

Symbiotic Polychaetes: Review of known species

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ABSTRACT

Although there have been numerous isolated studies and reports of symbiotic relationships of polychaetes and other marine animals, the only previous attempt to provide an overview of these phenomena among the polychaetes comes from the 1950s, with no more than 70 species of symbionts being very briefly treated. Based on the available literature and on our own field observations, we compiled a list of the mentions of symbiotic polychaetes known to date. Thus, the present review includes 292 species of commensal polychaetes from 28 families involved in 713 relationships and 81 species of parasitic polychaetes from 13 families involved in 253 relationships. When possible, the main characteristic features of symbiotic polychaetes and their relationships are discussed. Among them, we include systematic account, distribution within host groups, host specificity, intra-host distribution, location on the host, infestation prevalence and intensity, and morphological, behavioural and/or physiological and reproductive adaptations. When appropriate, the possible directions for further research are also indicated.

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INTRODUCTION

Living organisms are always connected in some way to other individuals of the same species and to individuals of other species living in the same area. Many of these established interactions are known as direct relationships (i.e. sex recognition, competition, predation). In these cases, the involved organisms are known as free-living. However, some species have become closely associated, often to mutual benefit (frequently referred to as “symbiosis”). These relationships usually convey a high degree of specificity, to the extent that at least one of the involved partners can no longer be considered a free-living organism.

Among the polychaetous annelids, which for the most part are free-living, crawling, burrowing and tube-dwelling, the setting-up of close associations with other marine invertebrates is a rather common phenomenon. This is not surprising because the polychaetes are probably the most frequent and abundant marine metazoans in benthic environments. They may be numerically less important on hard substrata, and some molluscs and crustaceans may co-dominate on soft bottoms, but of all metazoans only the nematodes are more ubiquitous (Fauchald & Jumars 1979). However, despite the obvious importance and increasing knowledge on the ecological role of polychaetes, the literature on symbiotic polychaetes remains largely anecdotal, likely with the exception of some widely known examples of commensalism practised by some species of the family Polynoidae. Moreover, the information is often scattered among studies dealing with many different subjects (e.g. systematics, descriptive ecology, biology).

The aim of the review is, therefore, to attract the attention of scientists to - and to encourage further studies on - the ecology of this particular and diverse group of symbionts. We make an attempt not only to summarise the available data on symbiotic polychaetes, but also to outline the lacunae in the knowledge of their ecology. However, an exception to these dispositions are the Myzostomida, a highly specialised Order of polychaetes which includes more than 130 species (Pettibone 1982) that live associated with echinoderms (Barel & Kramers 1977, Jangoux 1987). The aberrant characteristics of these worms and their special and intimate associations with echinoderms merit a specific approach that falls outside the scope of the present paper. Thus, the whole order has been omitted, for inclusion in a further generalisation. On the other hand, some associations previously considered as symbiotic, such as those between the orbinids *Orbinia latreilli* and *Phylo foetida* and the holothuroid *Leptosinapta gallieni* (Barel & Kramers 1977), appear to be fortuitous ecological associations (Beauchamp & Zachs 1913). As far as possible, these fortuitous associations were excluded from the present review. Similarly, the presence of epibionts (e.g. on the caparace of crabs, see Okuda 1934, Abelló et al. 1990), endobionts (e.g. inside the aquiferous canals of sponges, see Pearse 1932, Bacescu 1971, Frith 1976, Pansini & Daglio 1980-81, Westinga & Hoetjes 1981, Alós et al. 1982, Votsiadou-Koukoura et al. 1987, Koukouras et al. 1992, 1996, Pascual et al. 1996) or simple associates to other organisms (viz. bryozoans in Morgado & Amaral 1981a, b, c, 1984, 1985, vermetids in Ben Eliahu 1975a, b, 1976, corals in Arvanitidis & Koukouras 1994, wood-borer molluscs in Kirkegaard & Santhakumaran 1967) are not regarded as symbiosis without any demonstration of specificity, because most of the involved organisms will inhabit a wide variety of substrates and the presence or absence of the so-called “host” is irrelevant.

The present review provides a list of known symbiotic polychaetes arranged into several huge tables, including the symbiotic species from each polychaete family, the host group and species name, the type of association and the source of information. There are three main tables: non-boring commensals, non-boring parasites, and symbiotic borers. The main body of the review is divided into three main sections according to these three tables. Each section is sub-divided into several parts, starting with the analyses of the respective list of relationships. Then follow the information on morphological, biological, ecological and behavioural trends characterising the symbiotic polychaetes.

