New symbiotic associations involving Syllidae (Annelida: Polychaeta), with taxonomic and biological remarks on
Pionsyllis magnifica and Syllis cf. armillaris

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Several new symbiotic associations involving Syllidae (Annelida: Polychaeta) are reported. The number of known host sponge species infested by Hipsyllis spongivola is updated to 36, with seven hosts being reported for the first time (i.e. Aplysina corrigata, Aplysina sp., Chiona sp., Chiona viridis, Phorbas tenaciorn, one sponge from Iran, one sponge from Cambodja). Two infestation patterns (a few worms per host cm² in temperate waters and 10s or 100s in tropical waters) are identified. The taxonomic and ecological characteristics of the species are discussed. Five associations occurring between four syllid worms and decapod crustaceans are fully reported for the first time. Syllis cf. armillaris, S. ferrani and S. pontioi occurred inside gastropod shells occupied by hermit crabs as well as Pionsyllis magnifica, which was also found inside the branchial chambers of the giant crab Parathelphusoms cantschachia. The description of Pionsyllis magnifica is emended on the basis of the new specimens found, while some taxonomic remarks on Syllis cf. armillaris are given. In addition, further evidence of sexual (P. magnifica) and asexual (S. cf. armillaris) reproduction in symbiotic syllids is provided.

INTRODUCTION

The Syllidae are a very large and diverse polychaete family. Syllids are found in many different habitats, including the surfaces and inner channels and cavities of other marine invertebrates. About 28 species have been reported in association with cnidarians, crustaceans, echi- noderms and ascidians but they are particularly frequent and abundant in sponges (Martin & Britayev, 1998).

Sponges are one of the most common host group (including about 16% of the host species) for parasitic polychaetes (Martin & Britayev, 1998), where they often exceed the density of other inhabitants (Dauer, 1974; Tabachnikov, personal communication). Probably the most representative syllid harboured by sponges is the cosmopolitan species Hipsyllis spongivola (Grube). It is a typical example of a polyxenous relationship among symbiotic polychaetes, with 22 different host sponge species reported to date (Martin & Britayev; 1998). In this paper, the number of host sponge species harbouring H. spongivola is updated to 35, on the basis of both newly collected material, museum collections and bibliographical sources. Moreover, we discuss the ‘cosmopolitan’ character of the species based on the infestation characteristics of the sponge–worm associations.

There were a very few known symbiotic relationships between syllid worms and decapod crustaceans. The first reported association was that between Syllis cornuta Rahuche and an unidentified hermit crab (Fauvel, 1923). It was not until 1982 that other associations between a syllid (i.e. Essyllis blomstadi) and several species of pagurids were reported (Hoberg et al., 1982). Recently, some other associations involving Pionsyllis magnifica Moore and Syllis cf. armillaris (Müller) were also reported (Martin & Britayev, 1998). In this paper, the details of these associations are described and discussed. Moreover, the morphological description of P. magnifica is emended in the light of new specimens found during the present study, while some taxonomic remarks on Syllis cf. armillaris are given. In addition, further evidences of sexual (P. magnifica) and asexual (S. cf. armillaris) reproduction in symbiotic syllids are provided. Additionally, some new associations involving the species Syllis ferrani Alós & San Martin and Syllis pontioi San Martin & López are reported for the first time.

