
Hydroids (Cnidaria, Hydrozoa): A Neglected Component of Animal Forests

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Abstract

Hydroids, one of the dominant components of the zoobenthic communities, share comparable growth patterns with higher plants because of their modular body organization, high potential of asexual reproduction, and phenotypic plasticity. These features, together with the ability to enter dormancy to overcome unfavorable conditions, make hydroids successful organisms adaptable to a wide range of environmental scenarios. Depending on their wide range of shapes and sizes, hydroids form three-dimensional forests at different dimensional scales, establishing both trophic and non-trophic relationships with several other organisms, from virus to vertebrates.

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Despite numerous researches conducted to study the hydroid ecology, the putative importance of hydroids in structuring zoobenthic communities is underestimated. Here, information available about hydroid ecology is summarized, in order to emphasize the role of hydroids as forest formers, as well as their function in the benthic-pelagic coupling.

Keywords

Ecological role • Emerging threats • Hydroid forests • Protection • Seasonal and perennial habitat formers

Contents

1	Introduction	2
2	Deciduous Hydroid Forests	4
3	Perennial Hydroid Forests	7
4	Interactions with Other Organisms	16
5	Trophic Ecology, Feeding Behavior, and Reproductive Strategies	20
6	Emerging Threats for Hydroid Forests	24
7	Conclusions	26
	References	26

1 Introduction

Clonal animals, according to Jackson and Coates (1986), have either uniserial or multiserial growth patterns. Uniserial colonies are also called “runners” and do not form large assemblages, whereas multiserial colonies perform lateral and distal growth and tend to persist, with the possibility of forming large assemblages. Multiserial colonies, hence, are able to form “forests” and behave as trees, whereas uniserial colonies are more similar to weeds. The two strategies are also used to distinguish guerrilla from phalanx species (Humphrey and Pyke 1998). Philopatric colonies (Knowlton and Jackson 1993) can produce a high number of genetically identical colonies (each termed a ramet) that, together, form a genet: an assemblage of genetically identical ramets. This tendency is conducive to the formation of animal forests.

The colonies of the Hydrozoa show highly diverse growth forms that cover both categories (Bouillon et al. 2006). Small polyp colonies (usually less than 1 cm high) are reptant and tend either to grow on other organisms or to form “meadows,” growing directly on primary substrates where they can play a certain ecological role in becoming habitats for other species. Small hydroids are mostly overlooked, being considered as mere epizoides. Consequently, very little information is available on the ecological traits of small hydroids and the role they play in both benthic and pelagic communities. *Clytia hummelincki* (Leloup, 1935) represents a case of meadow-forming hydroid (Gravili et al. 2008).

Large colonies (ranging from 10 cm to 1 m) grow on primary substrates and become substrate for other organisms, forming forests comparable in sizes and

abundances to those of either algae or gorgonians, and likely play roles of habitat formers as those documented for anthozoan forests (Cerrano et al. 2010; Ponti et al. 2016; Valisano et al. 2016).

Hydroids are one of the main components of zoobenthic communities. At their relative dimensional scale, hydroids change the features of the geological habitat, becoming habitat formers by affecting water movement and light penetration and providing settling space, shelter, or food to several associated species, so enhancing local biodiversity. Moreover, hydroid forests release a consistent amount of planulae, medusoids, or medusae in the surrounding environment, contributing to benthopelagic coupling and affecting biogeochemical cycles (Gili et al. 1998; Rossi et al. 2012).

The modular organization of hydroids gives them a high plasticity and a potentially unlimited growth (Marfenin 1997; Kosevich 2006); hence they can adapt their shape, growth strategies, trophic behavior, and reproductive strategies to a vast array of environmental conditions (Boero 1984; Gili and Hughes 1995; Bouillon et al. 2006).

Even if hydroid ecology is rather well known (Fig. 1), their putative importance in structuring zoobenthic communities is underestimated by benthic ecologists. In spite of several documented cases of hydroids as formers of benthic assemblages comparable to algal forests, in fact, the formal definition of habitats rarely gave them much importance. For the Mediterranean Sea, for example, in the list of habitats assembled by RAC-SPA (2006), there is just a single item comprising all hydroid forests (i.e., facies with large hydrozoa), whereas each type of algal forests is carefully identified with the name of the main species; the same treatment is given to the Bryozoa. Frascchetti et al. (2008) proposed a rationale of benthic habitat classification that allows accommodating hydroid forests into the seasonal or even permanent habitat formers.

One of the reasons why hydroids are neglected is that hydroid specialists contributed less than marine botanists to the formal definition of habitats, and this led to underappreciation of the role of these animals, in respect to algae. Furthermore, at least in the Mediterranean Sea, field activities are mostly carried out in the favorable season when algae dominate benthic assemblages and most hydroids are dormant, leading to underappreciation of their importance in structuring benthic communities.

Analyzing papers focusing on hydroid ecology could help in understanding why hydroid ecological role is overlooked. From 1950 to today (Fig. 1), most of the papers were published during the decade 1980–1989 (over 45 per year); the most explored topic is the study of interactions between hydroids and other organisms (up to about 20 papers per year).

During the last years (2010–2016), there was an increasing interest in studying hydroids belonging to fouling communities, alien species, and effects of climate change on hydroid assemblages.

Among the researches published in the last two decades, very few papers put in relation hydroid distribution and population dynamics with abiotic and/or biotic factors (Azzini et al. 2003; Ronowicz et al. 2008; Orejas et al. 2013; Di Camillo et al. 2012a; Rossi et al. 2012).

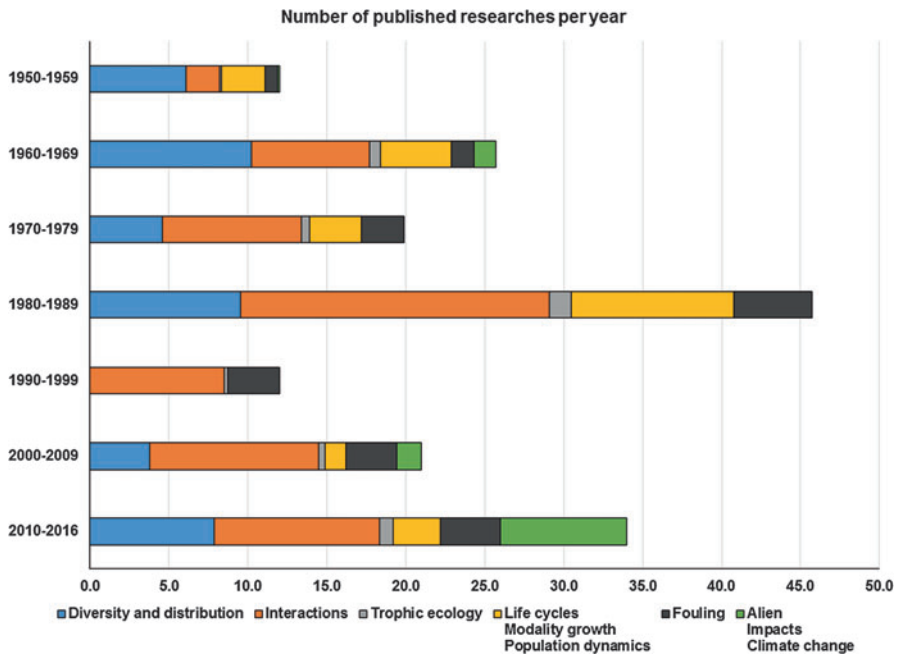


Fig. 1 Trend of published papers per year from 1950 to 2016. Over 1,500 papers focusing on hydroid ecology were considered (Data extracted from BiblioHydro, Gravili et al. 2000)

Similarly to what highlighted by Becerro (2008) regarding sponges, most of researches on hydroid ecology generally are descriptive and focus on one or few species, interesting a narrow readership. Lack of published quantitative data expressed in terms of biomass prevents estimation of the potential of hydrozoan forests in terms of trophic impact, food source, and reproductive output and does not allow the comparison with other animal forests or within the animal forests.

