

Associations between pycnogonids and hydroids from the Buenos Aires littoral zone, with observations on the semi-parasitic life cycle of *Tanystylum orbiculare* (Ammotheiidae)*

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SUMMARY. Abundance and seasonality of *Tanystylum orbiculare* Wilson, 1878 populations (Pycnogonida; Ammotheiidae) associated with *Sarsia sarsii* (Loven, 1836) and *Tubularia crocea* (Agassiz, 1862) (Hydrozoa; Anthomedusae) are analysed and the semi-parasitic life cycle of this species is described. In the analysed population, the first larval stages were found exclusively as parasites of *S. sarsii*. During the attachment to the hydranths, protonymphon larvae of *T. orbiculare* feed by sucking the hydranths of the cnidarian. Change of host is not obligatory; juveniles and adults were found both on *S. sarsii* as on *T. crocea*, and adults were also observed on other invertebrates. In the Mar del Plata intertidal, *Tanystylum orbiculare* was the most common pycnogonid species on colonies of *T. crocea* and *S. sarsii*. *Anoplodactylus petiolatus* was less abundant on both species and *A. assimilis* was found only on *T. crocea*. *Endeis spinosa* is absent on hydroids from the Mar del Plata intertidal zone but ectoparasitic larvae and adults were found on *Obelia longissima* colonies from Mar del Plata harbour together with adults of *T. orbiculare* and *A. petiolatus*. Endoparasitic larvae of *A. petiolatus* were found associated with colonies of Bougainvillidae.

Key words: hydroids, pycnogonids, association, parasitism, Argentina.

INTRODUCTION

Pycnogonids can be found in all marine habitats from the intertidal zone to abyssal depths. Although they are distributed worldwide, little is known about their biology.

Pycnogonids are usually found associated with other animals, the large majority of these associations involving sessile or sluggish invertebrates as food (Bain, 1991; Piel, 1991; Varoli, 1994 and others). The commonest recorded associates are cnidarians, including sea anemones (Mercier and Hamel,

1994) and especially hydroids (Staples and Watson, 1987; Staples, 1997) in which pycnogonid larvae often live as parasites within tissues of the colonies. Medusae records are relatively rare (Child and Harbison, 1986).

Although their larvae were described earlier, only recently has it been possible to describe the life cycle and population dynamics of some species (King and Jaervis, 1970; Munilla, 1979, 1980; Tomaschko, *et al.*, 1997; Wilhelm, *et al.*, 1997).

The pycnogonida of the Argentina continental shelf are poorly known. The available taxonomic accounts analysed species from the intertidal zone, harbour areas, and a few deep water samples of

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Buenos Aires province, and from the north-Patagonian sector (Río Negro province) (Castellanos, 1965; Stock, 1966; Larramendy, 1974; 1975; Larramendy and Castellanos, 1978; Minnard and Zamponi, 1984; Bremec *et al.*, 1986). Some species were reported as part of fouling communities (Bastida *et al.*, 1981; 1997) or as fauna associated to hydropolyps (Zamponi and Genzano, 1992) but there are no studies about their reproduction and larval stages.

Associations between pycnogonids and hydropolyps have been reported infrequently due to the few ecological studies on hydroids conducted in the intertidal fringe of Mar del Plata (Genzano, 1994 and subsequent). However, in recent years, studies on other intertidal and sublittoral hydroid communities have contributed more information on this association. In this paper, the pycnogonids found on hydroids in Mar del Plata are examined.

Abundance and seasonality of *Tanystylum orbiculare* Wilson, 1878 populations (Pycnogonida; Ammotheidae) associated with *Sarsia sarsii* (Loven, 1836) and *Tubularia crocea* (Agassiz, 1862) (Hydrozoa; Anthomedusae) are reported here and the semi-parasitic life cycle of the pycnogonid is described.

Records of association between hydroids and pycnogonids from other locations in the province of Buenos Aires were also analysed.

MATERIALS AND METHODS

This study results from numerous samples carried out since 1989 from the intertidal rocky shore and from a smaller data set from the sublittoral rocky bottom of Mar del Plata, Argentina. Information on association between hydroids and pycnogonids from other areas in Buenos Aires province were also included here.

Studies on taxonomic composition and abundance of pycnogonids were carried out in samples of *Sarsia sarsii* and *Tubularia crocea* colonies from the Punta Cantera intertidal (38°05'S 57°32'W), which were collected at monthly or bimonthly intervals from October 1989 to February 1992. After this period, colonies were monitored at irregular intervals until October 2000.

Pycnogonids were separated under a stereomicroscope and were identified according to Marcus (1940) Minnard and Zamponi (1984) and Bremec *et al.* (1986).

Sarsia sarsii is a common epizoic hydroid on the mytilid *Brachydontes rodriguezii* (d'Orbigny, 1846). Each sampled "clump" living on a bivalve was considered as one colony and the abundance of pycnogonids was indicated as number of individuals per colony. The relative abundance of the different larval stages within the population of *Tanystylum orbiculare* was observed. Due to the small size and cryptical colour of parasitic protonymphon larvae, which were attached among capitate tentacles, their abundance was estimated by counting under the microscope the larvae attached to 50 hydranths selected at random from each sample.

Abundances of pycnogonids associated on *T. crocea* were indicated as numbers of individuals / g colony dried for 48 h at 35-40°C. Pycnogonids found on other hydroid species were indicated only as present.

Colonies of *Obelia longissima* (Pallas, 1766) were collected seasonally in Mar del Plata Harbour (2-3 m depth) from spring 1999 to winter 2000. Collection data on other hydroids studied are indicated in the text.

RESULTS

Association between pycnogonids and hydroids in the Mar del Plata intertidal

During this study, a total of 503 pycnogonids associated with *T. crocea* and *S. sarsii* colonies were observed. Due to the abundance of *T. crocea* in the intertidal fringe, most pycnogonid specimens were found on this species. However, there were seasonal changes: *S. sarsii* was the more frequent host in autumn and *T. crocea* was the more frequent host in the cold months when *S. sarsii* was scarce or absent (Fig. 1).