MATERIALS AND METHODS

The study was based on preserved specimens, which are deposited within the author’s personal collections (except for those specimens where the corresponding museum and catalogue number are indicated in the Examined material section). For scanning electron microscope (SEM) observations, the preserved worms were washed three times in distilled water (30 min each), run through a series of ethanol concentrations, and stored in 70% ethanol until observation. Immediately prior to viewing in a Hitachi S.570 SEM (Laboratorio de Microscopia Electrónica of the Institut de Ciències del Mar of Barcelona, C.S.I.C), they were run through a series of ethanol concentrations ending with 100% alcohol, critical-point dried, attached to a stub, and coated with gold.
images were captured and stored in digital format using the
Printerface System hardware and software.
When possible, infestation intensities were estimated
after extracting the worms from each host (i.e. decapod
hosts, referred to as worms per host) or from a piece of
known volume (i.e. sponge hosts, referred to as worms per
host cm<sup>2</sup> of host). Worm extractions and counting were
made under a Leitz Diaplan stereomicroscope equipped with
interference contrast optics (Nornasky) and linked to a
camera lucida. Light microscope micrographs were made
with a Zeiss Axioscop stereomicroscope equipped with
the SPOT hardware and software (SP100 KAF1400
digital camera and software version 2.1) from Diagnostic
Instruments Inc.

RESULTS

Family SYLLIDAE Grube, 1850
Subfamily Syllinae Grube, 1850
Genus Haplosyllis Langerhans, 1879

Haplosyllis spongicola (Grube, 1855) (Table 1)


Material examined
More than 100 specimens from Aplysina coronata, A. fistularis and Aplysina sp., collected on July 1981 by H. M. Reiswig, 15–20 m depth; 115 specimens from A. batyphylla, collected in 1998 by M. Maldonado, 40–15 m depth; 210 specimens from Halichonia sp., collected on 7 December 1983 by T.A. Britayev, 3–4 m depth; 68 specimens from Aaptos cf. aaptos, collected on 4 April 1989 by T.A. Britayev, 2.5 m depth; 360 specimens from an unidentified pink sponge collected in October 1998 by E. Dutrieux, 14–15 m depth; 95 specimens from Cliona sp., National Museum of Natural History, Smithsonian Institution, USNM 50687; three specimens from C. vitidis in gamma (massive) growth stage, collected in early summer, 1999 by D. Martin, 9 m depth; three specimens from Phorbas tenaciura, collected in late spring, 1999 by D. Martin, 6 m depth; 10 specimens from unidentified white sponge collected on 12 November 1999 by Dr B. Tirsch and Dr Y. Kantor, 20 m depth.

All known geographical locations and infestation intensities for the currently known host sponge species are summarized in Table 1.

Ecology
Haplosyllis spongicola inhabited the host aquiferous system when the channels are large enough to harbour the worms. However, they could also inhabit the tissues of the sponge, often inside cavities surrounded by thick protective layers generated by the host sponge in response to the presence of the worms (Martin & Britayev, 1998). Among the studied associations, the first location was common for tropical hosts, which harboured small sized (often less than 0.5 cm in length) worms. The second location occurred in temperate hosts, which harboured much longer (reaching up to 5 cm in length) worms. In agreement with the above differences in location and worm's size, two infestation patterns were observed: (i) 10s or 100s of individuals per host cm<sup>2</sup> in tropical hosts; and (ii) less than one worm per host cm<sup>2</sup> in the Mediterranean (i.e. temperate) sponges (Table 1).

The species has been previously reported from detritic and muddy bottoms, 'maerl', intertidal algae, photophilic and sciaphilic algae on infraillitral hard bottoms, organogenic calcareous concretions (such as encrusting algae and corals) and Pseudodia oceanica meadows (fossil and rhizome strata). The species has been also mentioned in association with colonies of other organisms, such as hydroids (López et al., 1996), Microcosmus sp. and Phyllochaetopterus socialis (Campoy, 1982), and vermetid reefs (Amoureux & Gantès, 1976; Baratech & San Martín, 1987; Ben-Eliahu, 1977; Campoy, 1982; Núñez et al., 1992) or associated to organogenic calcareous concretions (Lauzier, 1966; López et al., 1996; Martin, 1987; Núñez et al., 1992).

World distribution
Cosmopolitan in warm (tropical and subtropical) waters. Occasionally reported from temperate boreal waters.

Pionosyllis magnifica Moore, 1906

Figures 1–3

Pionosyllis magnifica—Moore (1906), page 223, pl. 10, figures 9–11; Annenkova (1938) page 152; Uschakov (1950) page 176, figure 13; Hartman (1968), page 447; Kudennov & Harris (1995), page 54, figure 1.9.


