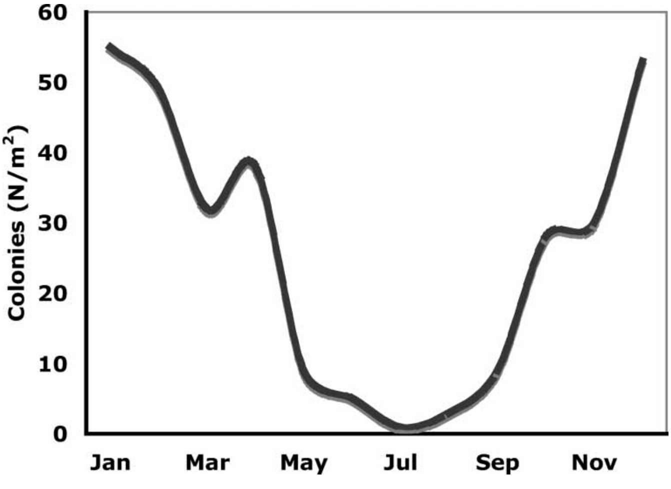

Figure 4. Annual trend of a *Eudendrium glomeratum* population from the Ligurian Sea (modified after [4]).

The gonads are produced from November to December. Generally, male colonies start to ripen before female colonies [25]. The newly released planula larvae are able to produce new colonies in the same winter, but the evidence that in the following year new colonies arise in places different from those of the colonies of the previous year supports the hypothesis that also planulae – probably those released at the end of the reproductive cycle – are able to cross the adverse season as resting stages [4].

The influence of environmental factors – water temperature, solar irradiance, and competition with macroalgae – in determining this cycle is strongly supported by the evidence that, below 50–60 m depth, where the environmental conditions are more stable and the macroalgae are almost absent, large colonies of *E. glomeratum* are active all around the year [25].

On the same rocky cliffs, the annual cycle of *E. racemosum* is opposite to that of *E. glomeratum*. The colonies become active in April and show a long period of fertility extended to the entire summer until the end of September degenerating in the autumn (figure 5A). Also, in this species, male colonies become ripe before female colonies [26, 27].

In harbour waters, the cycle of this species is very different (figure 5B). The colonies are active all year round, and the gonophores are present in three periods, a main period in the summer and two others in winter and spring [27].

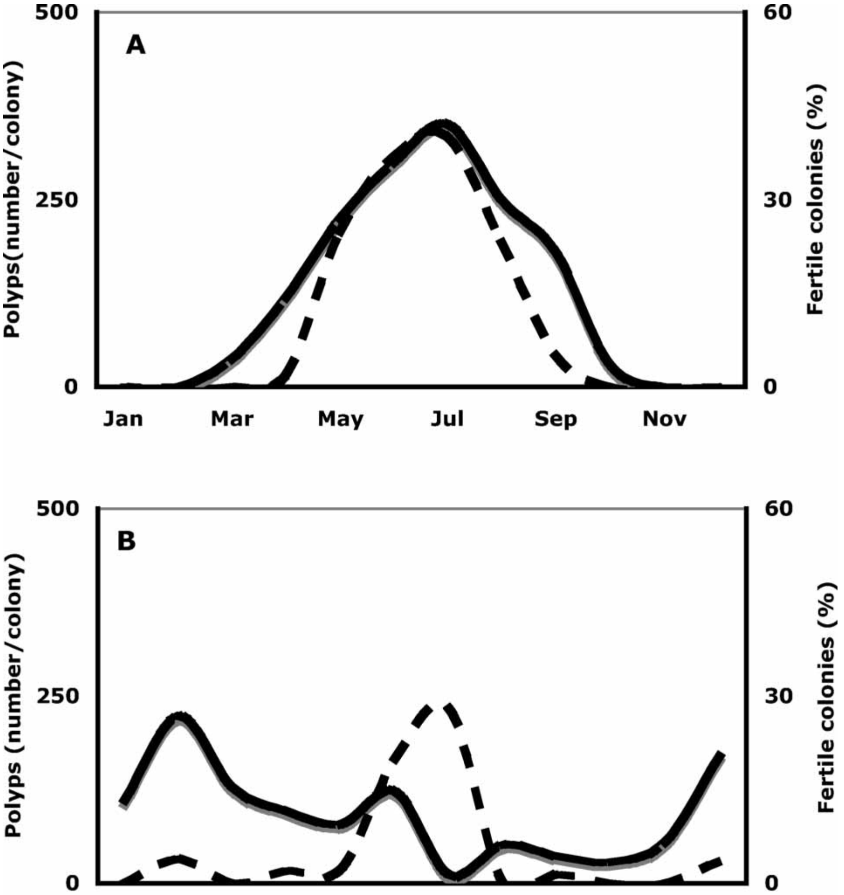

Figure 5. Annual trend of two populations of *Eudendrium racemosum* expressed as number of polyp per colony (continuous line) and percentage of fertile colonies (dotted line). A, Portofino rocky cliff; B, Harbour of S. Margherita Ligure (modified after [25]).