Tanystylum orbiculare (Ammotheidae) was the dominant pycnogonid on both species of hydroids. This ammotheid occurred throughout the year, with maximum numbers in summer and autumn correlating with warm water temperatures. *Anoplodactylus petiolatus* (Kroyer, 1844) (Phoxichilidiidae) was less abundant on *T. crocea* and occasional on *S. sarsii*. *Achelia assimilis* (Haswell, 1885) (Ammotheidae) was found only on *T. crocea* (Figs. 2 and 3).

Tanystylum orbiculare was occasionally found also on *Plumularia setacea* (Linnaeus, 1758) (Lep-tomedusae), another hydrozoan sharing the intertidal habitat with *T. crocea* and *S. sarsii*, but only during the warm seasons (Genzano, 1994).

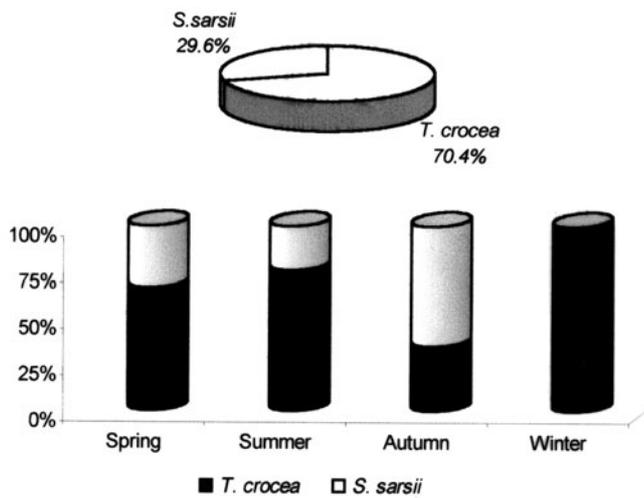


FIG. 1. – Frequency of hydroids as substrata of pycnogonids from Mar del Plata rocky intertidal.

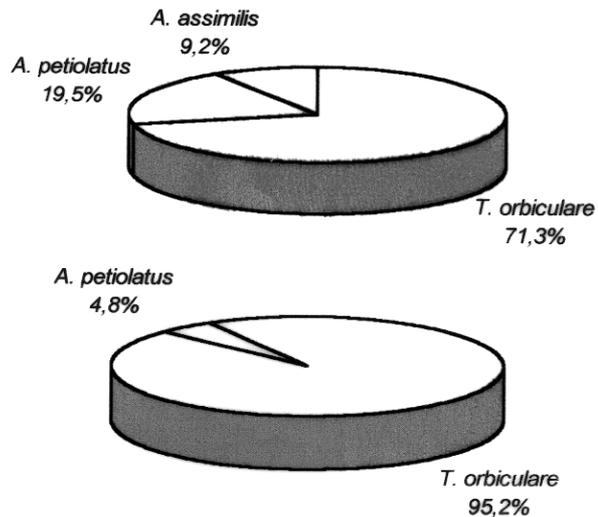


FIG. 2. – Frequency of pycnogonids associated with: a) *Tubularia crocea* and b) *Sarsia sarsii*.

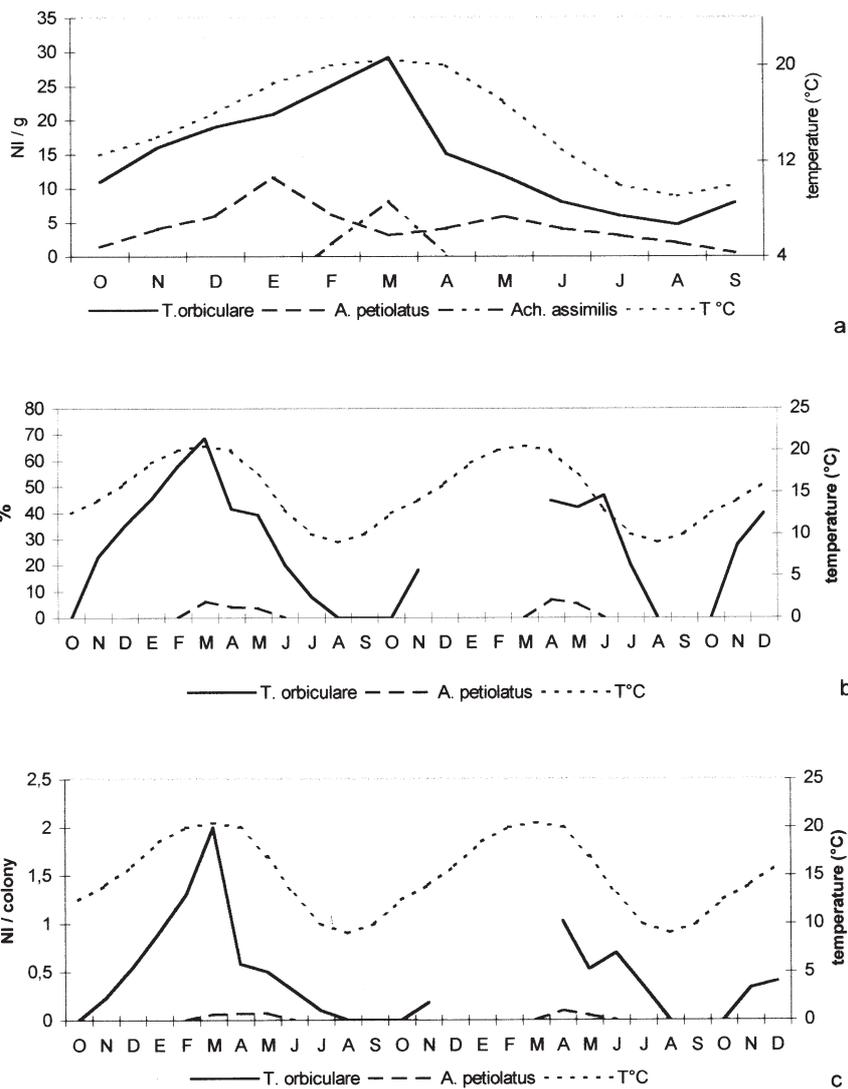


FIG. 3. – Abundance of pycnogonids on: a) *Tubularia crocea* (number of pycnogonids / g. colony), b) *Sarsia sarsii* (frequency of colonies with pycnogonids) and c) *Sarsia sarsii* (number of pycnogonids/colony).