Material examined
Bering Sea, 5752.05°–5756.04°N 17040.05°–17040.00°W, r/v Adler, cruise no. 18, station 150, 50 m depth, September 1973; two specimens collected by Victor N. Goriachev on Paralithodes camtschatica. Southern coast of Kamchatka peninsula, point Lopatka, 6–8 m depth, August 1983; one specimen collected by Andrey A. Adrianov in a gastropod shell occupied by Pagurus sp..

Emended description
Body long, thick, up to 28 mm long, 0.85 mm wide without parapodia, for 73 setigers. Colour white to yellowish (in alcohol) with brownish ventral spots or bodies at the base of posterior parapodia (Figure 3B). Prostomium subpentagonal, wider than long, with four eyes in trapezoidal to rectangular arrangement; median antenna originating between the anterior pair of eyes, longer than the length of prostomium and palps together; lateral antennae originating slightly in front of the anterior eyes, shorter than median antenna (Figure 1A). Palps wide, fused dorsally at their bases.

Two pairs of tentacular cirri, dorsal ones similar in length to median antenna and ventral ones shorter (Figure 1A). Parapodia with distinct anterior and posterior lobes; dorsal cirrall spindle-shaped, relatively short, similar in length to half of body width, but slightly longer on anterior segments; ventral cirral thick, shorter than parapodial lobes, thick and rounded in anterior parapodia to conical in mid-body and posterior parapodia (Figures 1B & 2A). Anterior parapodia bearing about 30 compound setae, with distally spinose shafts, relatively long bidentate

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<table>
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<th>Host sponge</th>
<th>Geographical location</th>
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* mentioned as 'Phanopongoia (Chondropsis) sp. (Magnino & Gaino, in press)' in Martin & Britayev (1998); b, number of worms found inside a single host of unknown volume.

blades, with both teeth distinctly separated and similar in length, and short straight marginal spines (Figures 1D & 2B); the number of setae decreasing backward. Each posterior parapodia bearing about 22 compound setae, with short, triangular, bidentate blades, with proximal tooth somewhat longer and bigger than distal tooth (Figure 1E). The blades showed slight antero–posterior and dorso–ventral gradation in length, having 26–32 m on anterior parapodia and about 20 m on posterior ones (Figure 1D,E). Simple setae not seen. Each anterior
parapodia with four aciculae (Figure 1C), decreasing to two on posterior ones (Figure 1F). The aciculae are slender, with rounded, irregular tips. All specimens with thin supporting acicula in the base of cirrophores and several thin, small capillary natatory setae (Figures 1G & 2A,C). Each segment with numerous ventral tufts of cilia (Figure 2A,D,E) and surrounded by one transverse ciliary ring interrupted by parapodia (Figure 2A,D).

Pharynx short, extending about 4–7 segments, with an anterior large tooth, and a crown of about ten papillae (Figure 3A). Proventriculus similar in length to pharynx extending from setiger 8 to 15 in specimen from giant crab, and from setiger 9 to 16 in specimen from hermit crab, barrel-shaped, with about 40 rows of muscular cells.

Remarks

_Pionosyllis magnifica_ is a relatively unknown species. Kudenov & Harris (1995) reported the species as known only from the North American Pacific coast. However, they included the specimens found by Annenkova (1938) within the synonyms. These worms were collected at the Japan Sea and, thus, closer to the occidental coast of the Pacific Ocean where our specimens were found. _Pionosyllis magnifica_ was originally drawn in the first description of the species, this iconography being repeated by Hartman (1968) and, after reviewing the holotype, also by Kudenov & Harris (1995). Now new drawings and SEM micrographs based on our specimens are provided, which show several slight differences with the original description. The specimens examined have a smooth pharyngeal tooth, which is not surrounded by small denticles. The median antenna is inserted between the anterior pair of eyes, while it was previously described as inserted in front of them and at the same level as the lateral antennae. In addition, they had segmental pairs of brownish bodies, which have never been previously reported. The shape of the pharyngeal end fully justifies the original inclusion of the species in _Pionosyllis_, instead of _Eusyllis_ (Bane & Hobson, 1974; Pettibone, 1934). On the other hand, the position of the antennae is not enough to define our worms as a new species while the presence of segmental brownish bodies has no taxonomic relevance. After dissecting and studying them under SEM, numerous long cilia on their inner surface were observed. This allows us to assume that could be nephridia modified to function as gonoducts in our specimens, which were all reproductive females.

