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The ecology of protists epibiontic on marine hydroids

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Several hydroid species have an epibiontic lifestyle, living associated with organisms of many different phyla. On the other hand, hydroids can also host dense assemblages of microflora and microfauna, mainly composed of protists and bacteria. Among protists, diatoms are the most abundant and diversified group, followed by foraminifera and sessile ciliata such as Vorticella *and suctorians. Regarding the spatial distribution of epibionts, hydroid colonies represent a mosaic of different microhabitats: in some species, each colony portion (base of the stem, branches, pedicels, inner space between the polyp and the theca) hosts different diatom species. Moreover, three foram species have been shown to occupy different positions according to the plasticity of their shell. A host specificity has been also observed: some epibionts are typical of only one or a group of species, such as* Vorticella *living on the teeth of the* Aglaophenia *thecae or coralline algae that cover mainly* Aglaophenia *and* Sertularella *colonies. The microassemblage associated to* Eudendrium racemosum *showed a typical seasonal cycle and a vertical distribution which reflects the selective advantage of the different life forms. Experiments with plastic structures miming hydroid colonies demonstrated that the living hydroid affects the assemblage structure. Probably, the perisarc composition and secondary metabolites play a crucial role in the relationships between hydroids and their microassemblage.*

Keywords: Epibiosis, protists, hydroid microhabitats, perisarc, Mediterranean Sea

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The branched colonies of several hydroids are a suitable substrate for sessile (Hughes, 1975, 1978a,b) and vagile epibiontic organisms (Lagardère & Tardy, 1980; Bavestrello *et al.*, 1996). Generally the hydroid does not represent for these organisms a mere low-competition substratum but several examples of relationships occurring between the host and its epibionts are here described. Lagardère & Tardy (1980) recorded a complex behaviour of a syllid polychaete that fixes its tubes immediately under the polyps of *Tubularia larynx*. In this situation, the polychaete eats part of the food captured by the polyps, and is able to defend the host from nudibranch predation. Some species of caprellid amphipods living on *Eudendrium* are able to use the polyps as traps to collect planktonic prey. When a polyp has caught and engulfed prey, the caprellid opens the polyp mouth by its gnatopods and extracts and eats the prey (Bavestrello *et al.*, 1996). It was observed that the polyps of *Eudendrium* never eat the harpacticoids living on their colonies (Bavestrello *et al.*, 1996), while it was demonstrated that polyps of this genus are generalistic predators engulfing all the prey with a diameter compatible with their hypostome (Barangè, 1988).

Recently it was demonstrated that several microorganisms, such as protists and bacteria, are able to live on hydroid colonies. Stabili *et al.* (2006) have shown that chitinolitic, luminous bacteria of the genus *Vibrio* live on the perisarc of several species and Romagnoli *et al.* (2007) have recorded bacterial and cyanobacterial mats on the branches of *Eudendrium*.

Benthic diatoms are very common on the hydroid branches where they produce dense assemblages or exploit more specific microenvironments such as the inner side of hydrothecae or the narrow grooves between the annuli of branches (Di Camillo *et al.*, 2005; Romagnoli *et al.*, 2007). Sessile ciliates such as *Ephelota* have commonly been recorded on several hydroid species (Di Camillo *et al.*, 2005), while *Vorticella* is a typical epibiont of some species of *Aglaophenia* where it settles on the edge of the theca (unpublished).

The aim of this paper is to summarize recorded data about the protists associated with marine hydroids, pointing out some ecological aspects of these epibiontic communities.

Diversity and abundance

The microassemblages recorded on the hydroid colonies are often very rich. The main epibionts are diatoms (Figure 1) followed by protozoans, both sessile ciliate (Figure 2) and forams (Figure 3). On the branches of *Eudendrium racemosum* collected in the Ligurian Sea at shallow depths, almost 107 species of diatoms belonging to 52 genera were recorded during an annual cycle (Romagnoli *et al.*, 2007) (Figure 1A,B). The maximum diatom abundance exceeded 45,000 cells mm^{-2}. This datum is particularly impressive if compared with others recorded on living substrata: 1000 cells mm^{-2} on gastropod shells (Gillan & Cadée, 2000);