Other hydroid species from this intertidal fringe were scarce, often occurring as small epizoic colonies on *T. crocea* (Genzano, 1994; 1998, Genzano and Rodriguez, 1998). No pycnogonids were associated with any of those species except *Bimeria vestita* Wright, 1859 (see below).

Post embryonic development of *Tanystylum orbiculare*

Records of *T. orbiculare* specimens were not frequent enough to estimate the relative abundances of all developmental stages (juveniles, mature females, mature ovigerous males, etc.). However, relative abundances and frequency of larval stages on different host colonies helped to gather information on the life cycle of this pycnogonid.

Pycnogonids are one of few groups of animals in which the males exclusively care for the developing eggs. *Tanystylum orbiculare* males carrying egg batches on the ovigerous legs were found throughout the year on both *S. sarsii* and on *T. crocea*.

Males carried the eggs until hatching. The protonymphon larvae (the first larval stages) leave the male and become associated with *S. sarsii* hydranths. The few males observed carrying

protonymphon larvae suggested that attachment to hydranths occurs shortly after hatching.

The protonymphon larvae were present among the capitate tentacles of hydranths and their tegument provided a defense against the nematocysts. The colour (brown) matched that of the hydranths. The larvae were characterised by a small proboscis flanked by chelate cheliphores. Two pairs of clawed lateral appendages were present. Body length ranged from 121 to 202 μ (Figs. 4a and 5a-b). During the study period, the protonymphon larvae occurring on a total of 900 hydranths of *S. sarsii* were analysed. Larvae were found from October to June, with maximum numbers from November to March (Fig. 6).

The subsequent larval stage resembled the protonymphon, but the cheliphores were shorter and it was characterized by the appearance of the first permanent legs (Figs. 4b and 5c). Other stages, found either on hydranths or on the hydrocaulus of *S. sarsii*, possessed the second and third pair of legs (Figs. 4c-d and 5d).

Free-living juvenile stages were found not only on *S. sarsii* but also on *T. crocea* colonies. The major changes during metamorphosis to the first juvenile stages is the disappearance of the cheliphores. In the

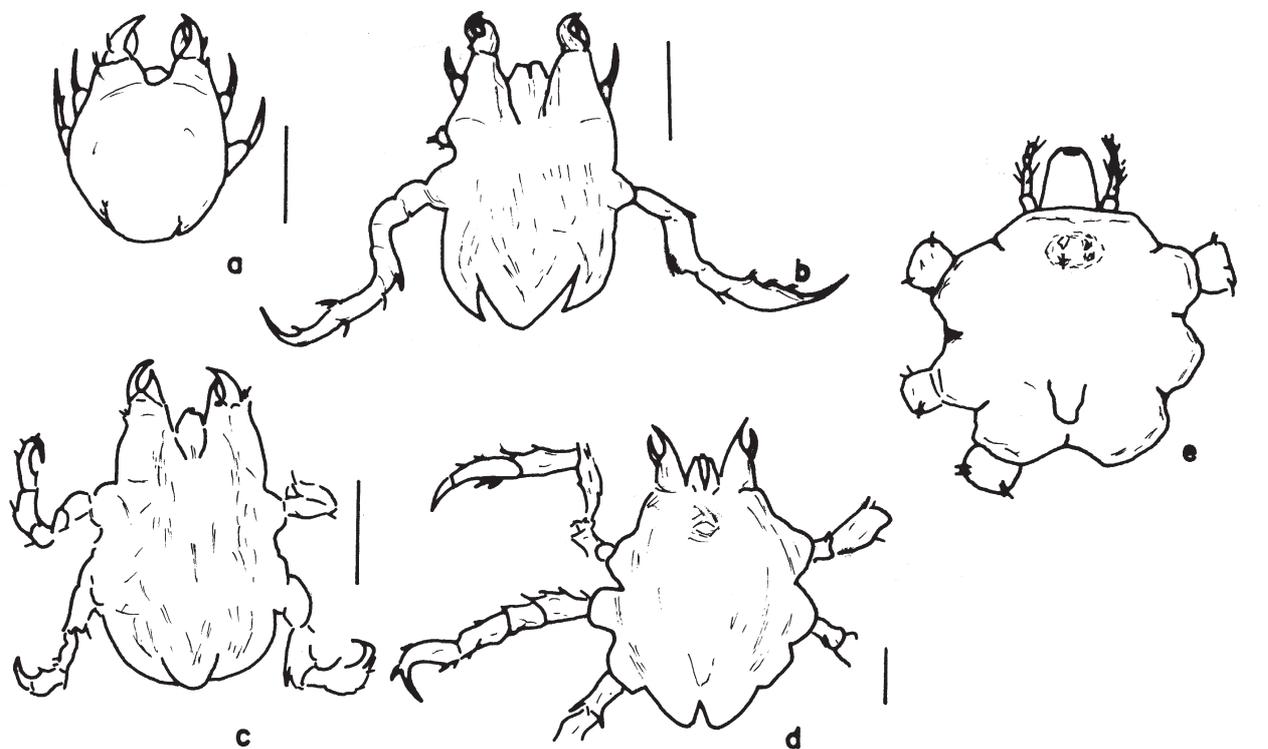


FIG. 4. – *Tanystylum orbiculare*: a) protonymphon larva, b, c and d) Larval stages with the first, second and third pairs of permanent legs respectively. e) Juvenile stage. Scale bar = 100 μ .

