

Life history of *Perarella schneideri* (Hydrozoa, Cytaeidae) in the Ligurian Sea*

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SUMMARY: *Perarella schneideri* is a cytaeid hydroid living in association with the bryozoan *Schizoporella longirostris*. In this study we have distinguished the presence of two kinds of polyps in its colonies: large gastrozooids and very extensible filiform polyps with 4 short tentacles. A study of the relationships between the hydroid and its host indicates a parasitic behaviour of *P. schneideri* on bryozoan adult colonies, and predation on bryozoan larvae. Study of hydroid stomach contents indicates that the trophic strategy of *P. schneideri* depends on two food sources: (i) a benthic one, mainly constituted of nematodes and polychaetes and (ii) a bryozoan source, which is performed in various ways. The *Perarella schneideri* colonies are, in turn, a food source for halacarids which perforate the hydranth wall and, penetrating the gastrovascular cavity, suck the semi-digested prey without evident damage to the polyps.

Key words: Hydrozoa, Cytaeidae, life cycle, trophic strategy, parasitism, commensalism, Bryozoa.

INTRODUCTION

The family Cytaeidae includes the genera *Cytaeis*, *Paracytaeis*, *Perarella* and *Stylactella* (Calder, 1988; Bouillon, 1995). In an earlier review of the family, Rees (1962) included five species in the genus *Perarella*: *P. affinis* (Jäderholm), *P. clavata* (Jäderholm), *P. spongicola* (Haeckel), *P. abyssicola* (Haeckel) and *P. schneideri* (Motz-Kossowska). *Perarella affinis* grows on algae in the Patagonian Sea, its gonophores are unknown and its systematic position is uncertain (Rees, 1962). *Perarella clavata* is found on shells in the Antarctic Ocean at a depth of 360 m (Jäderholm, 1905). Its gonophores have a styloid structure with an apical process and a

basal perisarc collar. *Perarella spongicola* and *P. abyssicola* were described by Haeckel (1889) living on sponges in the north and central Pacific at 4200-5300 m depths. The distinction between these two species is based on differences in the shape and arrangement of the hydrorhiza.

Perarella schneideri is one of the two species of the genus recorded in the Mediterranean Sea. It is always associated with colonies of the red cheilostome bryozoan *Schizoporella longirostris* and is characterised by having a gonophore with radial and circular canals, and tentacular bulbs (Motz-Kossowska, 1905). The other species collected in the Mediterranean is *P. propagulata* (Bavestrello, 1987) which is found on shells of the gastropod *Hinia incrassata*, either with living molluscs or inhabited by the hermit crab *Cestopagurus timidus*.

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The association between hydroids and other organisms such as sponges, cnidarians, bryozoans, molluscs, polychaetes, decapods and vertebrates is well-known (for a review see Gili and Hughes, 1995). The symbiosis of hydroids and bryozoans involves several genera including *Zanclaea*, *Perarella*, *Halocoryne*, *Hydranthea*, *Octotiarra* and *Zanclella* (Boero and Hewitt, 1992; Piraino *et al.*, 1992). The hydrorhiza of *Zanclaea*, *Octotiarra* and *Halocoryne* is covered by the bryozoan substrate, while in the other genera it grows on bryozoan surfaces in the grooves among the zoecia. Osman and Haugsnes (1981) demonstrated that the association of bryozoans and zancleid hydroids increases the survival and the competitive ability of both partners.

The aim of this work has been to define the annual cycle of *Perarella schneideri* in the Ligurian Sea, focusing our attention on the relationships with its bryozoan host.

MATERIAL AND METHODS

The observations were conducted at Cala Niasca in the Portofino Promontory (Ligurian Sea, Western Mediterranean). In this zone the bryozoan *Schizoporella longirostris* grows on natural hard substrata from 1 to 10 m in depth but is also very abundant on discarded glass bottles settled on the sandy sea bottom. On this substratum the bryozoan is confined to