2 Deciduous Hydroid Forests

Deciduous hydroids, typical of shallow waters at cold and temperate latitudes, range from less than 1 mm (many Campanulariids, Campanuliniids) to about 20 cm in height (i.e., several Eudendriids, Pennariids, Tubulariids, Aglaopheniids, etc.). In these seasonal species, hydranth resorption or shedding occurs in response to periodic adverse environmental conditions, followed by dormancy of remaining fragments of tissue (coenosarc) enclosed in stems or hydrorhizae acting as resting stages (Bouillon et al. 2006). When environmental conditions become favorable again, the regeneration of the colonies takes place from the dormant tissue.

Seasonality drives the succession of species with different ecological characteristics; consequently, winter and summer species may occupy the same space, but in

distinct temporal windows (Boero and Fresi 1986; Coma et al. 2000; Bavestrello et al. 2006; Puce et al. 2009). The duration of dormancy/active phases can change along bathymetric or geographical ranges characteristic of each species. Deciduous forests undergo strong seasonal variations in their biomass in relation to fluctuation of an intricate mixture of abiotic/biotic factors (i.e., temperature, irradiance, salinity, sedimentation, oxygen concentration, food availability, space competition, predation). Further studies are needed to understand physiological processes triggering quiescence or renovation and to test the duration of dormancy in relation to different ranges of environmental constraints since research focused on a limited number of species (Boero 1994 for a review).

Many studies on hydroid seasonality were conducted in the Mediterranean Sea. Boero and Fresi (1986) were the first to generalize a seasonal pattern of community structure in the Mediterranean benthos while giving paramount importance to hydroids, highlighting the importance of seasonal fluctuations in the composition of the sessile benthos, with a dominance of the algal component in the spring and summer and a prevalence of hydroids in the fall and winter. This was studied in detail for the dominant winter species *Eudendrium glomeratum* Picard, 1951 (Boero et al. 1986) and later better formalized in general studies (e.g., Boero 1994; Coma et al. 2000). Bavestrello et al. (2006) showed that, in the Mediterranean Sea, 50% of the species thrive in the winter, 30% in the summer, and only 20% tend to be always present.

Because of their plasticity and fast growth, deciduous hydroid forests have a prominent role in shaping zoobenthos dynamics. A good example is supplied by the comparison of the different life strategies of *Eudendrium racemosum* (Cavolini, 1785) from different localities. At the Medes Islands (MI), *E. racemosum* is also constantly present (Rossi et al. 2012), whereas it is sharply seasonal in the Adriatic Sea (AS), where temperatures are significantly lower in the winter (Di Camillo et al. 2012a) (Fig. 2). The longer duration of the fertility period and the highest polyp production in the population from the AS are likely related to the conspicuous food availability of this area. The considerable food amounts ingested by the polyps from the AS (Di Camillo et al. 2012a) suggest that (i) the hydroid plays a role in energy cycling and in removing particles from the water column and that (ii) local trophic levels are a key factor regulating variations in biomass of this suspension feeder. Indeed, in the MI, the summer regression of the population of *E. racemosum*, as well as the low polyp production, is probably related to the summer food paucity (Coma et al. 2000; Rossi et al. 2012). Moreover, in the MI, the hydroid growth could be limited in summer due to competition with algae, as occurring at other localities of the Western Mediterranean (Boero 1984; Boero and Fresi 1986; Boero et al. 1986; Rossi et al. 2012).

Under different local conditions, the life cycle patterns of *Eudendrium racemosum* can further differ from those described above: for example, in the Ligurian Sea, *E. racemosum* living on artificial substrates and in eutrophic conditions was observed all year round, while the population living on a natural rocky cliff was present in summer only (Azzini et al. 2003).

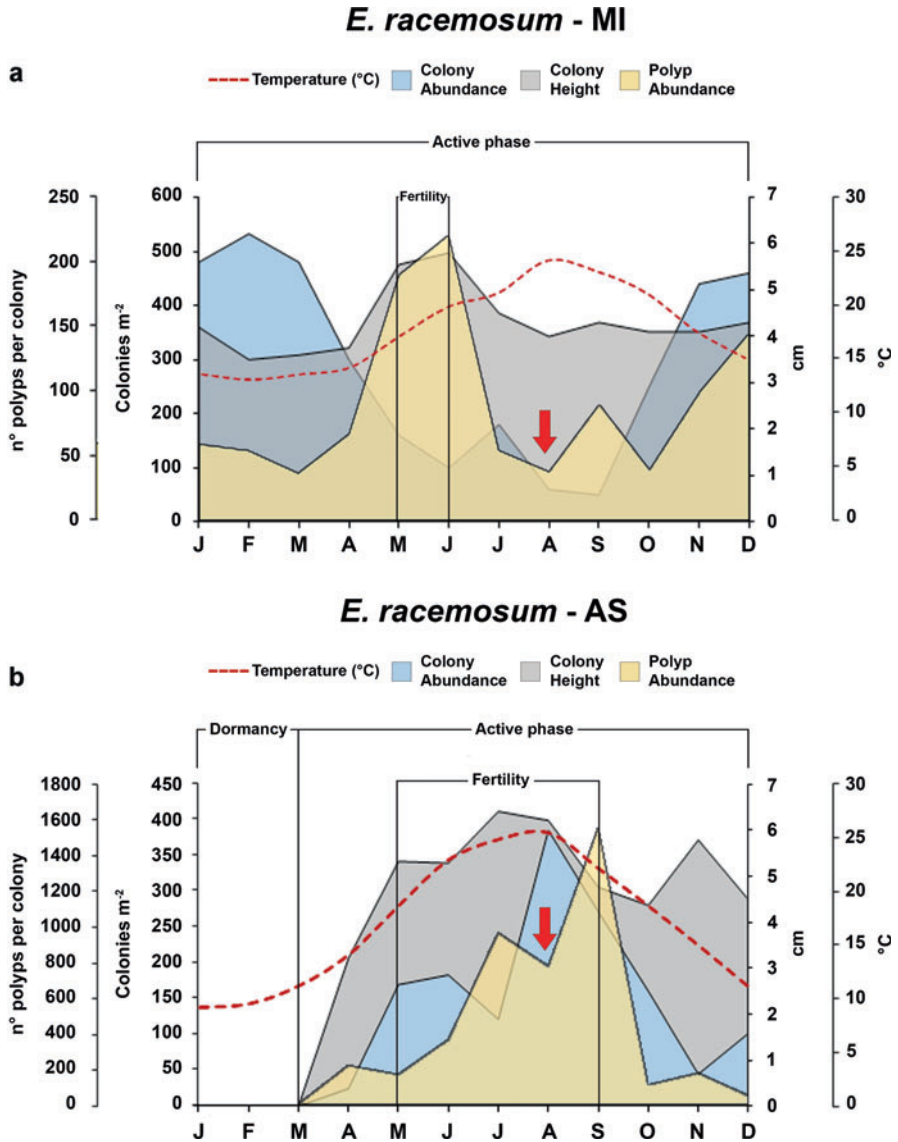


Fig. 2 Comparison of different population dynamics of *Eudendrium racemosum* (Cavolini, 1785) from Medes Islands (MI) (a) and Adriatic Sea (AS) (b) Red arrows indicate when the nudibranch predation is most intense

These considerations highlight that studies on fast-growing suspension feeders are indispensable to understand how population dynamics mirror environmental pressures and that the natural variability of these phenomena is great.

In tropical areas, seasonality is due to rainfalls, and biomass fluctuations are probably related to variations in food abundance during the wet and dry season (Boero 1994). In Indonesian waters, the maximal density of hydroids coincides with the period of heavy rainfall and river inputs (Di Camillo et al. 2008). However, most of the projects carried out in tropical waters focused on the census of marine organisms, while long-term monitoring programs are scant. Similar knowledge gaps are present at the poles, where a dark and ice-dominated season alternates with a long period of total darkness (Orejas et al. 2013).