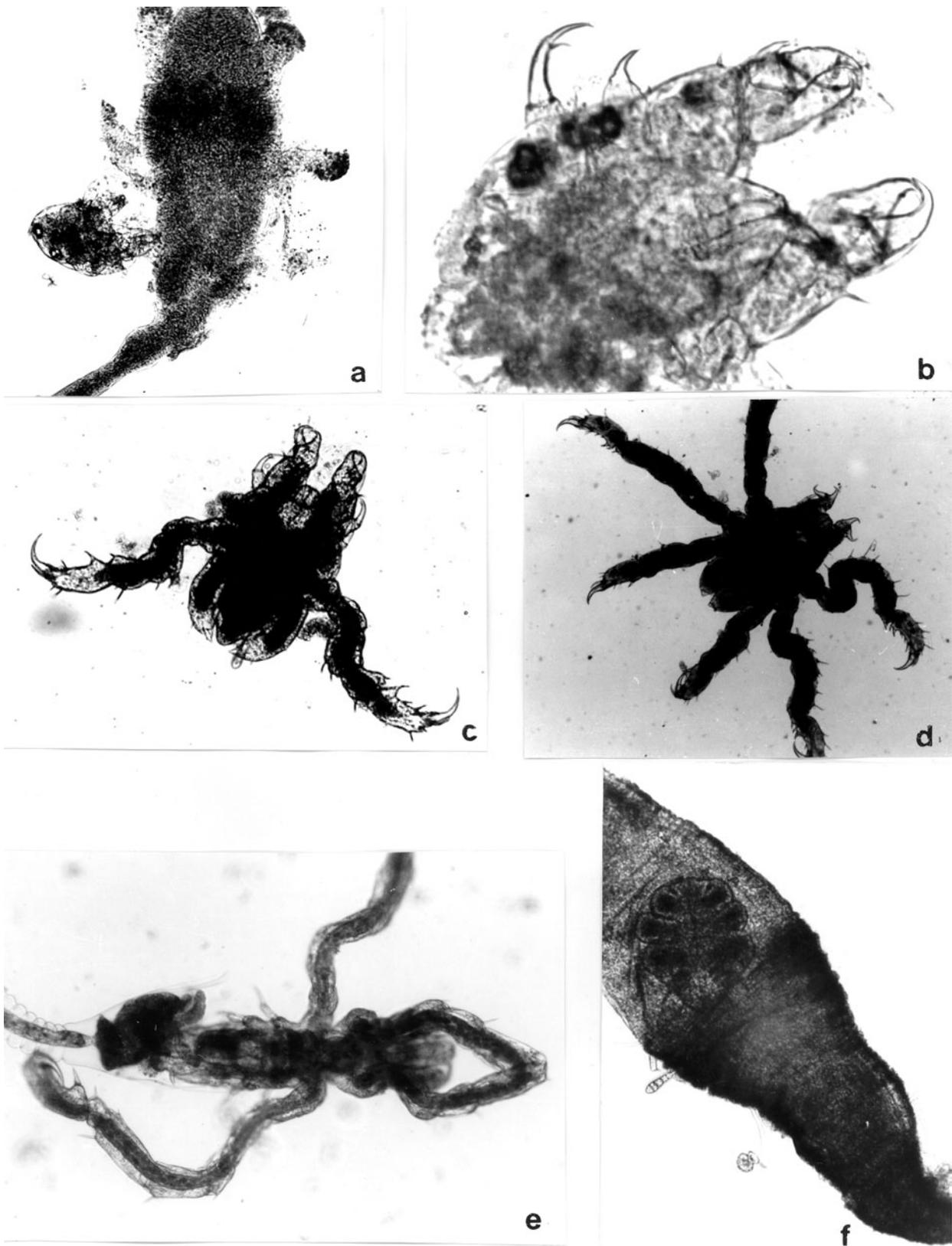


FIG. 5. – a) Protonymphon larva of *Tanystylum orbiculare* attached to hydranth of *Sarsia sarsii* (100 x), b) Detail of protonymphon larva (400 x), c) Larva stage of *Tanystylum orbiculare* with the first pair of permanent legs (40 x), d) Larva stage with the three pairs of permanent legs (40 x), e) Ectoparasitic larva of *Endeis spinosa* in hydrotheca of *Obelia longissima* (100 x), f) Endoparasitic encysted larva of a Phoxichilididae producing deformation of *Bimeria vestita* hydranth (40 x).

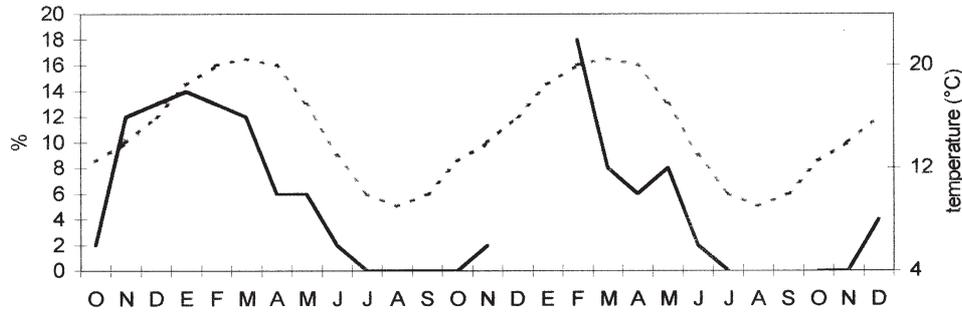


FIG. 6. – Frequency of hydranths of *Sarsia sarsii* with ectoparasitic protonymphon larvae of *Tanystylum orbiculare*.