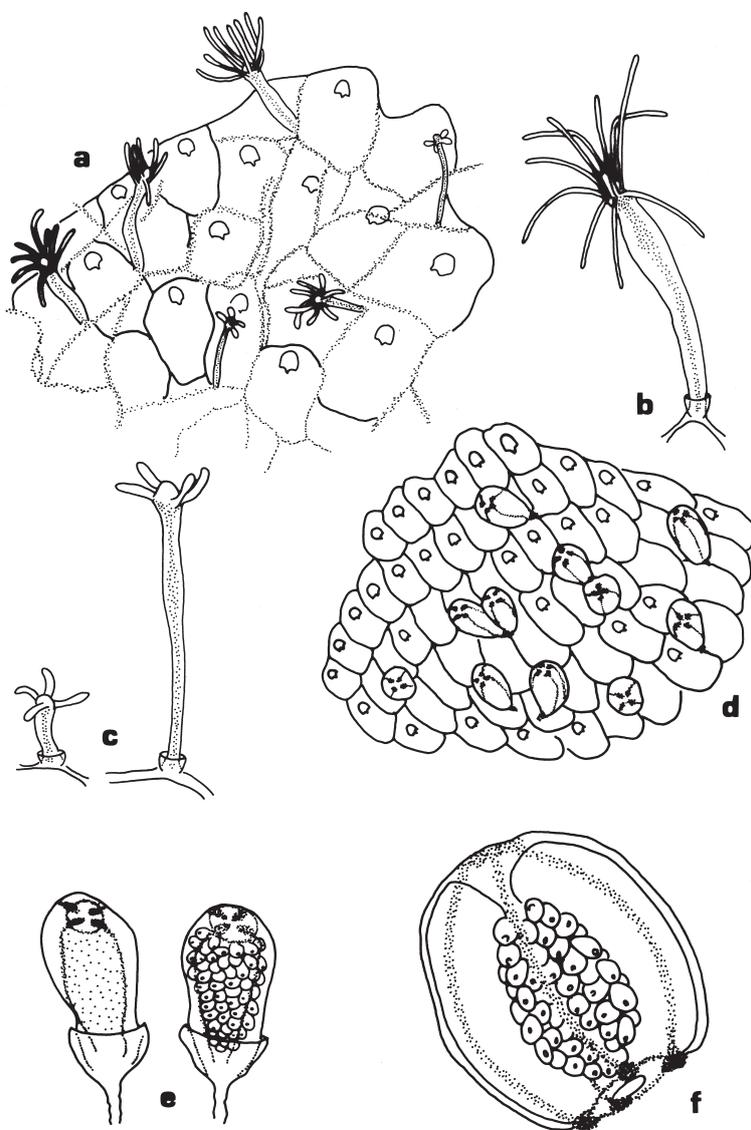


FIG. 1. – *Perarella schneideri*. a) a colony with large and small gastrozooids b) large gastrozooid; c) small gastrozooid, showing its extensibility; d) a summer colony that has lost gastrozooids but retained gonophores; e) male and female gonophores; f) free swimming female medusoid. Scale bar: a,d = 1cm; b,c,e,f = 1mm

a restricted sciophilous belt in direct contact with the bottom. Owing to its manageability, this artificial substratum was remarkably useful for our study. Each month, from July 1997 to July 1998, we collected five bottles. On these bottles all the bryozoan colonies were mapped and their area estimated by a digitizer, distinguishing the living portions from the dead ones. Moreover, for each colony the number of polyps of *Perarella* were counted. Observations on living hydroids were conducted on animals reared in natural seawater aerated by bubbles, and fed by *Artemia nauplii* at 20°C.

RESULTS

Hydroid morphology

The colonies of *Perarella schneideri* possess two distinct types of polyps (Fig. 1a): i) long and tubular hydranths with a whorl of 8-14 filiform tentacles around a conical hypostome (Fig. 1b) and ii) very extensile filiform hydranths with four short tentacles (Fig. 1c). Both kinds of polyps have bases surrounded by a perisarc collar. Nematocysts are microbasic euryteles (8.1 x 3.1 µm) and desmonemes (6.3 x 3.6 µm).

The gonophores of both sexes are medusoids (Fig. 1d-e), 1 mm in length, surrounded at the base by a collar of perisarc with four distinct radial canals, four tentacular bulbs, and a circular canal. The female gonophores contain about 80 eggs, 80-100 µm in diameter, which surround a non-functional manubrium (Fig. 1f). They detach from the colonies and swim for five days until the ejection of the eggs. The complete ejection of the eggs lasts about one hour. Two days after spawning, the medusoids degenerate. No swimming activity was observed in male gonophores.

The colonies of *Schizoporella* are generally composed of a living area and a non-living one. The two areas are easily distinguishable by their colour: vermilion red and white, respectively. The polyps of *Perarella* are located on the living areas of bryozoan, and are almost absent on the non-living areas.