Seasonal forests can regress as a result, for instance, of the impact of global warming on species of cold-water affinity, such as *Eudendrium glomeratum* in the Ligurian Sea (Boero et al. 1986). The regression of seasonal species is usually given less importance than that of perennial species, such as those of gorgonians in the Ligurian Sea (Cerrano et al. 2000). Seasonal species are preadapted to undergo long periods of adverse conditions with dormant phases but, nevertheless, if negative situations become permanent (e.g., with constantly higher temperatures than previous ones), species might become locally extinct.

3 Perennial Hydroid Forests

Perennial hydroids are always present in their erect forms (e.g., the calcareous Milleporidae and Stylasteridae) and are more common than seasonal species where variations in environmental conditions are small. Habitat stability allows enduring species to develop large and sturdy colonies and to reach considerable sizes ranging from 20 cm up to 2 m: for example, *Plumularia elongata* Billard, 1913, *Solanderia* spp., or *Millepora* spp. at tropics; *Lytocarpia myriophyllum* (Linnaeus, 1758) on soft bottoms; *Errina* spp., and *Amphisbetia operculata* (Linnaeus, 1758) on hard substrates from temperate regions (Table 1, Figs. 3 and 4). Perennial hydroids can give rise to animal forests comparable to those formed by gorgonians. Those with calcified skeletons are probably slow growing, but their growth rates are poorly estimated (Lewis 2006). During their theoretically unlimited life span, perennial hydroids host several taxa of sessile and vagile organisms, represent a food source for several animals, and, in their turn, likely collect great amounts of feeding particles from the water column. These forests undoubtedly have a significant – but little explored – role in energy transfer from plankton to benthos (Gili et al. 1998; Gili and Coma 1998). Enduring hydroid forests can be indicators of habitat health conditions: for example, the presence of intact *Errina* gardens on hard substrates (Häussermann and Försterra 2007; Salvati et al. 2010), *Plumularia elongata* on tropical reefs (Di Camillo et al. 2010), and *Lytocarpia myriophyllum* on sandbanks (Di Camillo et al. 2013; Cerrano et al. 2015) is linked to the existence of pristine or scarcely disturbed habitats.

Loss of their habitats would lead to decline or disappearance of the enduring hydroid forests and their ecosystem services, as observed for *L. myriophyllum* in Northern Ireland because of intense bottom trawling (Goodwin et al. 2011). In Ireland and Great Britain, the hydroid is considered a priority species (Goodwin

Table 1 Summary of the ecological characteristics of some large forest former hydrozoans (*A.*, Anthomedusae; *L.* Leptomedusae)

Order	Species	Geographic distribution	Vertical zonation	Substrate	Shape and skeleton	Reproduction	Associated organisms	Threats
A	<i>Millepora</i> spp.	Circumtropical	From reef crest	Hard	Larger colonies branched; calcified skeleton	Eumedusoids	Zooxanthellae, <i>Wanella elongatum</i> (Hiro, 1931) (barnacle), <i>Hermodice carunculata</i> (Pallas, 1766) (polychaete, predator), several species of crustaceans, echinoderms, mollusks, nemerteans, polychaetes, and sipunculids	Global warming, bomb fishing, pollution
A	<i>Solanderia</i> spp.	Tropical and subtropical	Fore reef	Hard	Fan-shaped to bushy; perisarc stiff	Cryptomedusoids or eumedusoids	<i>Medioantenna</i> spp., serpulids (polychaetes), <i>Licnophora</i> spp. (protozoans), <i>Jason mirabilis</i> M.C. Miller, 1974 and <i>Pleurotidia juliae</i> Burn, 1966 (nudibranches, predators), bivalves, gastropods,	

							<p><i>Pseudosolanderia</i> spp.</p>	<p>A</p>
<p>tunicates, ophiuroids, copepods, barnacles, amphipods, bryozoans</p>	<p><i>Lagisca zibrowii</i> Hartmann-Schröder, 1992 (polynoid polychaete), <i>Pachyprocerastea hydrozoicola</i> (Hartmann-Schröder, 1992) and <i>Procerastea simpliseta</i> Hartmann-Schröder, 1990 (syllid polychaetes)</p>	<p>Eumedusoids</p>	<p>Fan-shaped to bushy; chitinous or from partly to quite totally calcified</p>	<p>Hard</p>	<p>Fore reef</p>	<p>Circumtropical</p>		
<p>Algae, other hydrozoans, scleractinians, <i>Epizoanthus</i> sp. (zoanthid), sponges, bryozoans, commensal polychaetes, <i>Pachylasma giganteum</i></p>		<p>Fixed gonophores in ampullae</p>	<p>Branched colonies; calcified skeleton</p>	<p>Hard</p>	<p>Deep waters</p>	<p>Temperate</p>	<p>Stylasterids</p>	<p>A</p>

(continued)

Table 1 (continued)

Order	Species	Geographic distribution	Vertical zonation	Substrate	Shape and skeleton	Reproduction	Associated organisms	Threats
L	<i>Amphisbeta operculata</i> (Linnaeus, 1758)	Temperate and subtropical	From shallow waters in cold regions	Hard substrates on soft bottoms	Bushy with pinnate cormoids; perisarc flexible	Cryptomedusoids	(Philippi, 1836) (barnacle), <i>Pedicularia</i> spp. (gastropods)	
L	<i>Sertularia diaphana</i> (Allman, 1885)	Tropical and subtropical	Fore reef	Hard	Fan-shaped to bushy; perisarc stiff	Cryptomedusoids	Diatoms, macroalgae, ciliates, other hydrozoans, entoprocta, <i>Doto eireana</i> Lemche, 1976 (nudibranch, predator), other mollusks, bryozoans, tunicates	
L	<i>Sertularia argentea</i> Linnaeus, 1758	Temperate	From shallow waters in cold regions	Hard	Spiralate colonies; pinnate branches; flexible perisarc	Heteromedusoids		Ornamental harvesting
L	<i>Hydrallmania falcata</i> (Linnaeus, 1758)	Temperate	From shallow to mesophotic zone	Hard substrates on soft bottoms	Pinnate cormoids spirally arranged;	Fixed gonophores	Other hydroids	Ornamental harvesting

L	<i>Aglaophenia cupressina</i> Lamouroux, 1816	Indo-Pacific	Between reef crest and fore reef	Hard	perisarc flexible Bushy with pinnate cormoids; perisarc very flexible	Fixed gonophores protected by corbulae	Zooxanthellae, <i>Cuthona diversicolor</i> Baba, 1975 (nudibranch, predator), cyclopoid copepods, <i>Hyastenus bispinosus</i> Buitendijk, 1939 (crab), fish	Global warming
L	<i>Lytocarpia myriophyllum</i> (Linnaeus, 1758).	From boreal to subtropical regions	Mesophotic and deep waters	Soft	Bushy with pinnate cormoids; perisarc very flexible	Fixed gonophores	Forams, other hydroids, <i>Amphianthus dohrnii</i> (Koch, 1878) (actinian), <i>Dondice banyulensis</i> Portmann & Sandmeier, 1960 (nudibranch, predator, egg deposition), bivalves, stalked barnacles, solenogaster, gastropods, caprellids and gammarids, bryozoans	Destructive fishing techniques

(continued)

Table 1 (continued)

Order	Species	Geographic distribution	Vertical zonation	Substrate	Shape and skeleton	Reproduction	Associated organisms	Threats
L	<i>Macrorrhynchia</i> spp.	Tropical and subtropical	Fore reef	Hard	Fan-shaped, pinnate cormoids; moderately flexible	Fixed gonophores or medusoids, protected by phylactocaps	Other hydroids (Heliellidae), decapod palaemonids	
L	<i>Streptocaulis dollfusi</i> (Billard, 1924)	Eastern Atlantic, Strait of Gibraltar	Mesophotic and deep waters	Hard	Erect and polysiphonic colonies, pinnate cormoids	Fixed gonophores protected by phylactocaps		
L	<i>Plumularia elongata</i> (Billard, 1913)	Indo-Pacific	Fore reef	Hard	Fan-shaped to bushy; with pinnate cormoids; strongly polysiphonic and stiff	Fixed or swimming gonophores	<i>Hydrozoanthus gracilis</i> (Lwowsky, 1913) and <i>Hydrozoanthus</i> sp.1 (zoanthids), pycnogonids	
L	<i>Pseudoplumaria</i> spp.	Temperate and subtropical	From shallow to deep waters	Soft	With pinnate cormoids	Fixed gonophores		
L	<i>Nemertestia</i> spp.	Cosmopolitan	Mesophotic and deep waters	Hard substrates on soft bottoms	Bushy due to very close unbranched cormoids	Fixed gonophores	Sponges, other hydroids, <i>Alcyonium digitatum</i> Linnaeus, 1758 (anthozoan), nemertean, bivalves,	Destructive fishing techniques