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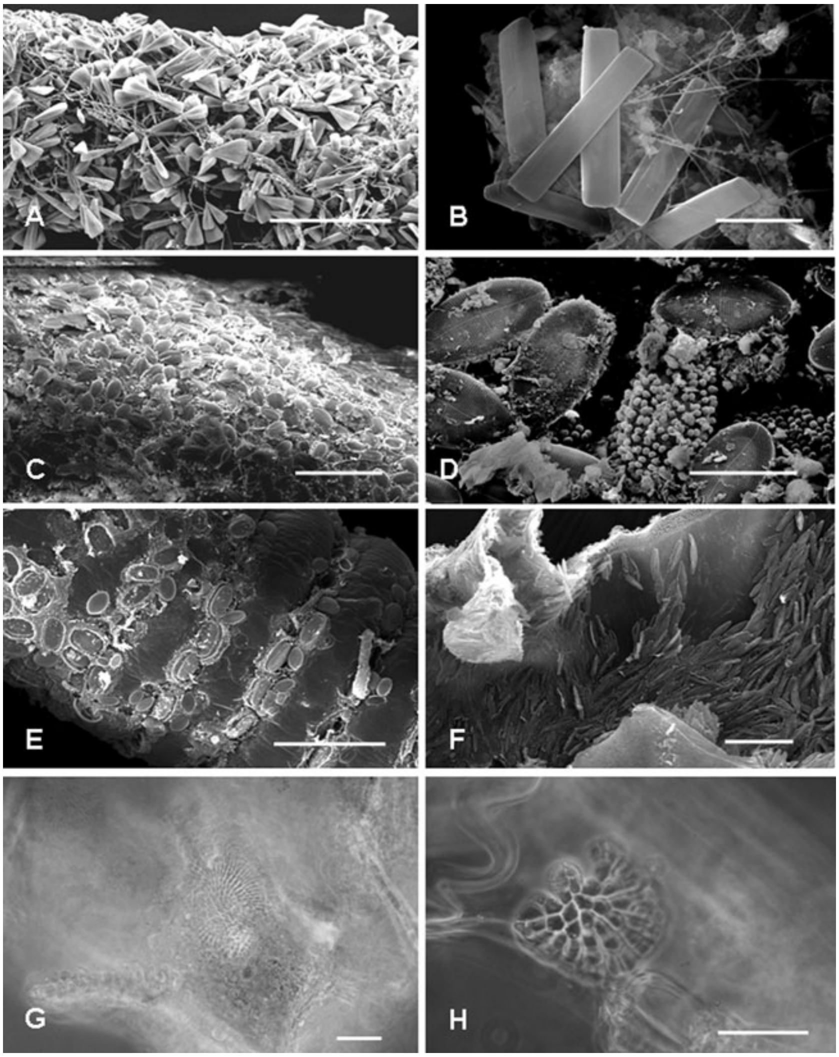

Fig. 1. Algal assemblages associated with marine hydroids. (A–F) Scanning electron microscope (SEM) pictures of diatom assemblages on hydroids. (A) *Licmophora* spp., erect diatoms that colonize the apical part of *Eudendrium racemosum*; (B) *Cyclophora tenuis* forming erect colonies on the *E. racemosum* skeleton; (C) *Cocconeis* spp., adnate diatoms covering the basal part of the *E. racemosum* colony; (D) *Cocconeis notata* on the inner side of *Campanularia hincksii* hydrothecae; (E) *Cocconeis pseudonotata* on the pedicel of *Clytia linearis*; (F) *Navicula* sp. inside the theca of *Synthecium evansi*; (G–H) light microscopy pictures of initial cells of coralline algae epibiontic on marine hydroids; (G) *Melobesia membranacea* on *Sertularella ellisii* hydrotheca; (H) *Hydrolithon farinosum* on *Aglaophenia tubiformis* hydrotheca. Scale bars: A, 200 μm; B, D, 20 μm; C, E, F–H 50 μm.