Annual cycle

The annual cycle of the hydroid has been evaluated as the percent of infested *Schizoporella* colonies (Fig. 2). In the Ligurian Sea, *P. schneideri* shows a typical winter seasonality: in February almost all the colonies of the bryozoan are infested,

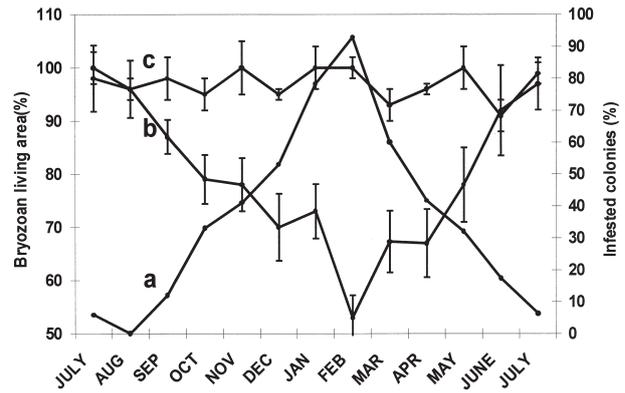


FIG. 2. – Annual cycle of the percent of bryozoan colonies infested by *Perarella schneideri* (a) compared with the annual cycle of the average percent of living bryozoan surface in infested (b) and not infested (c) colonies.

while in July-August no polyps are evident. The reproductive period has been observed between the second half of May and the end of June.

During the annual cycle the ratio between living and non-living areas in the colonies of *S. longirostris* is affected by the presence of the *Perarella* polyps. In non infested bryozoan colonies the living area is always greater than 95%, while in infested colonies the average monthly percent of living area is negatively correlated with the cycle of the hydroid (Fig. 2).

Colonies of bryozoans exhibited the presence of embryos in all the months of the year. We estimated the bryozoan recruitment as the percent of colonies less than 0.5 cm² (8-10 zooids). The trend of this parameter is negatively related with the abundance of the hydroid (Fig. 3) which demonstrates direct involvement of *Perarella* in the successful recruitment of bryozoans.

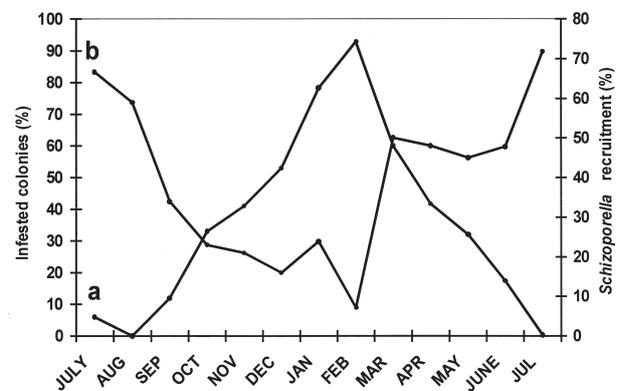


FIG. 3. – Annual cycle of the percent of bryozoan colonies infested by *Perarella schneideri* (a) compared with the annual cycle of the bryozoan recruitment estimated as the percent of colonies less than 0.5 cm² (8-10 zooids) (b).