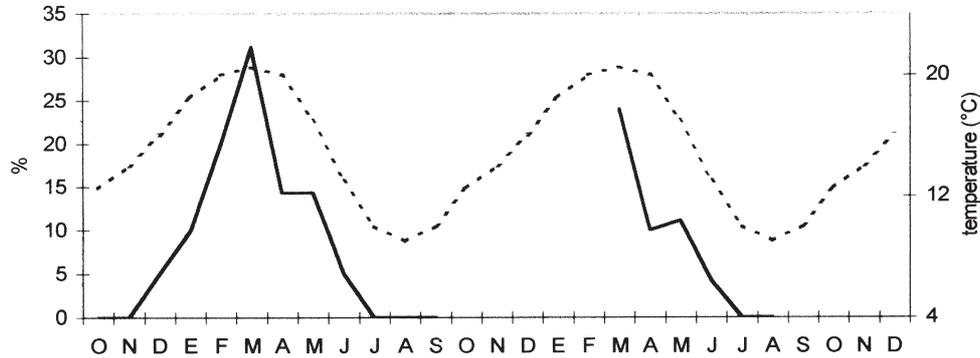


FIG. 7. – Frequency of juvenile stages of *Tanystylum orbiculare* on *Sarsia sarsii* colonies.

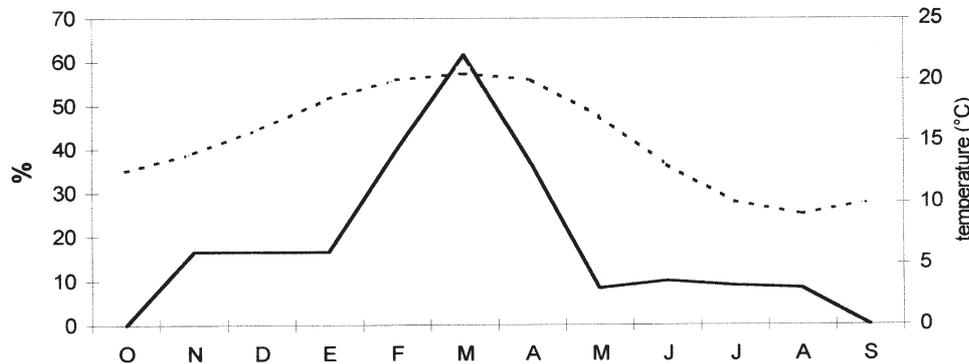


FIG. 8. – Frequency of juvenile stages of *Tanystylum orbiculare* on *Tubularia crocea* colonies.

last juvenile stage, the specimens developed the final large proboscis, which was significantly larger than the larval proboscis, and lost their larval extremities, retaining three pairs of walking legs and then adding the fourth pair. Body length varied considerably from 1.5 to 2.4 mm (Fig. 4e). The first juvenile stages appeared from November to August, with a peak in late summer (Figs. 7 and 8).

The last juvenile stages had four pairs of permanent legs. Adults can be distinguished from them by the genital pores and by the fully developed oviger in males. The adults were usually covered with mud particles and diatoms which acted as a camouflage.

Last juveniles and adults occurred all year on both hydroid species.

Other ecto-parasitic larvae

Colonies of *Obelia longissima*, epizotes on ascideans, are abundant in Mar del Plata harbour. Adult pycnogonids of *Tanystylum orbiculare*, *Anoplodactylus petiolatus*, and *Endeis spinosa* (Montagu, 1808) were associated with these colonies. During summer only (March 13, 2000), a few hydranths were infested by parasitic larvae inside the hydrothecae. These larvae were assigned to *Endeis spinosa*.

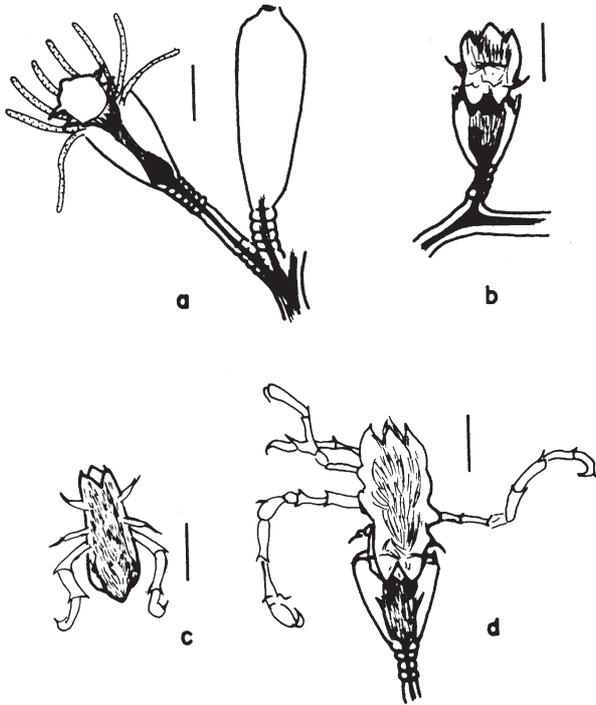


FIG. 9. – a, b) Protonymph larvae of *Endeis spinosa* in hydrothecae of *Obelia longissima*. c, d) Larvae with the first and second pairs of permanent legs, respectively. Scale bar: 200 μ m.

Protonymph larvae were found among filiform tentacles of the hydranths (Figs. 9 a-b). Permanent legs developed progressively in late larval stages (Figs. 9c-d and 5e).

Helfer (1932; in Staples and Watson, 1987) recorded larvae of *Anoplodactylus pygmaeus* (Hodge, 1862) attached to the hydranths of *Obelia* sp. without any obvious deformation on the hydrotheca. However, some of the *E. spinosa* larvae observed here had destroyed the hydrothecae and the last large permanent legs projected out of them.