Ecology

The commensal specimens from Bering Sea were found inside the branchial chambers of the giant crab _Paratilithodes canstatichus_ living on a sandy bottom. The commensal specimen from Lopatka Point was sheltered inside the apex (i.e. upper teleconch whorls) of a gastropod shell occupied by _Pogonurus_ sp. All the studied specimens are ovigerous females bearing coelomic oocytes. The oocyte diameter varied from 91–121 μm (the Bering Sea) to 240–290 μm (Lopatka point). The presence of notopodial setae indicates transformation to the epipodial stage.

_Pionosyllis magnifica_ has been previously reported from mud, pebble-mud and shelly-sand bottoms, intertidal to 150 m depth (Hartman, 1968; Kudenov & Harris, 1995). There are no mentions of the species in association with other benthic organisms.

![Figure 1. _Pionosyllis magnifica_.](image)

_**Figure 1.**_ _Pionosyllis magnifica_. A, Anterior end in dorsal view; B, posterior parapodium, setae not drawn; C, aciculae from an anterior parapodium; D, compound setae from an anterior parapodium; E, compound setae from a posterior parapodium; F, aciculae from a posterior parapodium; G, parapodium from mid body with noto- and neurosetae; the arrow indicates the position of notosetae. Scale bars: A, 0.7 mm; B, 0.12 mm; C–F, 20 μm; G, 0.52 mm.

World distribution

North Pacific: southern coast of Kamchatka, Japan Sea, Bering Sea, coast of North America.

Syllis cf. armillaris (Müller, 1776)

Figures 4&5


_Typosyllis aciculata orientalis_.—Imajima & Hartman (1964), page 130, pl. 31 figures e–f, pl. 32 figures a–t.

Material examined

Pacific Ocean, Sala-Y-Gomez submerged ridge, 2540–2537’S 8525–8526’W, 26 April 1987, r/v Shokman, cruise no. 18, station 1923, 162–190 m depth, 20 specimens; station 1993, 230–280 m depth, one specimen Indian Ocean, sea mount ‘Error’, 1019.7–1016.25’N 5607.3’W, September 1988, r/v Vitíaz II, cruise no. 17, station 2573, one juvenile and five adult specimens from _Pogonurus_ sp.

Description

Body long and slender, without colour marks. 2.1–14.5 mm long and 0.14–0.29 mm wide (at proventriculus level without parapodia), 38–124 setigers. Prostomium
Figure 2. SEM micrographs of *Pinnantis magnifica*. A, Mid-body segments in ventral view; B, compound setae from mid-body region; C, notosetae from mid body; D, ventral surface of mid region under higher magnification; E, detail of the ventral tufts of cilia. dc, dorsal cirrus; ns, natatory setae; ptc, parapodial tufts of cilia; src, segmental rings of cilia; vtc, ventral tufts of cilia.

oval, wider than long. Eyes not seen (perhaps an artefact of fixing). Palps broad and triangular. Median antenna originating from middle of prostomium, with a well-developed ceratophore and 16 articles. Lateral antennae originating from near the anterior margin, with 11–12 articles.