L	<i>Polyplumaria flabellata</i> G.O. Sars, 1874	Temperate and subtropical	Deep waters	Hard	Fan-shaped; with pinnate cormoids; stiff perisarc	Fixed gonophores	gastropods (prosobranchs and opistobranchs), <i>Ophiothrix fragilis</i> (Abildgaard, in O.F. Müller, 1789) (ophiuroid), <i>Anedon bifida</i> (Pennant, 1777) (comatulid), polychaetes, gammarid and caprellid amphipods, copepods, cirripeds, cumaceans, isopods, decapods, pycnogonids, entoprocts, bryozoans, tunicates
L	<i>Halecium</i> spp.	Boreal and temperate	Mesophotic and deep waters	Hard	Fan-shaped to bushy, pinnate cormoids	Fixed gonophores	
L	<i>Hartlaubella gelatinosa</i> (Pallas, 1766)	Temperate	Deep waters	Mixed substrates	Bushy	Fixed gonophores	Amphipods and caprellids

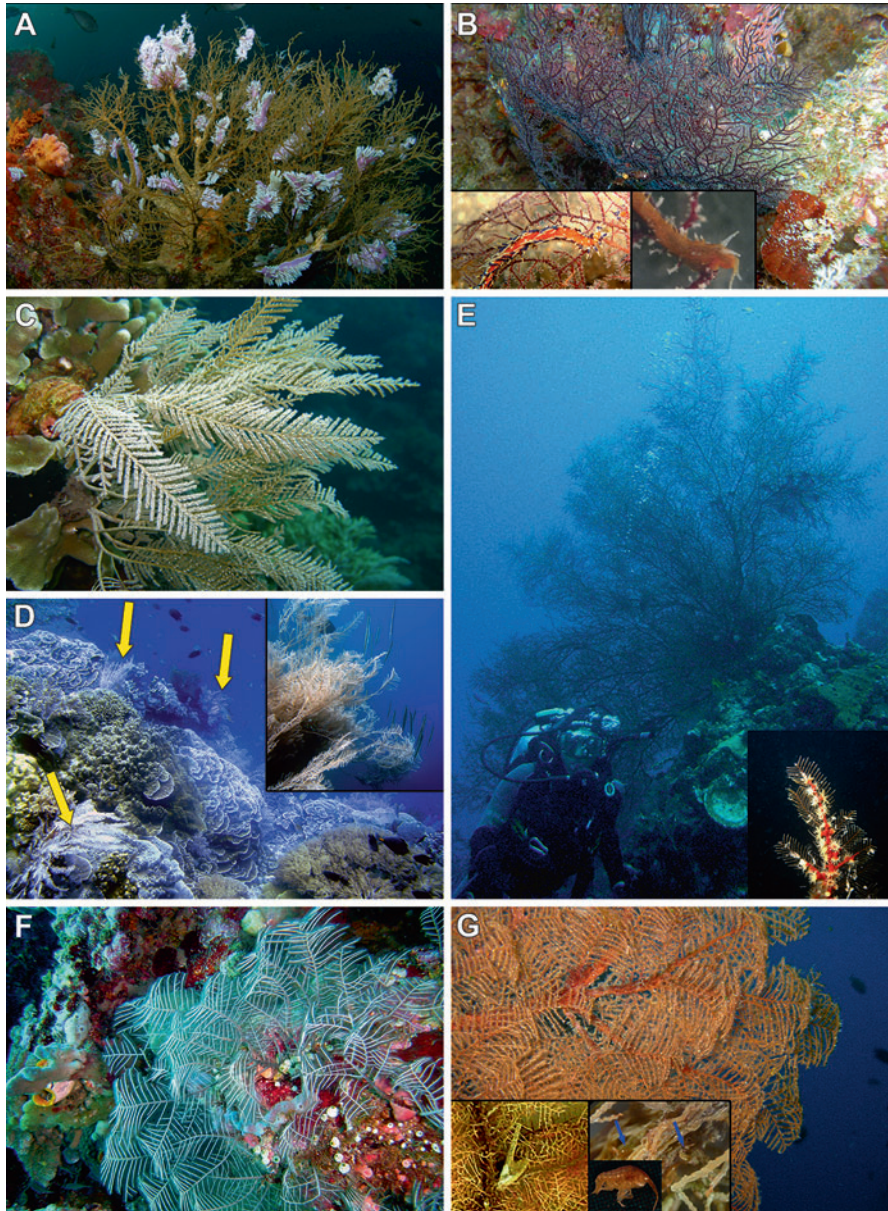


Fig. 3 Some large warm-affinity hydrozoans. (a, b) The subtropical *Solanderia ericopsis* (Carter, 1873) (a) from New Zealand predated by the nudibranch *Jason mirabilis* M. C. Miller, 1974 (photo courtesy of Ian Skip, <http://www.ianskipworth.com> and *Solanderia secunda* (b) from the North Sulawesi. The insets show the polynoid *Medioantenna variopinta* and the nudibranch *Pleurolidia juliae*. (c–d) *Aglaophenia cupressina* from the North Sulawesi; the inset shows a colony explored by razor fish. (e) *Plumularia elongata* from Bali: a large colony completely covered with the zoanthid *Hydrozoanthus* sp. 1 (inset). (f–g) *Macrorhynchia spectabilis* (f) and *Sertularella diaphana* (g) from the North Sulawesi. The insets in Fig. (g) show a pterid bivalve and numerous amphipods respectively on the main axis and on hydrorhiza of *S. diaphana*