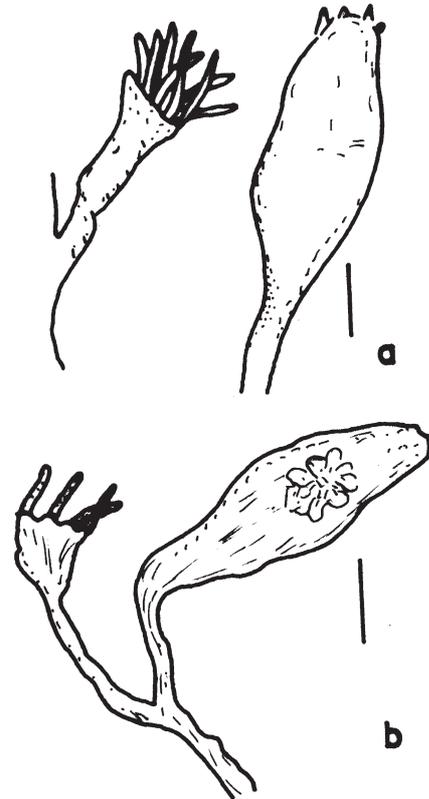


FIG. 10. – Endoparasitic encysted larva of a Phoxichilidae into hydranths of: a) *Bougainvillia muscus* (scale bar: 500 μ m) and b) *Bimeria vestita* (scale bar: 1000 μ m).

Endo-parasitic larvae

The larval type to hatch from the eggs is the protonymph. Usually, after leaving the male's ovigerous legs, the protonymph undergoes a series of moults during which it adds appendages until the adult number of appendages has been reached (Marcus, 1940; Tomaschko *et al.*, 1997; Wilhelm *et al.*, 1997).

TABLE 1. – Records of associations of pycnogonids with hydroids in the Buenos Aires littoral (records from the literature are indicated between bracket). T.o: *Tanystylum orbiculare* Wilson, 1878; A.a: *Achelia assimilis* (Haswell, 1885); A.p: *Anoplodactylus petiolatus* (Kroyer, 1844); A.s: *Anoplodactylus stictus* Marcus, 1940; E.s: *Endeis spinosa* (Montagu, 1808); e.l: encysted larva.

	Ammonotheidae		Phoxichilidae			Endeidae E.s.
	T.o	A.a	A. p	e l, A.p	A.s	
Anthomedusae:						
<i>Sarsia sarsii</i>	1	1	-	-	-	-
<i>Bimeria vestita</i>	-	-	-	1	-	-
<i>Bougainvillia muscus</i>	(4)	-	4	(4)	-	(6)
<i>Tubularia crocea</i>	1	1	1, (6)	-	(6)	(6)
Leptomedusae:						
<i>Obelia longissima</i>	2,3	-	2	-	-	2
<i>Obelia</i> sp.	-	(6)	-	-	-	-
<i>Amphisbetia operculata</i>	3	3	-	-	-	-
<i>Plumularia setacea</i>	1, (5)	(6)	-	-	-	-

1: 38°05'S 57°32'W, Mar del Plata, intertidal; 2: Mar del Plata, Harbor, 2-3 m depth; 3: Mar del Plata sublittoral rocky bottom, 6 m); 4: 38°50'S 61°05'W, Reta, intertidal (Bastida *et al.*, 1997); 5: 39°00'S 61°17'W, Monte Hermoso (Bremec *et al.*, 1986); 6: 38°45'S 62°12'W, Ingeniero White Harbor (Bremec *et al.*, 1986).

In another less frequent pathway of development, larvae acquire endoparasitic behaviour in a hydranth, undergoing one or more moults (exact number unknown), and emerging as juveniles. These endoparasitic larvae usually produce deformed hydranths. The manner in which the larvae locate and penetrate the hydranths is unknown (see Staples and Watson, 1987 for a review).

In the Buenos Aires littoral zone, endoparasitic larval was found in two athecate hydroids (Bougainvillidae): *Bimeria vestita* (Wright, 1859) and *Bougainvillia muscus* (Van Beneden, 1844).

Many epizoic colonies of *B. vestita* from the Mar del Plata intertidal were studied over more than a decade (Genzano, 1998; Genzano and Zamponi, 1999) but only recently (samples from March and October, 2000) have endo-parasitic Phoxichilidiidae larvae (possibly *Anoplodactylus petiolatus*) been found in four hydranths.

Bougainvillia muscus colonies were recorded in different places from Buenos Aires littoral (Genzano, 1995: *B. ramosa*). Different adult pycnogonids were found associated with them (see Table 1), and endoparasitic larvae of *A. petiolatus* were found in some hydranths of colonies from the intertidal at Reta (Bastida *et al.*, 1997: *B. ramosa*).

In both athecate hydroids a few dilated hydranths with their tentacles stunted or absent were observed. Pycnogonid larvae occupied these hydranths and were the cause of their deformation (Figs. 5f and 10a-b).

Larvae of pycnogonids in the coelenteron of *T. crocea* were reported by Staples and Watson (1987), but there was no evidence of such an infestation in the tubularids studied here.

Records of associations of pycnogonids to hydroids in the Buenos Aires area

Pycnogonids associated with athecate and thecate hydroids are shown in Table 1. There were 20 records of pycnogonids associated with eight hydroid species, mostly *T. crocea* and *B. muscus*. The Ammotheidae (*T. orbiculare* and *A. assimilis*) were the pycnogonids most frequently found on hydroid colonies.

DISCUSSION AND CONCLUSION

Few studies have analysed the taxonomic composition of pycnogonids from Buenos Aires province and the north-Patagonian sector (Río

Negro province) on the Argentina continental shelf (Castellanos, 1965; Stock, 1966; Larramendy, 1974; 1975; Larramendy and Castellanos, 1978; Minnard and Zamponi, 1984; Bremec *et al.*, 1986), none of them dealing with pycnogonid ecology and reproductive biology. Studies on hydroid populations from the Mar del Plata intertidal zone provided information on associated pycnogonids and on their seasonal dynamics.

Tanystylum orbiculare was the most common pycnogonid species on colonies of *T. crocea* and *S. sarsii*. *Anoplodactylus petiolatus* was less abundant on both species, and *A. assimilis* was found only on *T. crocea*. *Endeis spinosa* was absent on hydroids from the Mar del Plata intertidal, but ectoparasitic larvae and adults were found on *Obelia longissima* colonies from Mar del Plata harbour together with adults of *T. orbiculare* and *A. petiolatus*. From deeper water, only epibionts on *Amphisbetia operculata* (L.) colonies were analysed, and few adults of *T. orbiculare* were found there.