Two pairs of tentacular cirri, the dorsal one (20–25 articles) 1.5 times longer than the ventral one (13–14 articles), both having well-developed cirrophores. Dorsal cirri spindle-shaped, showing a slight alternation in length, with 12 (long) and 8–9 (short) articles at mid-body region (Figure 4A,B), and also a slight antero-posterior gradation in length (up to 17 articles in anterior setigers and shorter in the posterior ones). Ventral cirri shorter than parapodial lobe. Up to 18 articulated setae per parapodial lobe in the anterior parapodia, the blades being long and finely serrated, bearing a subdistal tooth smaller than the distal one but clearly developed and slight dorso-ventral gradation in blade length (dorsal 4.5 m, ventral 3.7 m) (Figure 4C). Up to five setae per parapodium in median and posterior parapodia, bearing only three at the posterior most ones; blades short, stout and triangular with a very small subdistal tooth, sometimes difficult to distinguish from serration, without clear dorso-ventral gradation (blade length from 20.5 to 26.5 m) (Figure 4E). Two to four aciculae per parapodium in the anterior segments; 1–2 with straight tip, the others with rounded tips (Figure 4D). One or two aciculae per parapodium in median and posterior segments, one with straight and blunt tip, the other with oblique and subdistally enlarged tip (Figure 4F). The latter is the single type in the last 20 setigers.
Figure 3. *Pionayllis magnifica*. A, Anterior end in ventral view; B, posterior end in ventral view.

Pharynx long, extending through 14 setigers. Tooth not seen (although expected to be near anterior end of pharynx). Proventriculum long, cylindrical, extending through 8–10 setigers, with 42 rows of muscle cells.

**Remarks**

*Syllis cf. armillaris* was first described from Arctic waters (Greenland), although it is currently considered cosmopolitan (Licher, 2000; Uebelacker, 1984). Our material differs slightly from re-description of the species by Licher (2000). The posterior setal blades in our specimens are shorter and proportionally stouter. Furthermore, they do not show any dorso–ventral gradation in length, contrary to Licher’s description, and the shape of dorsal cirri is more definitely spindle-shaped in our specimens. Finally, their pharynx is longer, extending through 14 instead of 9 setigers. However, Uebelacker (1984), mentioned a slight dorso–ventral gradation in blade length, as well as a range of pharynx length extending from setigers 4 to 13. Although a review of the different morphologies of the populations of the species reported around the world is out of the scope of the present paper, we suggest that they could support the existence of a sibling species–complex, perhaps with overlapping geographical distribution. As a consequence, we decided to fully describe our specimens to allow a future assessment of the geographical range of an eventual new species described within the frame of a new study on this complex.

**Ecology**

The commensal specimens were found in upper teleococonch whorls of the shells occupied by *Paragapagurus boletifer* De Saint-Laurent, 1972 and *Paguristes* sp., and under the base of actinian polyp attached to the upper surface of shells. The usual number of worms per one host ranged from 1 to 3. Up to ten worms were found in only one case, four of them having regenerated anterior ends.
Figure 6. Syllis pontxioi. A, Setae from a posterior parapodium; B, acicula from posterior parapodium; the arrow indicates the position of the acicula.

(Figure 5A). These worms showed a distinct border between old and new segments, well-defined by the posterior edge of proventriculum and the small size of segments in the regenerated anterior part (Figure 5A,B). The number of regenerated setigers was invariably equal to 11, indirectly supporting asexual reproduction.

Syllis cf. aemillaris has been previously reported from muddy detritus bottoms, calcareous encrusting algae, intertidal rocks, rhizomes of Cymodocea nodosa and Posidonia oceanica meadows and photophilous and scaphilous algae on infralittoral hard bottoms. The species has been also mentioned in association with hydroids (López et al., 1996), sponges (Alós, 1988; Amourex et al., 1980), colonies of the ascidiacean Microcosmus sp. (Campoy, 1982), vermetid reefs (Ben-Eliahu, 1977; Campoy, 1982) and Sabellaria reefs (Gruet, 1972).

World distribution
Cosmopolitan.