4. Causes of seasonality

The campanularid *Laomedea flexuosa*, reared under laboratory conditions for long time (10 °C, 17 °C, and 24 °C and in complete darkness) showed a luxuriant growth with a mid-winter phase of curtailed growth and a summer phase of sparse growth. The uniformity of growth oscillations, despite changes in ambient temperature and lack of light, demonstrated the presence of a circannual endogenous clock regulating the seasonal rhythm in this species [17].

Several authors indicate the environmental abiotic factors as light, temperature, salinity, and sedimentation [10] as the main causes of the seasonality. Boero and Fresi [12] propose that water temperature is the main cause of the seasonal cycle of hydroids on the Portofino cliff. Nevertheless, the authors suggest that other factors could be involved: for example, for winter species, the water temperature at the start of the active cycle (October–November) is higher than at the end of the same cycle (March–April). The effect of water temperature on hydroid metabolism, evaluated as the rate of oxygen consumption, was tested by Arillo *et al.* [25] on the winter species *Eudendrium glomeratum* along its entire cycle. Oxygen consumption of hydranths, when measured under normothermic conditions (14–19 °C) showed a maximum in October and a minimum in winter, and tended to increase again in spring. Probably, this species needs a relatively high temperature to reach an energy turnover compatible with its optimal activity, and this may explain why the reproductive activity and maximum growth rates occur in autumn, when the environmental temperature ranges between 18 and 20 °C [4].

Another environmental factor taken into consideration as determining the seasonal cycle of hydroids is the amount of solar radiation (irradiance). The first evidence of this was given by Rossi [28], who demonstrated that solar light is necessary for the growth, measured as polyps production, of the summer species *E. racemosum*. Moreover, Bavestrello and Arillo [29] demonstrated that temperature works synergistically with irradiance in determining the seasonal cycle of *E. glomeratum* (figure 6). In contrast to *E. racemosum*, in this last species, high levels of solar irradiance, coupled with high temperature, induce a quick decline of the colonies. In fact, laboratory exposure to 5 h of solar light results in a dramatic depletion of glycogen concentration at the two experimental temperatures of 14 and 22 °C. On the other hand, solar light exposure does not affect the oxygen consumption of the colonies maintained at 14 °C but drastically decreases the respiration of those tested at 22 °C.

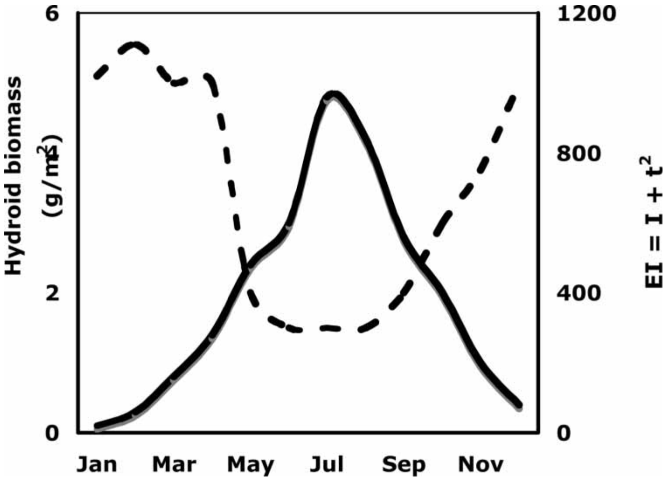

Figure 6. Annual trend of the biomass of a population of *E. glomeratum* (dotted line) from the Ligurian Sea compared with the trend of the environmental index, EI (continuous line), I = solar irradiance, t = water temperature (modified after [27]).

Light → ABA → PKA → cyclase activation → $\uparrow[\mathrm{cADPR}]_i$ → $\uparrow[\mathrm{Ca}^{++}]_i$ → regeneration

Figure 7. Biochemical pathway of the light activated stolon regeneration in *Eudendrium racemosum* (modified after [31]).

The influence of solar light on hydroid metabolism is demonstrated by the role of this factor in allowing egg hatching and in stimulating larval settlement and metamorphosis in *E. glomeratum* [30].

Probably, also biotic factors such as food availability and competition for substrate act synergistically with abiotic factors to determine the annual cycles of hydroids [9]. Colonies of *Plumularia setacea*, typically growing and reproducing throughout the year, show a phase of winter dormancy and reproduce only from June to August when living in areas of low productivity, characterized by periodical food shortage [31].

More recently, Azzini *et al.* [27] confirmed, by field studies, that physical factors such as temperature and solar irradiance are important in regulating the seasonal cycle of *E. racemosum* when the colonies live in natural, oligotrophic habitats. The cycle of the hydroid, however, is strongly modified for colonies living in harbours, in highly eutrophic waters, and on substrates characterized by low levels of competition.