The absence of pycnogonid records on hydroids belonging to some hydrozoan families (e.g. Haleciidae, Lafoeidae) is probably due to the rarity of representatives of these families in the study area (Genzano and Zamponi, 1997). Except for the well-studied thecate *A. operculata* (Sertulariidae), information on large sublittoral thecate colonies are still scant.

Bastida *et al.* (1997) reported, from another intertidal location in Buenos Aires, that *A. petiolatus* was the most common pycnogonid on *Bougainvillia muscus* colonies, and encysted larvae of this species were only found associated with Bougainvillidae colonies (see Table 1). These observations suggest that species-specific associations between pycnogonids and hydroids may occur, supporting the observations of other authors (Staples and Watson, 1987; Tomaschko *et al.*, 1997; Wilhelm *et al.*, 1997).

The interactions of pycnogonids with their invertebrate hosts and their life cycles are still poorly known. In *Pycnogonum litorale* Strom, the first larva stage is ectoparasite on the hydroid *Clava multicornis* (Forsk., 1775); and the metamorphosis to juvenile is accompanied by an obligatory change of host from the hydroid to the sea anemone *Metridium senile* (Linnaeus, 1767) (Tomaschko *et al.*, *op cit.*; Wilhelm *et al.*, *op cit.*).

Observations on larval stages of *T. orbiculare*, and on their host, allowed the life cycle of this pycnogonid to be reconstructed (Fig. 11). In the analysed population, the first larval stages were

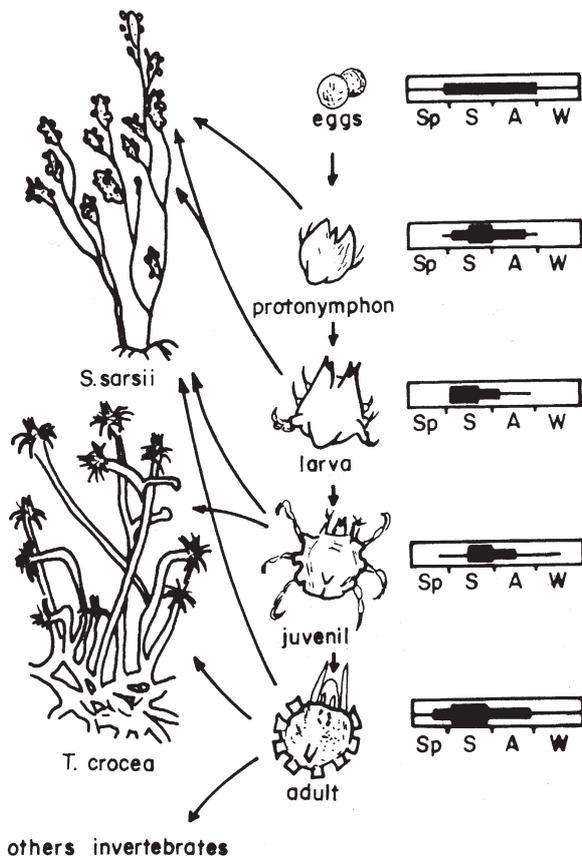


FIG. 11. – Life cycle diagram of *Tanystylum orbiculare* (see text for more details).

found exclusively as parasites of *S. sarsii*.

Change of host is not obligatory in this species, as juveniles and adults were found both on *S. sarsii* and on *T. crocea*. Adults were also reported on other invertebrates, such as the sponge *Hymeniacidon sanguinea* Grant, 1827 (Cuartas and Excoffon, 1993) in the community associated with the small mussel *Brachydontes rodriguezii* (d'Orbigny, 1846) (Scelzo *et al.*, 1996), and on organisms associated with the sea anemone *Anthothoe chilensis* (Lesson, 1830) (Excoffon, *et al.*, 1999).

Very little is known about pycnogonid feeding habits. Some species are generalized predators that feed on hydroids, polychaetes, nudibranchs and other invertebrates (Bain, 1991, Piel, 1991, Varoli, 1994).

During the attachment to the hydranths, protonymphon larvae of *T. orbiculare* feed by sucking. Some nematocysts (stenoteles) were found in their proboscides.

Adults were found browsing on hydroids and on their hydrocauli, where many protists and diatoms live as epizoites of the colonies (Zamponi and Genzano, 1992).

Further studies about the life cycle of *T. orbiculare* under laboratory conditions will be of interest to ascertain the number of instars and moults, and the duration of each larval stage up to maturity.