Syllis pontxioi San Martín & López, 2000
Figure 6


Material examined
Indian Ocean, sea mount ‘Error’, 1019.7°–1016.25’N 5607.3’W, September 1988, r/v Vitiaz II, cruise no. 17, station 2573, one juvenile and one broken specimen from Clibanarius sp., one juvenile and five adult specimens from Paguristes sp.

Remarks
According to Licher (2000), the worms reported (erroneously) as Syllis truncata cryptica Ben-Eliahu in the Iberian Peninsula since Campoy (1982) corresponded, in fact, to Syllis gelachi Hartmann-Schröder, 1960 while those reported as Syllis (or Typyllis) gelachi must belong to a different species. These worms have been recently redescribed as a new species, S. pontxioi (San Martín & López, 2000). Syllis pontxioi is characterized by its very short antennae, tentacular cirri and dorsal cirri (which, in addition, are very slender) and its thick and bidentate ventral simple setae. However, the most characteristic features for this species are the mid-body and posterior falciger blades, which are very short and with enlarged proximal tooth, and its stout posterior aciculae, whose tips are provided with hollow and convex edge. The specimens found living commensally with hermit crabs perfectly fitted with the description of S. pontxioi, particularly in the last two characteristics (Figure 6A,B).

Ecology
The commensal specimen was found inside the apex of gastropod shells occupied by the hermit crabs Paguristes sp. and Clibanarius sp.. Syllis pontxioi has been previously reported from Amphioxus sands, muddy sands and muddy gravels (between 11 and 200 m depth). The species has been also reported as sponge endobiont (Alós et al., 1982).

World distribution
Northern coast of Spain (Basque Country, Asturias, Galicia), Western Mediterranean, Indian Ocean.

Syllis ferrani Alós & San Martín 1987

Typyllis ferrani—Licher (2000), 221–223, figure 93.

Material examined
Mediterranean Sea off Cartagena, Medits 97 cruise, trawl 34; one complete specimen collected on May 1997
by Pere Abelló from a shell occupied by *Pogus caschatus*, 81 m depth.

**Remarks**

The single specimen found perfectly matched with the original description of the species.

**Ecology**

The commensal specimen was found inside a gastropod shell occupied by the hermit crab *Pogus caschatus*. *Syllis ferrani* has been previously reported from precruraligenous aggregates of calcareous algae and rhizome stratum of *Posidonia oceanica* meadows from 8 to 33 m depth and in association with sponges (López et al., 1996).

**World distribution**

Western Mediterranean Sea, Cape of Creus (Catalan coast of the Iberian Peninsula) and Chafarinas Islands (Alboran Sea).

**DISCUSSION**

Up to 33 species of syllids have been reported as living in close association with other marine invertebrates, representing about 9% of the total known symbiotic polychaetes (Martin & Britayev, 1998). Twenty-three species have commensal habits, while 11 have been considered as parasites. The former are associated with sponges, cnidarians, sipunculids, echinoderms (i.e. asteroids, ophiurids, holothuroids), hydroids and decapods. The latter are mainly parasites of sponges, but some species parasitize cnidarians, polychaetes, nemerteans and tunicates.

With a few exceptions, symbiotic syllids showed only slight adaptations to their particular mode of life. Among the few known (see Martin & Britayev, 1998 and references therein), there are: (i) life-cycle adaptations, such as the presence of isolated heterosexual pairs on the same host individual in *Amblyopsis cincinnata* (commensal); (ii) reproductive adaptations, such as the ichneumon-like lifecycle (i.e. direct oviposition inside living host hydroid; with subsequent feeding of juveniles on polyp tissues) in *Procernea* sp. (parasite); (iii) behavioural adaptations, such as host recognition in *Haplonyssus chamaeleon* (parasite); (iv) colour mimicry in *H. chamaeleon, Branchiochelys oculata* (parasite) and *Branchiochelys exilis* (commensal); (v) specialized attachment structures such as hooked setae in the symbiotic species of the genera *Haplonyssus, Haplonyllis, Trypanyllis, Bollandia, Procerus and Branchiochelys*.