BACKGROUND: PREVIOUS REVIEWS

Although the oldest known review of commensal organisms is probably that by van Beneden (1869), the first - and certainly the only known - reviews entirely dedicated to symbiotic polychaetes are those by Paris (1955), Clark (1956) and Britayev (1989). The former is a collection of some (but not all) of the typical commensal and parasitic relationships involving polychaetes known to date. The second includes a very full list of symbiotic polychaetes (about 73 species from 22 families, involved in about 160 associations), and a description of one new association. The latter, although known only from a Russian version, is certainly the first modern attempt to summarize the main trends of polychaetes as symbionts. There have also been a number of reviews in the past which have addressed particular aspects of symbiotic polychaetes. Dales (1957) reviewed the commensal interactions in marine organisms and mentioned several associations involving polychaetes. The extensive review of symbionts of Echinodermata from the NE Atlantic by Barel & Kramers (1977) included an annotated check list of symbiotic polychaetes, whereas Alvà & Jangoux (1989) updated the known relationships between polychaetes and ophiuroids. Overstreet (1983), in his review on the metazoan symbionts of crustaceans, briefly mentioned some polychaetes. Britayev (1981) described two new polychaete species commensal with coelenterates, and reviewed the bibliography on their associated polychaetes. The symbiotic invertebrates associated with the sea urchin *Echinus sculentus* and with the polychaete *Chaetopterus appendiculatus* were reviewed by Comely & Ansell (1988) and Petersen & Britayev (1997), respectively. The symbiotic relationships within benthic organisms from South California, polychaetes included, were reviewed by Fox & Ruppert (1985). The symbiotic polychaetes from more or less restricted geographical areas have more often been reviewed within the framework of systematic papers (e.g. Gibbs 1969 for the Solomon Islands, Okuda 1936a, 1950, and Uchida 1975 for the Japanese waters), whereas some systematic reviews referred to taxa whose members included well-known symbiotic species, such as the families Caobangidae (Jones 1974), Oeonidae (Pettibone 1957), Histriobdellidae (Moyano et al. 1993), Iphitimidae (Fage & Legendre 1933, Gaston & Benner 1981) and Polynoidae (e.g. Hanley 1989, Pettibone 1993, 1996). The shell-boring spionid species of *Polydora* and related genera were reviewed by Blake (1969, 1971, 1996). Finally, the physiology of commensal polychaetes was discussed by Davenport (1966a, b).

All these review articles, though comprehensive, address individually only particular aspects of the complex symbiotic interactions involving polychaetes. There has been a more or less steady dribble of information on symbiotic polychaetes over the years since Paris (1955) and Clark (1956). Therefore, it is now becoming possible to begin a synthesis of the available information. The present review will attempt to summarise current knowledge on symbiotic polychaetes as well as discuss the main systematic, biological, ecological and behavioural trends of these associations. When appropriate, possible directions for further research will also be indicated.

Before considering the interrelationships between polychaetes and their associated hosts, it is necessary to define the different concepts which are most often used when describing symbiotic associations. However, it would not be appropriate here to discuss extensively the different conceptual approaches, because this aspect has been largely discussed (e.g., Dales 1957, Rhode 1981, Boucher et al. 1982, Margolis et al. 1982, Addicott 1984). The particular terms adopted for the present review and the reasons for this adoption will, however, be considered in more detail.

DEFINITION OF TERMS

Although many attempts to classify the interrelations between organisms have been proposed, distinctions between different types of associations are not always clear. There are many factors that further define the nature of the interactions (e.g. the degree of association among the species, the degree to which the association is necessary for survival, the kinds of benefits, the extent of reciprocal specialisation by one species in response to the other, the temporal pattern, the stage of the life-cycle at which the interaction occurs, the location of the guest on or inside the host). Moreover, there are almost as many definitions as there are authors writing about close associations. In practice, it is difficult to obtain unequivocal demonstrations of all factors affecting a given interaction: the terms should preferably be used as stepping stones in helping to understand the real relationships in any particular association.

A partnership in which the advantage is wholly on one side, usually at the expense of the other partner, will be referred to as “parasitism” (Dales 1957). Where an association is clearly to the advantage (not necessarily from a trophic point of view) of one of the members without seriously inconveniencing or harming the other, the relationship will be referred to as “commensalism” (Dales 1957). Any interaction in which two (or more) species reciprocally benefit from the presence of the other species is referred to as “mutualism” (Addicott 1984). There is also a typical system of symbols to describe these three types of relationships: “+”, “-” and “0” indicate positive, negative and neutral effects for a given associate, respectively. Therefore, the associations can be represent as “++” (mutualism), “+0” (commensalism), and “+-” (parasitism).