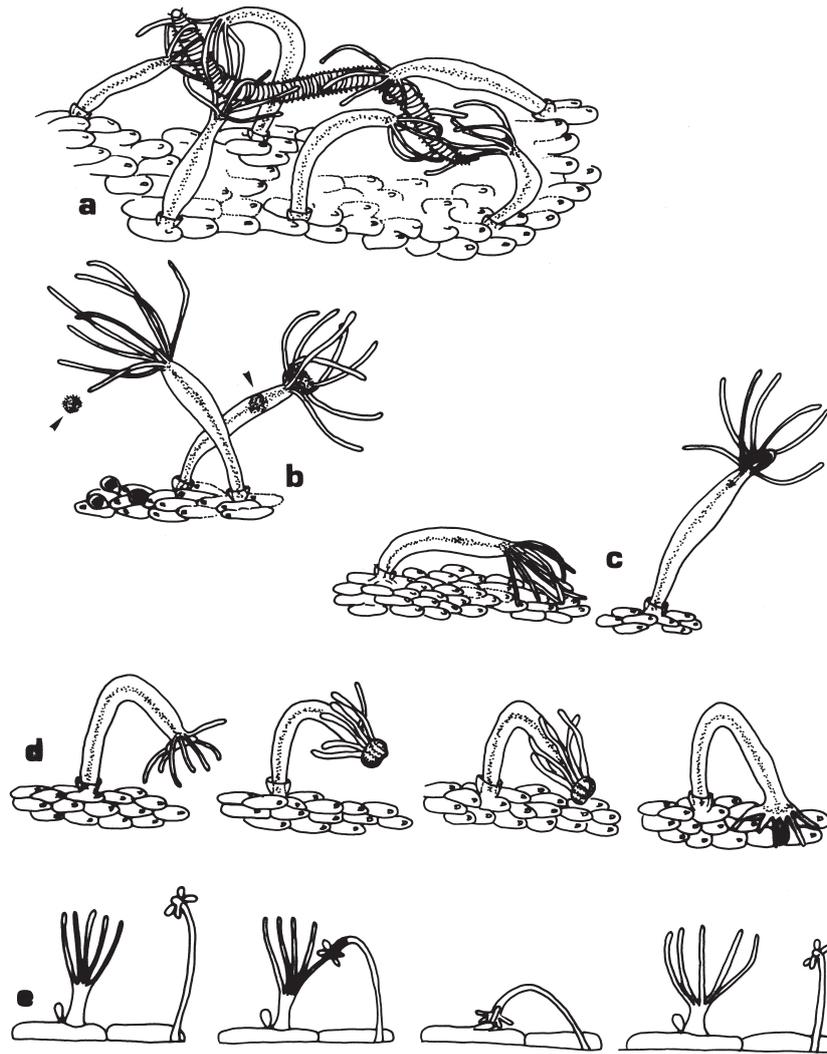


FIG. 4. – Trophic strategies of *P. schneideri*. The large gastrozooids feeding on meiobenthic organisms (a); the capture of newly released bryozoan larvae (arrows) (b); tentacles pick up the organic matter distributed on the bryozoan surface and introduce it, one at a time, into the mouth, sucking the material adhering to them (c); protrusion of the gastrovascular wall that adheres to the bryozoan epidermis (d). The filiform gastrozooids with four tentacles are specialised in engulphing the tip of a single lophophoral tentacle (e).

Trophic strategies

Perarella schneideri has two kinds of gastrozooids that are related to different trophic strategies. While the small filiform gastrozooids are very specialised, the large gastrozooids are involved in the exploitation of different food sources. The latter feed on meiobenthic organisms, particularly nematodes and polychaetes, but are also easily fed with *Artemia* nauplii under laboratory conditions. If the prey is very large many polyps participate in the capture. In this case the prey is ingested by a cluster of surrounding polyps (Fig. 4a). Another food source for large gastrozooids is newly released bryozoan larvae. As these larvae are caught in tentacles, they are quickly

ingested: each polyp can engulf two or three larvae at the same time (Fig. 4b).

Sometimes the tentacles of the polyps pick up organic matter on the bryozoan surface and then introduce the matter, one piece at a time, into the mouth which removes the material adhering to them (Fig. 4c). There is often a protrusion on the gastrovascular wall of the gastrozooids that, for several minutes, adheres to the bryozoan epidermis (Fig. 4d). It is not clear whether this behaviour is harmful to the bryozoan though the coelenteron of the gastrozooids is always filled with a red material resembling the color of the bryozoan epidermis.

The filiform gastrozooids with four tentacles are specialised for engulphing the tip of a single lophophoral tentacle of the bryozoan. These exten-

sile zooids wait for lophophore eversion, then prudently approach the lophophore and touch its tentacles very softly. Then the polyp engulfs the distal portion of a single lophophoral tentacle for several minutes. When the lophophore retracts, the polyp is dragged into the bryozoan orifice for several seconds (Fig. 4e). Unlike *Halocoryne epizoica* (Piraino *et al.*, 1992) the hydroid never breaks portions of bryozoan tentacles. The polyp seems to suck the lophophoral tentacles, feeding on the food particles caught by the bryozoan.

Commensalism

Perarella colonies are a food source for halacarids, which climb up the hydranth and penetrate the coenosarc with the proboscis for several minutes. The halacarids probably feed on the semi-digested contents in the gastral cavity of the hydroid (Fig. 5). During the perforation process the polyp is motionless. The hole caused by the penetration is visible immediately after the retraction of the proboscis, but it then disappears whereupon the polyp begins to move and to feed. The halacarids feed only on large gastrozooids, never utilising the smaller polyps. This selective behaviour is probably due to the different kinds of trophic resources exploited by the two kinds of polyps.

The behaviour of the halacarids is like that of pycnogonid larvae which infest the hydroid *Halocordyle wilsoni* (Staples and Watson, 1987). The pycnogonid larvae settle on the hydranth, which is grasped by the cheliphores while the proboscis penetrates the coenosarc.