120 cells mm^{-2} on mussel shells (Bodeanu, 1988); and 1 cell mm^{-2} on the carapace of horseshoe crabs (Patil & Anil, 2000). On the bryozoans *Electra pilosa*, *Membranipora membranacea*, *Flustra foliacea* and *Alcyonidium gelatinosum* from the German Bight, members of 26 diatom genera were found with densities of 71–547, 77–110 and 1–27 cells mm^{-2} respectively for *E. pilosa*, *M. membranacea* and *A. gelatinosum* while on *F. foliacea*, diatoms were present with very low abundances (<5 cells mm^{-2}) (Wuchter *et al.*, 2003).

On rocks, the maximum diatom densities reported range from 2200 to 5600 cells mm^{-2} (Hudon & Bourget, 1981; Brandini *et al.*, 2001; Totti *et al.*, 2007). The values observed on hydroids were higher and comparable with those recorded on highly productive soft intertidal sediments (Admiraal *et al.*, 1982; Delgado, 1989; Delgado *et al.*, 1991; Peletier, 1996).

Together with diatoms, the colonies of *Eudendrium racemosum* are also rich in assemblages of filamentous cyanobacteria (up to 30,000 cells mm^{-2}) (Romagnoli *et al.*, 2007).

Also protozoans are often very abundant on the colonies of several hydroid species. On pinnate colonies of *Aglaophenia elongata*, 7 cm high, living at 25 m depth on the Portofino Promontory (Ligurian Sea), about 3000 cells of *Vorticella* sp. were recorded, with an average number of about 4 cells per theca (Figure 2A & D) (unpublished).

Few works have focused on the diversity and the abundance of foraminifera on hydroids: Dobson & Haynes (1973) described about 70 species settled on the hydroids dominating the benthic communities of the deep shelf of the Irish and the Malin Seas. Some species, such as *Rupertina stabilis*, *Planulina ariminensis* and *Cibicioides wuellerstorfi* were observed on the hydrocauli of some hydroids (Lutze & Altenbach, 1988; Lutze & Thiel, 1989). Recently, we observed on average 25 cells of *Rosalina globularis* living on *Eudendrium* colonies (Figure 3A,B) from the northern Sardinia coast (Di Camillo *et al.*, in press), while on specimens from the Portofino Promontory more than 3500 cells per colony were counted (unpublished).