The term “symbiosis” has been considered as synonymous of mutualism (e.g. Rhode 1981). However, it may also refer to the extent to which two species live in close association. Thus, in a wider sense, symbiosis is more often used to describe all kinds of organism associations (Henry 1966). In this review, we preferred to retain the generic sense of symbiosis, which will thus include parasitism, commensalism and mutualism. In this case, the partner s involved in “symbiotic” associations will be referred to as “the symbiont” (or “the guest”) and “the host”. The host harbours the symbiont, which is usually smaller than the host and always derives benefits from the association. In addition, the symbionts tend to have a more active role in the formation of associations than the hosts. In the case of commensalisms and parasitisms, however, the symbiont may be more specifically referred to as “the commensal” and “the parasite”, respectively.

Because of the difficulties of applying the experimental method to such a complex network of interactions, we often know little about their nature. Strict borderlines can not be easily drawn between the various types of associations. For instance, a parasite may become a predator by killing the host, or it may become beneficial to the host species, i.e. the relationship may become mutualistic. A commensal may affect the host and sometimes damage it, and thus become a parasite. In practice, it is difficult to infer unequivocal demonstrations of benefit (be it reciprocal or not) from the analysis of an association or from the existing literature. Moreover, the interpretations of the relationships become peculiarly susceptible to anthropomorphic bias: the parasites simply seem “bad”, the mutualists and commensals seem “good”. There are, however, many examples of associations which where initially considered as parasitisms that, with increasing knowledge, have been redefined s commensalistic or even mutualistic. Some examples will be mentioned in coming chapters. For the purposes of this review, we will thus consider two broad groups of associations, parasitisms and commensalisms. The cases of mutualism involving polychaetes are very few, so we have included them within the commensalisms, with indications of the bi-directional trends if known. Some species will be labelled as parasites or commensals according to the original criteria of their descriptors, without it being possible to give much more information so that the character of the interactions can be determined. However, when possible, special care will be taken to pinpoint the known relevant trends of the associations, so allowing the readers to judge. Moreover, a special chapter will be dedicated to the polychaetes that bore into living organisms (i.e., those that produce burrows mainly, but not exclusively, in organisms with calcareous structures), which are often difficult to catalogue into the two types of associations.

Other labels that will be frequently used to define the nature of an association are: “ecto-” and “endo-” (for guests living outside or inside the host, respectively), “obligatory” and “facultative”

(for guests that can not survive without the host or that can also be free-living, respectively), “permanent” and “temporary” (for guests living as symbionts during their whole life or only during one phase of their life-cycle, respectively), and “monoxenous” and “polyxenous” (for symbionts inhabiting one or a few hosts and inhabiting many different hosts, respectively). Moreover, by considering the close associations as infestations, some specific terminology applied (Margolis et al. 1982). The relationship between the number of infested hosts and the total number of hosts will be referred to as “prevalence”, whereas “intensity” will be the number of symbionts present in each infested host, “mean intensity” will be the mean number of individuals of a particular symbiotic species per infested host in a sample, and “abundance” or “relative density” will be the mean number of symbiont individuals per host examined (i.e. equal to prevalence multiplied by mean intensity).

COMMENSAL POLYCHAETES

Commensalisms are the most abundant relationships among symbiotic polychaetes. This statement may reflect a real dominance of “+/0” associations. However, the low level of knowledge and scattered available information on the biology of the species involved may artificially exaggerate their relevance. Most known symbiotic polychaetes have been considered as “commensals” as their associations with other organisms lack clear “parasitic” features. However, their status may be further modified with the appraisal of new information on host-symbiont relationships. For example, the relationships involving the scaleworms *Arctonoe vittata* (with its gastropod host *Diodora aspera*) and *Gastrolepidia clavigera* (with its holothuroid hosts), rather than commensalisms, are closer to mutualism and parasitism, respectively (Dimock & Dimock 1969, T.A. Britayev personal observations). However, we decided to include within the commensals those species often considered as parasites but lacking specific behaviour descriptions. For example, the highly modified species of the family Spintheridae are often described as feeding on their host sponges (Pettibone 1963, 1982). However, whether this feeding activity damages the host or benefits it by cleaning its surface has not yet been demonstrated. A high morphological specialisation is not in itself a demonstration of parasitism, as pointed out with the re-evaluation of the histriobdellids as commensals of their host crustaceans (Jennings & Gelder 1976, Cannon & Jennings 1987).

TAXONOMICAL DISTRIBUTION OF COMMENSAL POLYCHAETES

292 species of commensal polychaetes belonging to 28 families are reported to be involved in 713 different commensal relationships in the present review (Tables 1 and 2; Fig 1). The total number of polychaete families may range between 84 (Fauchald 1977) and 87 (Pettibone 1982), with more than 16,000 known species (Blake 1994). Commensals are thus present in just over 31% of the known polychaete families and comprise about 1.8% of the known species. For the most part, commensal polychaetes are obligatory symbionts (67%) and belong to families formerly grouped in the artificial Errantia group. However, some others are included in the so-called Sedentary families, namely the Capitellidae, Fauveliopsidae, Flabelligeridae, Sabellariidae, Serpulidae and Spionidae, with symbiotic species being more abundant in this last family (see Tables 1 and 8).