While the involvement of some environmental factors, mainly temperature and sun light, in determining the seasonal cycles of the hydroids is clearly demonstrated, the biochemical patterns implicated in the perception and transduction of environmental cues are widely unexplored. Recently, the biochemical pathway mediating temperature signalling in sponges was elucidated [32]. This pattern involves abscissic acid (ABA), a plant hormone, and the ADP-ribosyl cyclase that converts NAD to cyclic ADP-ribose (cADPR). Puce *et al.* [33] demonstrated the involvement of the same biochemical pathway in light-induced growth in *Eudendrium racemosum*. In this species, light exposure activates ABA synthase, which stimulates ADP-ribosyl cyclase, and the consequent increase in the intracellular cADPR concentration then leads to an increase in the intracellular calcium concentration, stimulating cell proliferation (figure 7). In the same species, ABA acts as inhibitor of differentiation: polyp production, in fact, decreases when growth is stimulated by ABA. Therefore, in *E. racemosum*,

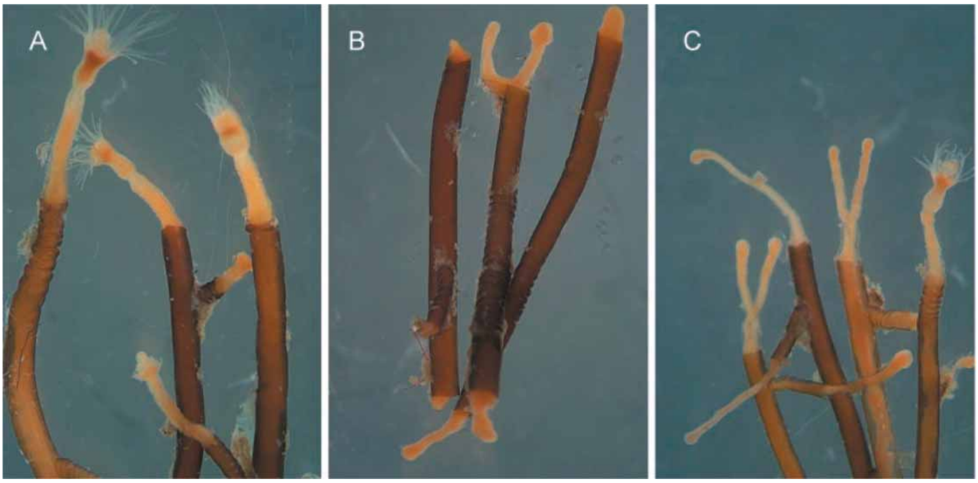

Figure 8. Regeneration of E. *racemosum* fragments observed under a low-power microscope. *E. racemosum* fragments (10 mm) were cut from different colonies, randomized, divided into three Petri dishes, and incubated in sea water at 17 °C under artificial light (A) or in the dark without (control, B) or with 50 µM ABA (C) (from [31]).

another hormone is probably present, inhibiting ABA release and activating differentiation (figure 8).

5. Significance of seasonality in hydrozoans

In marine environments, the cycle of phytoplankton is the main biological trigger of seasonal variations, regulating the cycles of holoplanktonic zooplankton, the reproduction of benthic organisms characterized by meroplanktonic larvae, and the reproduction of pelagic fishes. At least in temperate environments, it is possible to recognize the involvement of the phytoplankton cycle at every level of the trophic chains, from shallow to deep water. According to Coma *et al.* [2], the differences in seasonality between benthic communities of cold and temperate waters derive from a shift in the phytoplankton cycle. Also, the benthic macro and microalgae show annual variations similar to those of phytoplankton. It is obvious that the rhythmic behaviours related to the phytoplankton cycle are mainly due to trophic requirements: with the biomass production being variable along the year, the consumers adjust their life cycles to better exploit the available resources.

Apparently, the seasonal variations of benthic hydroids are largely independent of the regulating capability of the plankton cycle. Some species are in fact active throughout the year, while others are active in different seasons. Moreover, hydroids are seasonal also in more stable habitats like the equatorial habitats. This evidence suggests that the cyclic strategies of hydrozoans are not only related to trophic reasons.

The seasonality recorded in several species probably evolved for reasons related to avoiding competition for substrate: seasonal cycles allow hydroids to occupy the same substratum by the alternation of different species, each with a definite period of activity. Moreover, this strategy obviates competition with macroalgae. On the rocky cliffs of the Portofino Promontory, during summer, the belt of 5–10 m is completely characterized by the brown alga *Dictyopteris membranacea*, and very few, small epibiontic hydroid species are present. In autumn, when most macroalgae degenerate, the substratum becomes free for different hydroids, sometimes developing extremely abundant populations (*Eudendrium glomeratum* and *E. ramosum*) that, in spring, leave in their turn the substratum available for algae [34]. In this way, the environment shows, in a particular period, an expressed biodiversity that represents only a part of the standing species pool. The potential biodiversity, present under the form of resting stages, is normally higher [1].

From a biogeographic point of view, a seasonal life style allows hydroids to exploit geographic areas that are, only for a part of the year, suitable for the requirements of the various species. This fact is particularly evident in the Mediterranean sea that, in different seasons, shows a hydroid community characterized by boreal (*Eudendrium glomeratum*) or subtropical species (*Ectopleura crocea, Pennaria disticha*, and *Corydendrium parasiticum*) [35].

The available data suggest therefore that the cyclic behaviour is triggered by a mosaic of physical factors, biotic interactions and internal clues, but our knowledge on this subject has been, until now, very superficial.

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