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REFERENCES

- Bain, B.A. – 1991. Some observations on biology and feeding behavior in two southern California pycnogonids. *Bijdr. Dierk.*, 61(1): 63-64.
- Bastida, R., M. Trivi de Mandri, V. Lichtschein de Bastida and M. Stupak. – 1981. Ecological aspects of marine fouling at the port of Mar del Plata, Argentina. *Actas del Congreso Internacional de Corrosión Marina e Incrustaciones*, 5, España: 299-320.
- Bastida, R., J.P. Martín and E. Ieno. – 1997. Comunidades incrustantes de áreas costeras del sur de la provincia de Buenos Aires (Argentina). *Cidepint-Anales*, 1997-1998: 171-197.
- Bremec, C.S., D.E. Martínez and R. Elias. – 1986. Pícnogónidos de los alrededores de Bahía Blanca (Argentina). *Spheniscus*, 3: 31-49.
- Castellanos, Z.J.A. – 1965. Adiciones a la pantopodofauna Argentina. *Physis*, 25(69): 13-17.
- Child, C.A. and G.R. Harbison. – 1986. A parasitic association between a pycnogonid and a scyphomedusae in midwater. *J. Mar. Biol. Ass. U. K.*, 66: 113-117.
- Cuartas, E. and A.C. Excoffon. – 1993. La fauna acompañante de *Hymeniacidon sanguinea* (Grant, 1827) (Porifera: Demospongiae). *Neotropica*, 39(101-102): 3-10.
- Excoffon, A.C., G.N. Genzano and M.O. Zamponi. – 1999. Associated macrobenthos to a population of *Anthothoe chilensis* (Lesson, 1830) (Cnidaria, Actinaria) from Mar del Plata Harbour, Argentina. *Cienc. Mar.*, 25(2): 177-191.
- Genzano, G.N. – 1994. La comunidad hidróide del intermareal rocoso de Mar del Plata (Argentina). I. Estacionalidad, abundancia y períodos reproductivos. *Cah. Biol. Mar.*, 35(3): 289-303.
- Genzano, G.N. – 1995. New records of hydropolyps (Cnidaria) from south western Atlantic Ocean. *Misc. Zool.*, 18: 1-8.
- Genzano, G.N. – 1998. Hydroid epizoites on *Tubularia crocea* (Agassiz, 1862) and *Sertularella mediterranea* Hartlaub, 1901 (Hydrozoa-Cnidaria) from intertidal of Mar del Plata (Argentina). *Russ. J. Mar. Biol.*, 24(2): 123-126.
- Genzano, G.N. and G.M. Rodríguez. – 1998. Associations between hydroid species and their substrates from intertidal of Mar del Plata (Argentina). *Misc. Zool.*, 21(1): 21-29.
- Genzano, G.N. and M.O. Zamponi. – 1997. Frequency of study and diversity of benthic Hydrozoa of the Argentine Continental Shelf. *Cienc. Mar.*, 23(3): 285-302.
- Genzano, G.N. and M.O. Zamponi. – 1999. Natural history of *Bimeria vestita* Wright, 1859 (Hydrozoa, Bougainvillidae) from rocky intertidal of Mar del Plata (Argentina). *Cienc. Mar.*, 25(1): 63-74.
- King, P.E. and J.H. Jaervis. – 1970. Egg development in a littoral pycnogonid *Nymphon gracile*. *Mar. Biol.*, 7: 294-304.
- Larramendy, M.L. – 1974. Anotaciones sobre *Colossendeis geoffroyi* (Mañe-Garzon, 1944). *Neotrópica*, 20(63): 149-152.
- Larramendy, M.L. – 1975. Un nuevo *Pallenopsis* Wilson, 1881 para

- el Mar Argentino (Pycnogonida, Pallenidae). *Neotrópica*, 21(65): 94-98.
- Larramendy, M.L. and Z.J.A. Castellanos. – 1978. Sobre un nuevo picnogónido del Mar Argentino (Pycnogonida, Palleidae). *Neotrópica*, 24(72): 91-97.
- Marcus, E. – 1940. Os pantopodas brasileiros e os emais sul-americanos. *Bol. Facult. Filos., Ciên. Letr.*, 19(zool. 4): 3-179.
- Mercier, A. and J. Hamel. – 1994. Deleterious effects of a pycnogonid on the sea anemone *Bartholomea annulata*. *Can. J. Zool.*, 72: 1362-1364.
- Minnard, V.A. and M.O. Zamponi. – 1984. Estudios sistemáticos de algunos pantópodos de la región subantártica. *Historia Natural*, 4(28): 257-279.
- Munilla, L. – 1979. Desarrollo anual y reproducción de *Achelia echinata* Hodge, 1864 (Pycnogonida). *Cah. Biol. Mar.*, 21: 115-121.
- Munilla, L. – 1980. Ciclo postlarvario anual de *Ammothella longipes* (Hodge, 1864) (Pycnogonida). *Cah. Biol. Mar.*, 21: 1-9.
- Piel, W.H. – 1991. Pycnogonid predation on nudibranch and ceratal autonomy. *Veliger*, 34(4): 366-367.
- Scelzo, M.A., R. Elias, E.A. Vallarino, M. Charrier, N. Lucero and F. Alvarez. – 1996. Variación estacional de la estructura comunitaria del bivalvo *Brachydontes rodriguezii* (d'Orbigny, 1846) en sustratos artificiales (Mar del Plata, Argentina). *Nerítica*, 10: 87-102.
- Staples, D.A. – 1997. Sea spiders or pycnogonids (Phylum Arthropoda). In: S.A. Shepard and M. Davies (eds.), *Marine Invertebrates of Southern Australian, Part. III*, pp. 1041-1072. South Australian Research and Development Institute.
- Staples, D.A. and J.E. Watson. – 1987. Associations between pycnogonids and hydroids, In: J. Bouillon, F. Boero, F. Cicogna and P.F.S. Cornelius (eds.), *Modern Trends in the Systematics, Ecology, and Evolution of Hydroids and Hydromedusae*, pp. 215-226. Oxford University Press.
- Stock, J.H. – 1966. Pycnogonida. Campagne de la Calypso au large des côtes atlantiques de l'Amérique du sud (1961-62). In: Résultats Scientifiques de la Campagne de la Calypso, 7. *Ann. Inst. Océanogr. Monaco*, 44: 385-406.
- Tomaschko, K.H., E. Wilhelm and D. Buckmann. – 1997. Growth and reproduction of *Pycnogonum litorale* (Pycnogonida) under laboratory conditions. *Mar. Biol.*, 129: 595-600.
- Varoli, F. – 1994. Aspectos da alimentação de *Tanystylum isabellae* Marcus e *Anoplodactylus stictus* Marcus (Pantopoda). *Rev. Brasil. Zool.*, 11(4): 623-627.
- Wilhelm, E., D. Buckmann and K.H. Tomaschko. – 1997. Life cycle and population dynamics of *Pycnogonum litorale* (Pycnogonida) in a natural habitat. *Mar. Biol.*, 129: 601-606.
- Zamponi, M.O. and G.N. Genzano. – 1992. La fauna asociada a *Tubularia crocea* (Agassiz, 1868). (Anthomedusae; Tubulariidae) y la aplicación de un método de cartificación. *Hidrobiológica*, 3/4: 35-42.

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