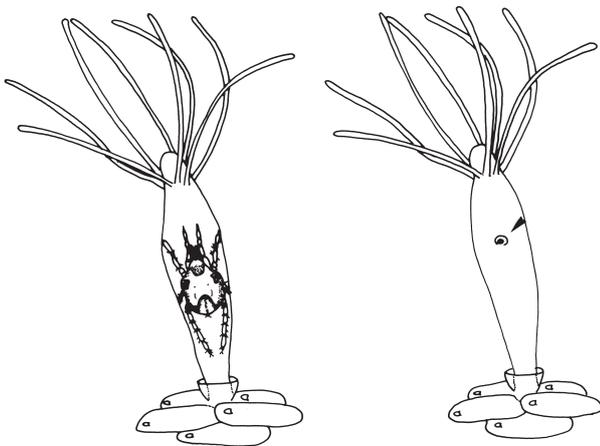


FIG. 5. — *Perarella* polyps are a food source for halacarids which penetrate the hydranth with their proboscis, whereupon they suck the semi-digested content of the gastral cavity. After the halacarid has detached itself, a hole (arrow) is evident on the hydranth.

DISCUSSION

The family Cytaeidae, belonging to the superfamily Bougainvillioidea (Petersen, 1979), also shows a resemblance to Hydractiniidae, particularly in the non-ramified colonies composed of naked polyps arising from a creeping hydrorhiza (Millard, 1975; Bavestrello, 1987). The main features traditionally considered common in the cytaeidid and in other bougainvillid families are: (i) gonophores arise directly from the hydrorhiza (or hydrocaulus or hydrocladia) rather than from specialised polyps; (ii) oral tentacles occur in medusae of *Cytaeis* and bougainvillids; (iii) the absence of polymorphism.

Our observations indicate that there is polymorphism in the genus *Perarella*, with the simultaneous presence of two gastrozooid types that are well-differentiated from both a morphological and a behavioural point of view. The filiform shape of one of these polyps, with their extensibility and shortened tentacles suggests that they may have a relationship with the dactylozooids of the hydractiniids. Bavestrello (1987) described in *P. propagulata* some cylindrical portions of naked coenosarc surrounded by a perisarc collar that were interpreted as propagules. In light of the present data these structures may be descendants of the small gastrozooids of *P. schneideri* which have lost their very short tentacles.

In our observations of the swimming activity of female medusoids of *P. schneideri*, described earlier, we found a trend of medusa reduction within the family: *Cytaeis* spp. with free medusae; *P. schneideri* with free medusoids; *Perarella* spp. with styloid gonophores. The same is seen in many families of hydroids, and species which have abolished the medusa stage are usually assumed to be descendants.

Piraino *et al.* (1992) demonstrated, as a provisional conclusion, that the symbiosis between hydroids and bryozoans originates from simple epibiosis and leads into parasitism. Our data indicate a parasitic behaviour of the *Perarella* colonies that highly affects the biological cycle of its host. Although the reproductive period of *S. longirostris* occurs throughout the year in the Ligurian Sea, an appreciable recruitment of young colonies is evident only in summer, which corresponds to the phase of regression of the hydroid colonies. This phenomenon is directly related to the active predation of the hydroid on the larvae of its host. A similar behaviour was observed in colonies of *Podocoryne exigua* which actively feed on the larvae of the hermit crab host (Bavestrello, 1985).

More difficult to understand is the way in which *Perarella schneideri* damages and kills the colonies on which it lives. The trophic behaviour of both large and small gastrozooids on lophophores and on the bryozoan surface probably produces negative effects on the *Schizoporella* colonies. It is possible that the grazing of the hydroid on the bryozoan epidermis, as evidenced by the red content of the gastrozooid coelenteron, exposes *Schizoporella* zoecia to infection by microorganisms. A feeding activity by the gastral cavity protrusion has already been observed in *Hydractinia vallini* and *H. ingolfi* living epibiotically on starfish in polar waters (Svoboda *et al.*, 1997).

Bavestrello *et al.* (1996) confirmed the presence of a cleptocommensalistic strategy in the relationships involving hydroids and caprellids. The case of *Perarella* is a new and interesting example of this strategy: the hydroid exploits the organic matter collected by the bryozoan lophophore and is, in turn, exploited by the halacarid. This complex pattern suggests that cleptocommensalism is probably widely diffused in trophic marine invertebrate relationships.

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