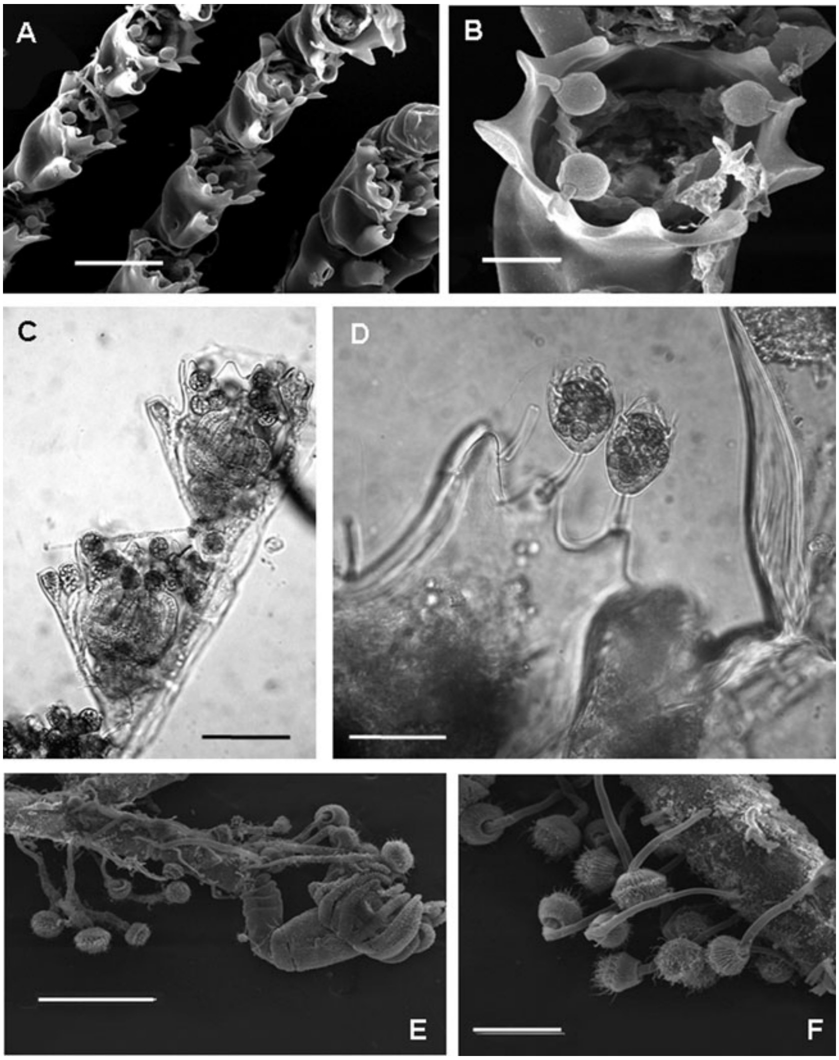

Fig. 2. Sessile ciliates. (A) The SEM image of *Vorticella* sp. on thecae of *Aglaophenia kirchenpaueri* from Messina Strait; (B) close-up image showing the protozoans attached on the inner side of the marginal teeth; (C) thecae of *Aglaophenia octodonta* from Conero Riviera hosting numerous cells of *Vorticella* sp.; (D) living *Vorticella* on the thecal margin of *Aglaophenia tubiformis* from Apulian Coasts; (E–F) suctorians of the *Ephelota* genus on the pedicel of *Eudendrium racemosum*. Scale bars: A, C, F, 200 μm; B, 50 μm; D, 100 μm; E, 500 μm.

Specificity

At the present state of knowledge, it is difficult to clarify the existence of species-specific relationships between protist epibionts and the hosting hydroids. The existence of host specificity was suggested for diatoms by Sullivan (1984), as certain epiphytic species were distributed only on particular macrophytes, but these have also been interpreted as a response to different physical conditions (Sullivan, 1981). Diatoms of the genus *Cocconeis* and *Navicula* were frequently observed on thecate hydroids (Figure 1C–F), but these two genera are also widely distributed in many benthic habitats.

A more specific relationship involving hydroids and protists hitherto recorded is that of the filter-feeder ciliates of the genus *Vorticella* and the hydroids of the genus *Aglaophenia* and *Plumularia*. We observed this association in several *Aglaophenia* species in different localities of the Mediterranean: *A. octodonta* and *A. elongata* from Portofino Promontory (Ligurian Sea), *A. elongata* from the Lebanon coast (eastern Mediterranean), *A. harpago* and *A. octodonta* from the Conero Riviera (central Adriatic Sea), *A. tubiformis* from Otranto (southern Adriatic) and *A. kirchenpaueri* from the Messina Strait (unpublished). The specificity of this relationship is demonstrated by the spatial position of the cells that are attached through their contractile peduncle exactly on the edge of the hydroid theca (Figure 2C,D). Up to 12 cells may settle on one theca (Figure 2C): if disturbed, the protozoans quickly retract into the inner wall of the theca.

Other relationships are less specific but it is clear that some hydroid groups are particularly suitable as substratum for epibionts. Several species belonging to the family Sertulariidae, both in the Mediterranean and in tropical waters, are covered by a coat composed of coralline algae mixed with benthic diatoms. Encrusting Corallinales were frequently recorded on *Sertularella ellisii* and *S. crassicaulis* from several Mediterranean localities (Figure 1G). Although more than 100 hydroid species were examined from Portofino Promontory, *Pneophyllum fragile*, *Hydrolithon* cf. *farinosum* and *Melobesia membranacea* were found only on these two species and, in one case, also on *Aglaophenia tubiformis* (Figure 1H) where they form only small spots on the hydrothecae. On the exoskeleton of the two species of *Sertularella*