The external morphology of *H. spongicola* is very well adapted to its life style and appears to be relatively simple, with all setae being simple and having two small teeth on its large main fang. However, there are a few very data on the relationships between *H. spongicola* and its host sponges (Martin & Britayev, 1998). Grazing of *H. spongicola* on individuals of the Mediterranean host *Cliona viridis* that had already attained its largest growth stage (i.e. gamma or massive stage, according to Rosell & Uriz, 1991) was observed (D. Martin, personal observation). In that case, for instance, one sponge specimen measuring about 62 cm³ harboured only one large worm (about 3 cm in length), located directly inside the sponge tissues. However, the presence of this worm (probably temporal) apparently did not disturb the normal growth of the sponge. The situation was similar to that found in *Phorbas tenacior, Axinella verucosa* and *Rhizosolenia pyriformis*, always harbouring less than one worm per host cm² (Table I). The last two species, however, react to the presence of the worms by producing a thick protective layer around them (Uriz, 1978).

In tropical seas, *H. spongicola* occurred inside the canals of the aquiferous system of their host, who did not show abnormal morphological structures in reaction to the presence of the worms. In addition, infestations by 10s or 100s of worms are typical in these hosts (Table I). The coral reef *Cliona* sp. from Puerto Rico harboured a few more than 600 worms in a piece of about 16.5 cm². The extremely numerous, small-sized tropical worms were continuously grazing and removing the host biomass without apparently causing a decrease in the host growth rate or in the sexual and asexual reproductive activities (Reiswig, 1973; Tsurumi & Reiswig, 1997). The host sponges *Ircinia ferox* and *Alphysina fistulosa* were able to survive and even grow when experimentally transplanted to more than 100 m depth (i.e. much deeper than their normal bathymetric distribution). The transplanted sponges loose their zooxanthellae and bacterial symbionts, while their respective polychaete populations were not stressed (Maldonado & Young, 1998a). *Haplonyllis spongicola* seems to be typically present in tropical asyndisic sponges, reaching high densities even in the small-sized *Alphysina bathyphila* (Table I), the single stalked species of the family Verongiidae, which inhabits vertical walls submitted to strong currents (Maldonado & Young, 1998b).

The differences between temperate and tropical populations of *H. spongicola* reported in this paper (i.e. worm’s size, location on hosts, host reactions, infestation intensity) cast severe doubts on the cosmopolitanism of the species. The species have been the subject of a long-lasting taxonomic controversy, recently summarized by Licher (2000), who listed more than 15 synonymized specific names, together with more than 350 of worldwide citations of the species, either as *Syllis spongicola, Syllis* (Haplonyllis) *spongicola or Haplonyllis spongicola*. In light of our results, however, we agree with Campoy (1982), who first suggested the possible (and still unexplored) relationships between the presence of the species inside many different hosts and the existence of different morphotypes. A detailed analysis of more than 30 populations around the world is currently being carried out to assess the validity of all previously synonymized specific names, as well as to determine if a sibling or pseudosibling species-complex is being hidden under the name of *H. spongicola* (D. Martin & T.A. Britayev, unpublished data).

From an ecological point of view (and supporting the possible existence of a sibling species-complex) the behavior of both temperate and tropical *Haplonyllis spongicola* populations appears to be different. We suggest that the temperate worms could behave as sponge predators. To assess if they are species-specific or generalist predators would be an interesting subject of a future experimental approach. As predators, the worms could either be able to move from one prey to another (feeding on different sponges) or to live sometimes inside their preys (providing they offer enough room to harbour the worms). Most reports of *H. spongicola* as free-living or associated to other
benthic invertebrates correspond to temperate locations. However, these reports should be viewed with caution, as the presence of sponges in the original samples may never be discarded. In fact, sponges may be avoided during the sorting process, without any further mention of this manipulation, or omitted in faunistic and/or taxonomic reports dealing with polychaetes. Thus, as already mentioned by Campoy (1982), the relationships of *H. spongicola* with the sponges may not be evident to the final reader (e.g., a polychaete taxonomist or ecologist).