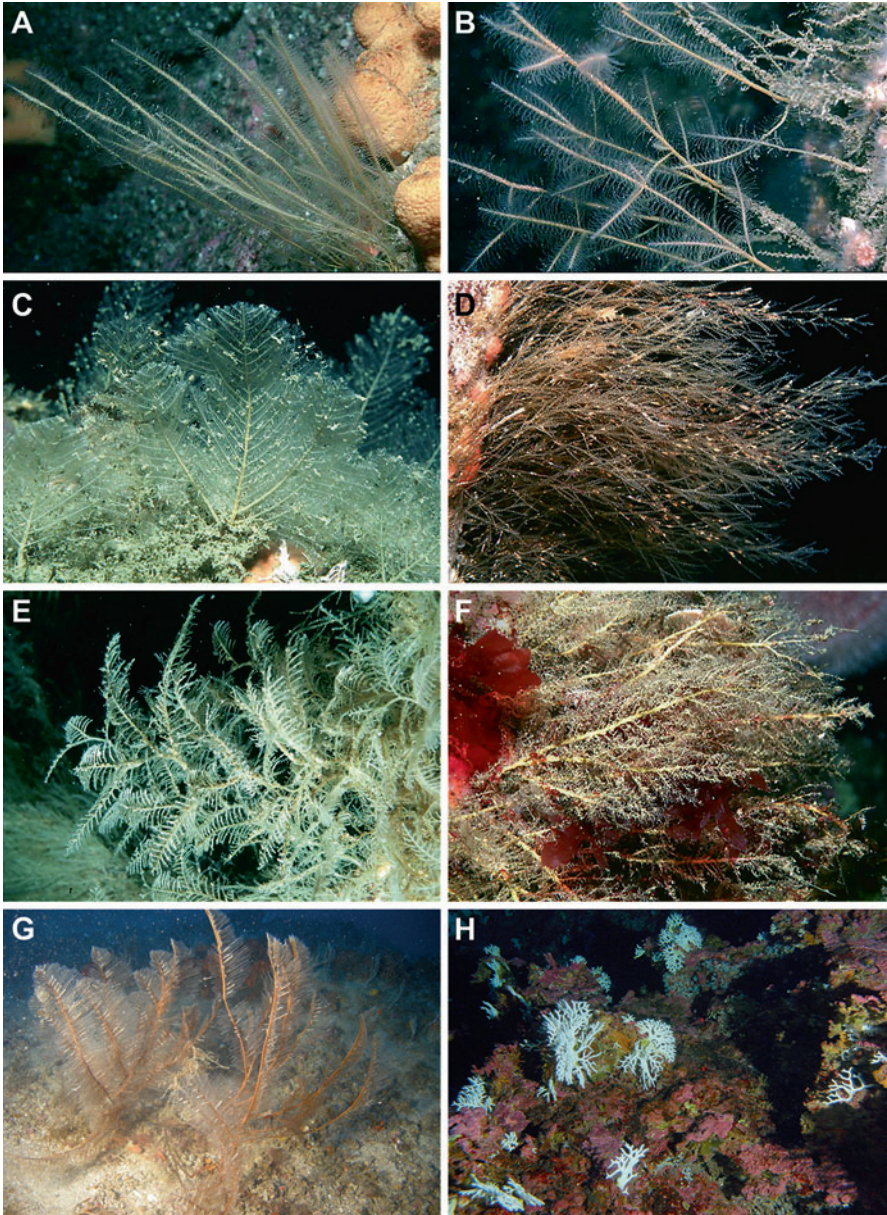


Fig. 4 Some large cold-affinity hydrozoans. (a–f). Hydrozoans from British Isles, photo courtesy of Dr. Bernard Pictet <http://www.habitas.org.uk/marinelife/>. (a) *Nemertesia antennina*. (b) *Nemertesia ramosa*. (c) *Polyplumaria flabellata*. (d) *Amphibestia operculata*. (e) *Hydrallmania falcata*. (f) *Halecium muricatum*. (g) *Lytocarpia myriophyllum* from the Western Mediterranean. (h) The deep stylasterid *Errina aspera* from the Strait of Messina

et al. 2011), while, in the Mediterranean, surveys of *L. myriophyllum* should be performed to collect much information about its distribution and abundance and to develop a proper conservation strategy of this species (Di Camillo et al. 2013).

Indeed, the extension of either perennial or seasonal hydroid forests has never been mapped as carefully as other benthic features, such as coralligenous formations or seagrass meadows.

Phenology and distribution of enduring species should be known to evaluate their importance for ecosystem functioning and to plan conservation programs.

4 Interactions with Other Organisms

Hydroids can establish different kinds of symbiotic relationships with several organisms from viruses to vertebrates, and, due to their wide size range, they can be both hosts and epibionts.

Hydroids increase habitat complexity and enhance biodiversity as demonstrated through the study of temporal variations in composition and biomass of the organisms associated to *Tubularia indivisa* Linnaeus, 1758 from the North Sea (Zintzen et al. 2008). The biomass of most of the symbionts was positively correlated to that of the host, and the maximal epibiont density reached very high values (about 450,000 ind. m⁻²).

Even if several papers describe the entire assemblage of fauna and flora associated to hydroids (e.g., Hughes 1975; Lagardère and Tardy 1980; Bavestrello et al. 1996; Genzano 2001; Zintzen et al. 2008; Meretta and Genzano 2015), the majority of the available literature studies associations involving few taxa, such as endosymbiotic algae (29% of published papers, Fig. 5) and mollusks (19%). There are over 600 papers focusing on interactions between hydroids and other taxa, highlighting that hydroid forests represent a mosaic of microhabitats, exploitable by numerous and diversified organisms. The perisarc composition and the production of secondary metabolites probably affect the attractiveness of hydroid basibionts; moreover, the organic matter trapped by hydroid colonies may support detritus-feeder communities (Bavestrello et al. 2008), whereas other organisms such as amphipods can use the inorganic fraction imprisoned under the hydrorhiza to build their burrows (Genzano 2001). Even the smallest hydroids can host a dense microbiome, composed both of prokaryotic and eukaryotic symbionts (Fig. 6). Stabili et al. (2006) found prokaryotic communities on the perisarc of *Aglaophenia octodonta* Heller, 1868, while Östman (2000) and Di Camillo et al. (2012b) reported bacteria on the bare epidermis of *Pennaria disticha* Goldfuss, 1820, and *Ectopleura crocea* (L. Agassiz, 1862). Schuett and Doepke (2009) recorded microbes inside the tissues of *Tubularia indivisa* Linnaeus, 1758. Among eukaryotes, the microbiome includes diatoms, sessile ciliata such as *Vorticella* and suctorians (Tazioli and Di Camillo 2013), foraminifera, and macroalgae (Bavestrello et al. 2008).

Millepora spp. and *Aglaophenia cupressina* Lamouroux, 1816, are the only large forest-forming hydroids with conspicuous presences in scleractinian-dominated

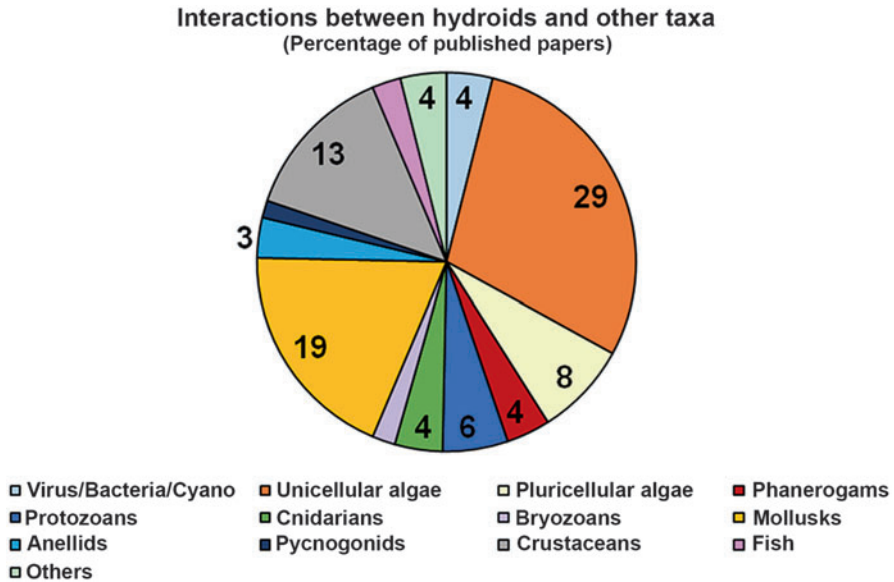


Fig. 5 Percentages of published papers concerning interactions between hydroids and other organisms

shallow reefs. The fact that both species host zooxanthellae (*Symbiodinium* spp.) suggests that the success of these hydroids on the upper part of the reef could be linked to their ability to obtain part of their nutrition from autotrophic sources (Lewis 2006). On the other hand, many zooxanthellate hydroids (e.g., *Hydra* spp., *Myrionema amboinense* Pictet, 1893, *Eudendrium moulouyensis* Marques, Peña Cantero, Vervoort, 2000, *Halecium nanum* Alder, 1859) do have zooxanthellae but do not form forests.

Large hydroids are basibionts for a conspicuous number of taxa due to (i) the large surface offered by their colonies; (ii) the high variety of microhabitats represented by the hydrorhiza, the proximal polysiphonic portions, and the thinner distal branches; (iii) the elevation from the substrate, allowing the settlement of acrophilous species; and (iv) in some case the stability over time of at least the elder and larger basal portions, where organisms are particularly abundant (Garcia et al. 2009; Hughes 1975, 1977).