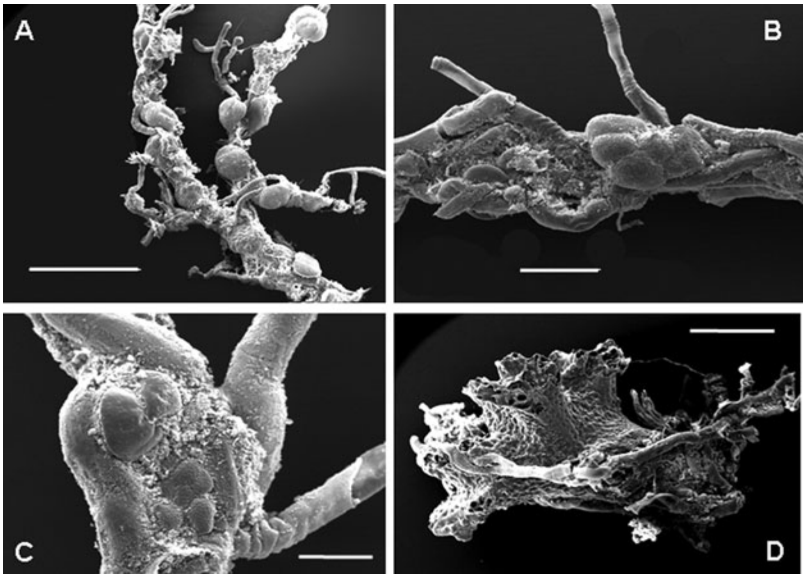

Fig. 3. Foraminifera epibiontic on *Eudendrium armatum*. (A) Several tests of *Rosalina globularis* on the thin apical pedicels; (B) *Lobatula lobatula* on a slightly polysiphonic branch; (C) *Acervulina inhaerens* between two tubes of a polysiphonic branch; (D) *Miniacina miniacea* growing around the hydroid stem. Scale bars: A, 2 mm; B, 500 µm; C, 200 µm; D, 1 mm.

coralline algae were observed forming a continuous coat completely covering the hydroid perisarc, except for the thecal opercula and gonothecae. During springtime, the coralline coat reaches its maximal development completely covering the colonies which appear pink in colour. The presence of hydranths inside the thecae indicated that the hydroid colonies were still living and probably the host was not damaged by its epibionts (Di Camillo *et al.*, 2006).

Sometimes, epibionts show preferences among different host species belonging to the same genus. On the Sardinia coast the abundance of some foram species (Figure 4) is related to the colonized species of *Eudendrium*. *Rosalina globularis* (Figure 4A) was observed on all the *Eudendrium* species recorded in the locality but its average abundance decreases from 25 tests per colony in *E. armatum* to 17 in *E. glomeratum* to 12 in *E. racemosum* and 8 in *E. molouyensis*. *Lobatula lobatula* (Figure 4B), *Acervulina inhaerens* (Figure 4C) and *Miniacina miniacea* (Figure 4D) are mainly present on *E. armatum*, rarely on *E. glomeratum*, and never on the other species (Di Camillo *et al.*, in press). These data confirm unpublished observations from the Portofino Promontory where the tests of *Rosalina globularis* present on *E. armatum* are two orders of magnitude greater than those recorded on *E. racemosum*. This specificity could be related to the interaction between foraminifera and their host but probably the ecological preferences of the host also affect the epibiont abundances.

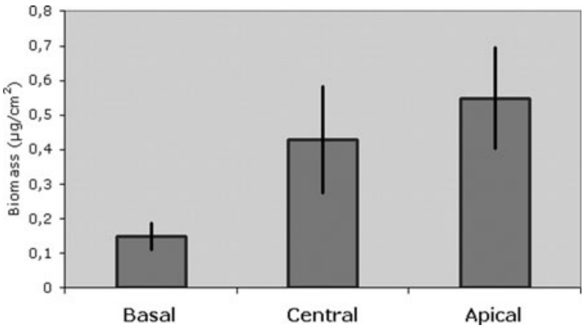

Fig. 4. Diatom abundance (means ± SE) on different portions of the colonies of *Eudendrium racemosum* from the Ligurian Sea.

Spatial distribution

Hydroid colonies represent an amazing mosaic of different microhabitats exploited by a variety of protists. The highly specific position of *Vorticella* sp. on *Aglaophenia* theca was described above. On *Eudendrium*, the suctorian *Ephelota* was present only on the pedicels, immediately under the polyps (Figure 3E,F) (Di Camillo *et al.*, 2005).