Conversely, the tropical worms seemed to be strict sponge endosymbionts, living always inside the host and probably behaving as parasites. In fact, the term 'good' parasite (sensu Ricklefs, 1990) could apply to these worms, as all phases of their life-cycle occurred inside the host, often during the whole year and without disturbing the normal growth and reproductive cycle of the sponges (Tsurumi & Reiswig, 1997; D. Martin, personal observations). The exact nature of the host/symbiont relationships as well as the host specificity of the different morphotypes that could be involved in the species-complex will be assessed as a part of the same study mentioned above (D. Martin & T.A. Britayev, unpublished data).

The associations between syllids and decapod crustaceans are apparently much less frequent than those between syllids and sponges (Martin & Britayev, 1998). They have been scarcely reported and are poorly known. They have been incidentally mentioned in faunistic papers (e.g. Faivel, 1923). Only one paper includes relevant ecological information on the association between a syllid, *Eusyllis blomstadii* and their pagurid hosts (Hofer et al., 1992). This species has been found in the Pacific coast of North America in a white parchment tube adhering and conforming to the upper interior surface of the whorl of the host shell. This location is similar to our observations on *Pionosyllis magnifica*, which also occurs in the branchial cavity of giant crabs. These peculiar locations suggest a high degree of specificity in their relationships with the hosts. In fact, the presence of possible host crabs may not be discarded for the previous records of the species (Moore, 1906; Pettibone, 1954). Consequently, they may either reflect the real existence of free-living populations, or a complex life cycle including both free-living and symbiotic stage or, also, they might result from loss of host during sampling. Thus, we suggest that *P. magnifica* could be tentatively considered as a facultative or temporary symbiont, while the exact nature of the association (i.e., parasitic, commensalistic or mutualistic) is still undefined.

Like *P. magnifica*, *Syllis cf. armillaris*, *S. ferrani* and *S. pontsio* did not show any specific morphological adaptation to the symbiotic mode of life, while these three species have been reported either as free-living or as incidentally associated to colonial or reef-building invertebrates. Like most species of the Superfamily Nereididae, the syllids are considered to be free-living predators (Fauchald & Jumars, 1979), often erroneously (Giagrande et al., 2000). Thus, in absence of morphological adaptations, further research should also be addressed to define the exact nature of these associations. Particularly to assess the possible existence of behavioural adaptations, like those developed by the well-known hermit crab commensal *Nanthes fascata* (Cram & Evans, 1980; Gilpin-

Brown, 1969; Goerke, 1971). The present data do not allow us to affirm whether the hermit crab associated syllids should be considered as commensal (i.e. feeding on the host food) or parasitic (e.g. feeding on the hermit crab eggs) symbionts or as merely inquilines.

Asexual reproduction has been also considered as an adaptation to the symbiotic mode of life, allowing the symbionts to reach high densities after colonization of a rare suitable substrate (i.e. the host) by a single larva (Martin & Britayev, 1998). This may be supported indirectly by the higher intensities of infestation among hosts sheltering symbiotic polychaetes showing traces of asexual reproduction (Tzetlin & Britayev, 1985). True asexual reproduction by architomy appears to be rare in syllids (Franke, 1999), the two only previously known species being *S. gracilis* and the parasitic *Pocerasteria halleiziana*. The regeneration of the anterior end in some specimens of *S. cf. armillaris* in our samples, as well as the invariable number of regenerated setigers, clearly supports the capacity of reproduction by architomy in this species. Additionally, the finding of asexually reproductive specimens of *S. cf. armillaris* supports its close phylogenetic relationships with *S. gracilis*. Both species also have short fusiform dorsal cirri in mid-body, similar compound setae and sexual reproduction by pentacereaceous stolons (Estapé & San Martín, 1991).

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