Some large hydroids such as *Nemertesia antennina* and *Lytocarpia myriophyllum* form a complex rootlike apparatus, which may be composed by several generations of hydrorhizae (Hughes 1977; Di Camillo et al. 2013). In proximity of the substrate, the anchoring system accumulates sediments due to the reduced current speed (Hughes 1978). This three-dimensional holdfast represents a perennial habitat for several organisms, such as those of meiofauna (Cerrano et al. 2015), sponges, pycnogonids, bryozoans (Hughes 1978), or amphipods. The biomass of associated organisms may reduce in distal portions due to the possible presence of defensive/

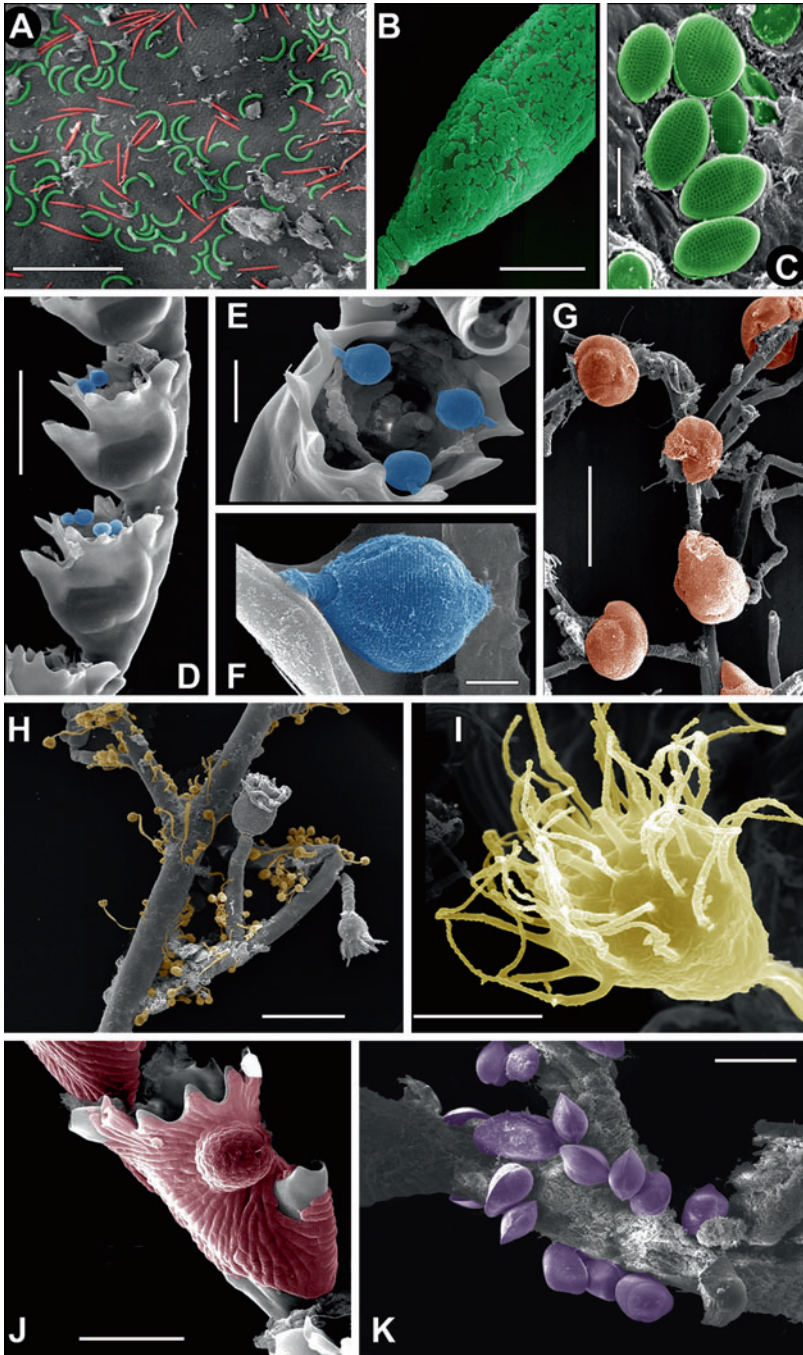


Fig. 6 (continued)

cleaning zooids (Gili and Hughes 1995; Hughes 1978) or because of a higher turnover of the apical branches.

Hydroid's colonies can be the primary substrate for the recruitment of other invertebrates, such as mussel's larvae (Standing 1976; Di Camillo et al. 2012a; Genzano et al. 2003). Big colonies of *Amphisbetia operculata* (Linnaeus, 1758) and *Plumularia setacea* (Linnaeus, 1758) represent the unique filamentous structure in sublittoral outcrops from temperate southwestern Atlantic (Buenos Aires coast), and blue mussel spats use these colonies as primary substrata (Genzano et al. 2003); colonies of *Symplectoscyphus subdichotomus* (Kirchenpauer, 1884) are the main primary settlement substrate of scallop spats in fishing grounds in Argentine sea (Bremec et al. 2008).

Some examples of relationships between large hydroids and associated organisms are summarized in Table 1. *Millepora* spp. form functional biogenic reefs positively influencing fish abundance and species richness, especially in scleractinian-poor Southwestern Atlantic (Coni et al. 2013; Lewis 2006; Pereira et al. 2012; Rogers et al. 2014). Besides fish, *Millepora* forests were found in association with a rich epi- and endofauna represented by crustaceans, echinoderms, mollusks, nemerteans, polychaetes, tunicates, and sipunculids (Cook et al. 1991; Garcia et al. 2009, 2010; Pérez and Gomes 2012).

In temperate waters from southwestern Atlantic Ocean, intertidal colonies of the Anthomedusan *Ectopleura crocea* (Agassiz, 1862) can form dense clumps that support many epizoical microcrustaceans. Colonies also trap sediments under their hydrorhizae where other sediment-associated fauna lives (Genzano 2001). In sublittoral outcrops, two large Leptomedusan hydroid, *P. setacea* and *A. operculata*, represent the most abundant available substrata for numerous vagile and sessile organisms (Meretta and Genzano 2015).

Stylasterid corals enhance habitat complexity offering refuge, food, and a hard substrate to several vagile and sessile invertebrates (Braga-Henriques et al. 2011; Salvati et al. 2010; Pica et al. 2015).



Fig. 6 Microforests living on hydrozoans at scanning electron microscope; recolored pictures. (a) Two microbial morphotypes, one horseshoe shaped (*green*) and another one fusiform (*red*), living on the bared epidermis of *Ectopleura crocea*. (b–c) Portion of the hydrotheca of *Clytia linearis* (b) almost completely covered by the diatom *Cocconeis pseudonotata* (c). (d–f) Sessile ciliated of the genus *Vorticella* settled on the thecal margin of *Aglaophenia kirchenpaueri*. (g) Foraminifers living on cauli of *Eudendrium armatum*. (h–i) A dense assemblage of suctorians settled on a colony of *Eudendrium racemosum*. (j) Hydrotheca of *Aglaophenia tubiformis* covered by the coralline alga *Hydrolithon* cf. *farinosum*. (k) Juvenile of *Mytilus galloprovincialis* on *Eudendrium racemosum*. Scale bars: (a, c, f) 10 µm; (b, d) 200 µm; (e) 50 µm; (g–h) 1 mm; (i) 20 µm; (j) 100 µm; (k) 500 µm

5 Trophic Ecology, Feeding Behavior, and Reproductive Strategies

Hydroid habitat formers do not give rise to large colonies and forests everywhere, suggesting that formation of forests occurs only where food availability can support their development.