On the branched, polysiphonic colonies of *E. armatum*, four species of foraminifera—*Rosalina globularis, Lobatula lobatula, Acervulina inhaerens* and *Miniacina miniacea*—occupied different positions, due to the shape and the plasticity of their tests and the size of the hydroid branches. In particular, *R. globularis* settled only at the apex of the thin branches; *L. lobatula* was found only at the level of branch bifurcation, while *A. inhaerens* colonized the vertical grooves between two adjacent tubes of a polysiphonic branch. Finally, the large colonies of *M. miniacea* were observed only in the highly polysiphonic basal region (Di Camillo *et al.*, in press).

Generally, diatoms occupy each part of the hydroid colony, like the base of the stem, the branches, the pedicels and the inner space between the polyp and the theca. At shallow depths, where enough light is available, the stem and branches of *Eudendrium racemosum* were covered by an extremely rich diatom assemblage (Romagnoli *et al.*, 2007). The assemblage is mainly composed of motile diatoms (*Navicula* spp.), followed by erect species such as *Licmophora* spp. (mainly *L. oedipus* and *L. flabellata*), *Tabularia tabulata* and *Cyclophora tenuis*, and adnate, such as *Amphora* spp. and *Cocconeis* spp. (*C. stauroneiformis*, *C. scutellum* and *C. neotumensis*) and tube-dwelling

(*Berkeleya rutilans* and *Parlibellus* sp.). As a rule, the erect diatoms colonized the upper part of the hydroid, while the adnate ones colonized the lower part of the stem. Diatom abundance showed a clear relationship with position on the colony. The number of cells increases from the base of the colony towards the apex indicating a direct effect of the polyps on the abundance of the epibionts (Figure 4). The diatom covering stopped at the base of pedicels which are sometimes colonized by *Ephelota* sp. (Di Camillo *et al.*, 2005). In any case, the abundance of diatoms increases from the base to the apex of the colony, suggesting a certain degree of interaction between algae and polyps (Romagnoli *et al.*, 2007).

On some hydroids like *Campanularia hincksii*, diatoms do not settle on the external side of the theca, while a monospecific diatom assemblage of *Cocconeis notata* living only on the inner side of the theca was recorded (Di Camillo *et al.*, 2005). On the external side of the theca of *Clytia linearis*, the colonization of *Cocconeis pseudonotata* starts from the vertical grooves present in each tooth and then continues downwards completely covering the theca and pedicel in a continuous layer. At the same time, inside the theca, a population of the pinnate diatom *Cylindrotheca* sp. occurs. The green colour and the movement of the cells clearly indicate that they are living and that apparently, their presence did not damage the polyps, which always remained alive. A similar situation was observed on *Synthecium evansi* where *C. neothumensis* var. *marina* colonized the perisarc surrounding stem, branches and thecae, while *Navicula* sp. was localized exclusively inside the thecae (Di Camillo *et al.*, 2005).

These examples indicate that a number of factors—shape of the host, life-form of epibionts, trophic relationships with the polyps, light exposition, competition between different epibionts—are involved in determining the spatial distribution on the colonies. The narrow space between the internal sides of thecae and polyps is a particularly interesting habitat colonized by diatoms. Probably, the thin perisarc is sufficiently transparent to allow light penetration but on the other hand several mixotrophic diatoms are known in habitats strongly favouring heterotrophic growth, where light is absent or limited and organic substrates are in great supply (Matsuda *et al.*, 1987). Several diatom species have evolved highly sophisticated and ecologically significant mechanisms for facultative heterotrophy, developing active transport systems for a limited number of organic substrates (glucose, lactate and glutamate) in response to low light or darkness conditions (Myklestad *et al.*, 1989).

Temporal distribution

Sometimes the protists epibiontic on hydroid colonies showed a clear seasonal trend. On *Aglaophenia* the *Vorticella* cells are present only in summer, with a maximum in May (unpublished). Also the foraminifera of the genus *Rosalina* on *Eudendrium* in the Ligurian Sea are present only in summer (unpublished). In these seasonal variations, the cycles of both the epibiont and the host are involved.

The best described case is the microalgal assemblage on *Eudendrium racemosum*. On colonies of this species, diatoms and cyanobacteria abundance showed opposite seasonal trends, with diatoms mainly abundant in winter and spring and cyanobacteria in summer (Figure 5). Within the diatom assemblage, the different life-forms—motile, adnate, erect and tube dwelling—showed a different pattern of annual cycle. Among them, adnate diatoms, which live attached to the substratum and have limited motility, showed an annual cycle which paralleled that of hydroid host, suggesting that they can benefit from the host association, probably through the nutrient supply from the host itself (Romagnoli *et al.*, 2007).