The experimental studies performed to define the trophic role of hydroids in marine communities (Table 2) show that hydroids can exploit large quantities of seston, contributing to control the secondary production in coastal waters (Gili and Coma 1998; Gili et al. 1998). Zooplanktonic preys, eggs, merobenthic larvae, phytoplankton, bacteria, and detritus represent the preferential food items of hydroids. The prey composition and predation rates vary in relation to hydroid species, sizes of preys and hydranths (feeding polyps), characteristics of the study areas, temporal fluctuations of environmental parameters (such as temperature, salinity, current intensity), and biotic factors (i.e., predation and competition). Captures are related to the food availability, which can vary daily or seasonally (Table 2). Predation rate is inversely correlated to digestion time (Coma et al. 1994) which, in its turn, is related to hydroid characteristics but also to environmental conditions (i.e., temperature and salinity, Kinne and Paffenhöfer 1965; Gili and Hughes 1995). Besides the size, other features of the ingested preys can condition digestion times, such as the presence of stiff exoskeletons (Orejas et al. 2013). Times required for digestion of some hydrozoans are compared in Table 3.

Different preys have diverse carbon contents; however, the total carbon intake ($\text{mg C m}^{-2} \text{ day}^{-1}$) of the considered hydroid species is comparable to that of other suspension feeders (Gili and Coma 1998, Table 1), suggesting that hydroids play a key role in energy transfer from the pelagic to the benthic realms (Coma et al. 1995, 1998). In particular, hydroids forming large, multibranched colonies could have a great impact on seston since they have a number of feeding polyps much higher than small hydroid species. Large colonies of *Lytocarpia myriophyllum* from the Ligurian Sea have about 1,300,000 feeding polyps m^{-2} (Cerrano et al. 2015), that, applying the lowest feeding rate reported for a cnidarian ($0.01 \text{ mg C polyp}^{-1} \text{ day}^{-1}$, Gili and Coma 1998), could remove up to 13,000 $\text{mg C m}^{-2} \text{ day}^{-1}$.

Standing (1976) and Sutherland and Karlson (1977) showed that hydroids resist overgrowth when present in dense aggregations (forests) being able to prevent the settlement of competitors by feeding on their approaching larvae. This behavior contributed to the proposal of the inhibition model as one of the modes of community development (Connell and Slatyer 1977) and can explain the processes that lead to the establishment of hydroid forests: once established, the forests inhibit the settlement of other species by eating the larvae of potential competitors.

The trophic role of hydroids with medusae is double since they predate both in the benthos and in the plankton. To our knowledge, the complete trophic role of a species with both polyps and medusae has never been studied in detail, accounting for both domains.

Concerning trophic behavior, Miglietta et al. (2000) reviewed a vast array of strategies in the various hydroid species, ranging from passive filter feeding, with the

Table 2 Predation rates of some hydroids from different localities

Species	Locality	Dominant preys	Predation rate	Carbon intake (mg C m ⁻² day ⁻¹)	References
<i>Campanularia everta</i> Clark, 1876	Western Mediterranean	POM (88), copepod eggs (7%)	From 4,000 (summer) to 800,000 (winter) preys m ⁻² day ⁻¹	6.4	Coma et al. 1995; Gili et al. 1998
<i>Ectopleura crocea</i> (Agassiz, 1862)	Mar del Plata	Diatoms (100% in winter), crustaceans (summer)	115 (summer), 93 (autumn), 77 (winter), 200 (spring) preys ind. ⁻¹ day ⁻¹	–	Genzano 2005
<i>Ectopleura larynx</i> (Ellis & Solander, 1786)	Cumbrae (SW Scotland)	Crustacean eggs, nauplii, copepodites	From 36 (day) to 360 (night) preys ind. ⁻¹ day ⁻¹	89.9	Gili et al. 1996, 1998
<i>Eudendrium racemosum</i> (Cavolini, 1785)	Medes Islands (Mediterranean)	–	372,000 preys m ⁻² day ⁻¹ in June	30.7	Rossi et al. 2012
<i>Eudendrium racemosum</i> (Cavolini, 1785)	North Adriatic Sea (Mediterranean)	Bivalve larvae (43%), tintinnids (32%), invertebrate eggs (7%), invertebrate larvae (6%), amphipods (4%)	Over 6,000 preys m ⁻² day ⁻¹ in summer (without considering POM)	13	Di Camillo et al. 2012
<i>Eudendrium racemosum</i> (Cavolini, 1785)	Western Mediterranean	Copepod eggs (28%), Copepods (22%), invertebrate larvae (10%)	120,000 preys m ⁻² day ⁻¹	12	Gili et al. 1998
<i>Eudendrium racemosum</i> (Cavolini, 1785)	Western Mediterranean	Above all zooplanktonic preys (crustacean fragments, copepods, larvae)	100,000 preys m ⁻² day ⁻¹	–	Barangé and Gili 1998
<i>Lytocarpia myriophyllum</i> (Linnaeus, 1758)	Ligurian Sea	–	–	13,000 ^a	Cerrano et al. 2015
<i>Millepora complanata</i> Lamarek, 1816	Barbados	Copepods (63%)	480,000 preys m ⁻² of the corallum's surface day ⁻¹	360,000 mg C m ⁻² of the corallum's surface day ⁻¹	Lewis 1992

(continued)

Table 2 (continued)

Species	Locality	Dominant preys	Predation rate	Carbon intake (mg C m ⁻² day ⁻¹)	References
<i>Nemalocium lighti</i> (Hargitt, 1924)	San Blas Islands (Panamá)	Diatoms (28%), POM (23%); invertebrate larvae (19%); bivalve larvae (11%)	400,000 preys m ⁻² day ⁻¹	6	Gili et al. 1998; Coma et al. 1999
<i>Obelia dichotoma</i> (Linnaeus, 1758)	Kongsfjorden (Spitsbergen, Arctic)	Fecal pellets (up to 57% of the total ingested food), phytoplankton (up to 50%), and organic matter (up to 35%)	261,182 preys m ⁻² day ⁻¹	5.5–8.9	Orejas et al. 2013
<i>Obelia geniculata</i> (Linnaeus, 1758)	Chile	Fecal pellets (48%), Copepod eggs (29%), diatoms (17%)	3,200,000 preys m ⁻² day ⁻¹	48	Gili et al. 1998
<i>Silicularia rosea</i> Meyen, 1834	King George Island (Antarctica)	Benthic diatoms (95%), eggs (2%)	4,000,000 preys m ⁻² day ⁻¹	66	Gili et al. 1996, 1998

^aEstimated applying the lowest capture rate calculated for cnidarians (0.01 mg C ind.⁻¹ day⁻¹, from Gili and Coma 1998)

Table 3 Digestion time of some hydroids estimated in experimental conditions

Species	Sampling site	Rearing conditions	Preys	Digestion time (h)	References
<i>Ectopleura larynx</i> (Ellis & Solander, 1786)	Cumbrae (SW Scotland)	15 °C	Small	2–3	Gili et al. 1996
			Large	5	
<i>Ectopleura crocea</i> (Agassiz, 1862)	Mar del Plata			4–5	
<i>Obelia dichotoma</i> (Linnaeus, 1758)	Arctic waters	6 °C	A single diatom	20	Orejas et al. 2013
<i>Hydractinia echinata</i> (Fleming, 1828)	Knähaken Reef (Øresund, NE Atlantic)	4 °C		40	Chistensen 1967
		16 °C		5	
<i>Silicularia rosea</i> Meyen, 1834	King George Island (Antarctica)	0–2 °C	Diatoms	12	Gili et al. 1996
<i>Campanularia everta</i> (Clark, 1876)	Medes Islands (NW Mediterranean)	18 °C		2	Coma et al. 1995
<i>Clava multicornis</i> (Forsskål, 1775)	Helgoland (North Sea)	12 °C (32‰ S)	Artemia larvae	8	Kinne and Paffenhöfer 1965
		17 °C (32‰ S)	Artemia larvae	6	
		22 °C (32‰ S)	Artemia larvae	4	
<i>Garveia franciscana</i> (Torrey, 1902)	Russia	23–26 °C		3–4	Simkina 1980
<i>Eudendrium racemosum</i> (Cavolini, 1785)	Medes Islands (NW Mediterranean)	18 °C		5	Barangé and Gili 1988

outstretched tentacles used as a filter, to active feeding achieved by movement of the whole polyp in a “searching” pattern, to rhythmic tentacle contraction causing microcurrents that convey small prey toward the mouth. As it might have been expected, specific studies (Gili et al. 1996; Miglietta et al. 2000) showed that small polyps mostly eat small food items, usually protists, whereas large polyps catch larger prey, ranging from crustaceans to other planktonic and benthic prey. Miglietta et al. (2000) distinguish active filter feeders that produce microcurrents that draw food particles toward the mouth (e.g., *Aglaophenia*) and passive filter feeders that extend their tentacles and wait for prey (e.g., *Tubularia*). The subantarctic hydroid *Silicularia rosea* Meyen, 1834, from the intertidal communities of King George Island ingests above all benthic diatoms resuspended by tidal current. The hydroid

rhythmically expands and contracts its tentacles in order to increase the flow of particles toward the mouth (Gili et al. 1996). Some species with small hydranths such as *Lytocarpia myriophyllum* and *Aglaophenia cupressina* produce conspicuous amount of mucus probably acting as a trap of organic matter (Puce et al. 2002).

Hydroids hosting zooxanthellae (i.e., *Myrionema* spp., *Eudendrium molouyensis*, *Millepora* spp., *Aglaophenia cupressina*) probably adopt a mixotrophic strategy and exploit products of the photosynthesis in oligotrophic waters.

Trophic strategies are finalized to optimize the hydroid reproductive effort: since the reproductive period overlaps, at least partially, with the higher food intake and the maximal colony size, it is hypothesizable that hydroids store the energy necessary to produce gametes or medusae (Rossi et al. 2012 and references therein). Thanks to their plasticity, hydroids can adapt the shape of their colonies to increase the feeding surface and to give rise to an efficient three-dimensional predation system (Gili and Hughes 1995; Rossi et al. 2012).

The reproductive patterns do have a major role in the persistence of perennial hydroid forests. Large polyp colonies with fixed gonophores such as the *Eudendrium* studied by Wasserthal and Wasserthal (1973) produce planulae that settle directly in the vicinity of the mother colony, so contributing to the persistence of the forest. Hughes (1977) observed similar patterns for *Nemertesia*. Furthermore, these large colonies do spend the adverse season as resting hydrorhizae and continue to occupy the substrate. Boero et al. (1986) showed that the forest-forming *Eudendrium glomeratum* has a mixed strategy, with new colonies deriving from planulae and old colonies that regenerate from the resting stolons. The life histories of most species, however, are unstudied, and further research is needed to substantiate these patterns. The presence of medusae, due to the high vagility of this life form, should have more opportunistic polyps, even though the medusa stage is present in most of the very specialized forms that live in strict symbiosis with other animals (Puce et al. 2008), whereas those associated with plants do not follow this rule.

6 Emerging Threats for Hydroid Forests

As other “animal forests,” hydroid assemblages represent fragile and diverse systems that could suffer severe threats from direct and indirect impacts and for the lack of a clear responsibility for some human activities in coastal and offshore benthic systems (Rossi 2013).

As shown in Fig. 1, researches on hydroids and environmental/anthropogenic stresses have been increasing. These papers highlight that the three-dimensional habitats formed by hydroids could be threatened from direct (bottom trawling, pollution, urban expansion, tourism, harvesting of precious corals, aquaculture, mining, introduction of alien species) and indirect (ocean acidification and global warming) anthropic impacts (Rossi 2013).

Bottom trawling, among fishing activities, is the most devastating practice for animal forests (Rossi 2013), due to the destruction of the fragile species and the

sediment compactness, leading to the simplification of the benthic ecosystems (Althaus et al. 2009; Clark et al. 2010; Rossi 2013). Hydroids living on dredgeable soft substrates, such as *Lytocarpia myriophyllum* and *Nemertesia* spp., are vulnerable to the effects of mechanical disturbances. Up to now, the role of soft-bottom habitat formers received little attention despite they create secondary hard substrata (Hughes 1975, 1977, 1978; Ammons and Daly 2008; Cerrano et al. 2015; Di Camillo et al. 2013).

Global warming is leading to changing in the benthic domain (Boero and Bonsdorff 2007; Lejeusne et al. 2010) favoring the establishment of tropical non-indigenous species (Coll et al. 2010; Lejeusne et al. 2010) and leading to the regression or disappearance of autochthonous, cold-affinity species (Boero et al. 2008; Rivetti et al. 2014; McCauley et al. 2015). Analysis of records over time can provide “early warning signals of species” that may encounter higher probabilities of local extinction involving several mechanisms at different spatial and temporal scales (Gravili et al. 2013, 2015). According to Puce et al. (2009) and Gravili and Boero (2014), in the Mediterranean Sea, larger *Halecium* species (e.g., *Halecium beanii*, *H. halecinum*, *H. labrosum*) are regressing compared to smaller ones (e.g., *Halecium petrosum*, *H. pusillum*, and *H. tenellum*). Large-size *Halecium* species, in fact, can be considered as habitat modifiers that create wide marine forests maintaining and modifying habitats (Fraschetti et al. 2008; Piraino and Fanelli 1999; Piraino et al. 2002). Ocean acidification could affect hydroid producing calcified skeletons, such as stylasterids and milleporids, or the partly calcified such as the Alaskan hydractiniid *Schuchertinia antonii* (Miglietta 2006).

Moreover, intensive aquaculture is responsible for composition changes of the animal forest by water eutrophication, pollution, introduction of invasive species with evident changes in the trophic chain, simplification of the ecosystems, and accumulation of sediments (Borja et al. 2009; Rossi 2013).

Some hydroid species are harvested for ornamental purposes, such as *Sertularia argentea* and *Hydrallmania* (Hancock et al. 1956); *S. cupressina* Linnaeus, 1758 (Wagler et al. 2009); or stylasterids (Cairns 2011), with presumably negative consequences on their conservation status. Moreover, this state is worsened by the deficiency of clear legal rules in the management of marine communities (Rossi 2013).

Other hydroids take advantage from anthropic impacts, such as those able to proliferate on artificial or modified substrates (e.g., among the genera *Clytia*, *Obelia*, *Ectopleura*, and *Pennaria*) (Morri and Boero 1986).

Deciduous and enduring hydroid forests probably respond in different ways to the effects of the abovementioned threats. Seasonal hydroids, due to their fast growth, plasticity, and above all their ability to enter dormancy, could overcome temporal unfavorable environmental conditions (Di Camillo and Cerrano 2015). Enduring forests formed by large, slow-growing hydroids could be more vulnerable to environmental changes (Di Camillo et al. 2013), especially considering species producing calcified or strongly polysiphonic skeletons or those associated with zooxanthellae (Banaszak 2003).

7 Conclusions

The scientific literature on hydroids here reported clearly highlights a gap in supplying quantitative data, limiting the possibility to compare information on hydroids with those available for other suspension feeders, to evaluate the impact of hydroids on seston, to calculate energy budgets, and therefore to define their actual role in benthic-pelagic coupling.

Moreover, most of studies focused above all on species easy to rear (i.e., *Hydra* spp.) or on shallow-water hydroids easy to study in situ. Since several species live in environments difficult and/or expensive to be explored, there are very few data available on cryptic, tropical, polar, and deep hydroids, suggesting that we have only a partial knowledge on hydroid ecology.

Data on enduring species – forming the largest hydroid forests – are still insufficient to understand their function in benthic communities and to assess their vulnerability to climate changes.

Knowledge on ephemeral hydroids allows using them as indicators of several environmental conditions (Mergner 1987). Long-term studies on hydroid diversity and life histories may allow to detect early signs of the effects of water warming and other environmental stresses or to pinpoint nonindigenous species, identifying variations in composition, abundance, and reproductive periods (Puce et al. 2009; Gravili 2016).

The importance given to algal canopies in the description of habitats and in the determination of conservation policies must be extended also to animals that, in the past, were named “zoophytes,” since they have a similar structural role to that of algae as habitat formers, extending also at depths where algal growth is not optimal. Hydroids do have a higher trophic level than algae and represent an important link between the benthic and the planktonic realms, due to the production of medusae and to predation on both benthic and planktonic organisms.

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