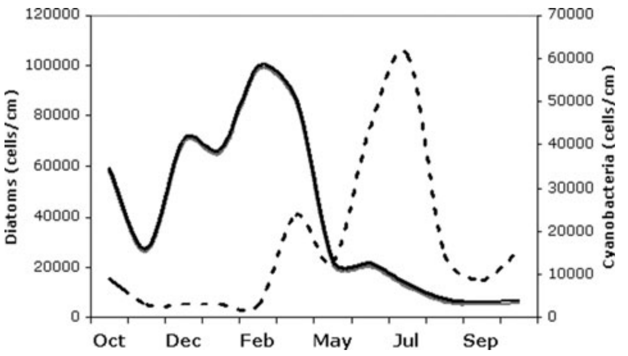

Fig. 5. Annual trends of the abundance of diatoms (continuous line) and cyanobacteria (dotted line) on the colonies of *Eudendrium racemosum* from the Ligurian Sea.

General considerations

The data here summarized clearly indicate that the colonies of large hydroids are not only hot spots of biodiversity hosting numerous, sometimes poorly known species, but also have repertoires of complex life histories co-evolved between epibionts and their hosts, presumably in a short span of time.

In the establishment of these relationships, a pivotal role is played by the perisarc enveloping stem and branches and, in the thecate hydrozoans, also the polyps. In all the revised papers diatoms and protozoans settle on different parts of the perisarc. In athecate hydroids, like *Eudendrium*, both diatoms and the suctorian *Ephelota* stop immediately under the polyps. Some diatoms may settle on the hydroid buds that are covered by a thin sheet of perisarc, but when polyps born from the bud, the diatoms disappear (Romagnoli *et al.*, 2007).

The perisarc is composed of chitin, sometimes linked with different proteins (Jeuniaux, 1963; Holl *et al.*, 1992). However, no comparative studies are available on the perisarc characteristics of different hydroid species. Different kinds of proteins presumably present in different hydroid groups could selectively influence epibiont colonization.

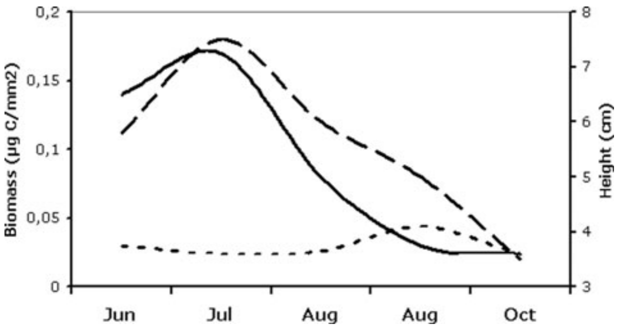

Fig. 6. Temporal trend of diatom biomass on the colonies of *Eudendrium racemosum* (continuous line) and on plastic mimes (dotted line) compared with the trend of the height of the hydroid colonies (stacked line).

The perisarc acts not only as an inert substratum but in fact it was experimentally demonstrated that on living colonies of *E. racemosum*, diatom communities showed significantly higher abundance and biomass values than on artificial mimic plastic substrata (Figure 6). When colonies died, on the remaining stems the number of diatom cells become similar to those recorded over the same period on the artificial mimes (Romagnoli *et al.*, 2007). This evidence demonstrates that the host's metabolism and life style is crucial in affecting the amount and compositions of the epibiontic communities.

Several field studies on the effects of habitat structure on species assemblages have indicated that habitat heterogeneity (Pimm, 1984) does not enhance biodiversity as expected theoretically (McGuinness & Underwood, 1986; Beck, 1998, 2000; Guichard & Bourget, 1998). This review shows that hydroid colonies can be a driving force in determining levels of biodiversity. This role of hydroid colonies was also demonstrated by Bradshaw *et al.* (2003) in the Irish Sea, where upright sessile epifauna structurally increased habitat heterogeneity leading to a general enrichment of biodiversity.

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