According to Clark (1956), almost two-thirds of the polychaetes that were reported as commensals were members of the scaleworm family Polynoidae. With the increasing number of commensal polychaete species described since then, this proportion has been slightly reduced. However, more than half of all currently known commensal species (55%) belong to this family (Fig 1A). In fact, the polynoids are a very large family, including diverse and numerous species inhabiting different marine habitats. The majority are sluggish and crawling and are found under stones, in crevices and in available tubes or burrows. Most of them are carnivorous, feeding on a great variety of animals. Thus, although the lack of information on most known associations prevented us speculating on the curious dominance of polynoids within commensal polychaetes,

the symbiotic habits of this family seem to be more or less easily inferred from their “normal” (i.e. free-living) modes of life (Fauchald & Jumars 1979). According to our present evaluation, the family consists of about 700 species, the commensals representing 22.7% of the total. Commensal and free-living scaleworms do not show a marked taxonomical differentiation, the former often belonging to genera that include free-living species as well. The huge genus *Harmothoe*, for example, consists of more than 120 species within which about 15 are commensal, whereas the “typically” free-living genus *Eunoe* includes 3 commensal species (Table 1). On the other hand, some genera (viz. *Arctonoe*, *Asterophyllia*, *Australaugeneria*) and one subfamily, the Arctonoinae (Hanley 1989), could be considered as wholly, or at least mostly, commensal.

The weight of commensal species within the non-polynoid polychaete families is significantly less than within polynoids. The relative number of commensals does not exceed 10% and the number of commensal species is always less than 10, with the exception of syllids, hesionids, spionids and serpulids (Fig 1A).

Three small polychaete families are entirely symbiotic. The Iphitimidae (*sensu* Fauchald 1970) includes a single genus, *Iphitime*, with 1 parasitic (see Table 6) and 7 commensal species, all the latter inhabiting the branchial cavities of decapod crustaceans (crabs and hermit crabs). Also belonging to the order Eunicida, the family Histriobdellidae consists of two genera and 9 species, all of them living epizoically in branchial chambers or carapaces of crustaceans. The single species of *Histriobdella* lives associated with marine lobsters in northern Europe and along the north-eastern American coast. The remaining species belong to *Stratiodrilus* and are known as commensals of freshwater crayfish (from Australia, Tasmania, Madagascar, and South and Central America) and marine isopods (from South Africa). The third commensal family, the Nautiliniellidae, has been recently described by Miura & Laubier (1989) and consists of 9 species, all them associated with bivalves (Table 1). The nautiliniellids inhabit deep-water hydrothermal vents and seep-site communities and are closely related to the monotypic “commensal” family Antonbruuniidae. *Antonbruuniaviridis*, the single species, is also associated with a bivalve. Both families are morphologically very close, suggesting that a further review would probably lead to their union under the older family name, Antonbruuniidae.

MARINE HOST TAXA HARBOURING COMMENSAL POLYCHAETES

Commensal polychaetes are associated with as many as 569 species included within the main taxa of marine Metazoans (excluding flatworms, nemerteans and nematodes) and even with Protozoans (i.e. foraminifers) (Fig 1B). However, they clearly prefer organisms providing them with good shelter, such as tube-dwelling or burrowing animals (viz. tubicolous polychaetes, sipunculids, balanoglossids) or relatively large animals possessing “advantageous” protective physiological or morphological characteristics. Among them, organisms having holes, grooves, chambers or channels (e.g. sponges, starfishes), as well as those showing good chemical or physical defences (e.g. sponges, cnidarians, sea urchins) are included. The highest number of host species harbouring polychaetes belong to the echinoderms, and the highest number of commensal polychaetes are also associated with this group. In fact, about 36% of all host species belong to one of the five echinoderm classes and the same percentage of all commensal polychaetes are associated with species of this group (Fig 1B). The following most dominant groups are the cnidarians (20% of the host species and associated commensal polychaetes) and the polychaetes themselves (16% of the host species and 17% of associated commensal polychaetes), whereas only 7.2% and 13% of the host species are included among such abundant and widely distributed marine animals as molluscs and crustaceans, respectively.

SPECIFICITY AMONG COMMENSAL POLYCHAETES

All degrees of host-commensal specificity may be found among commensal polychaetes. Although several polychaete species may be associated with many hosts from very different groups, most of

them are symbiotic with only one or a few closely related hosts ([Table 1](#)). In fact, 59% are strictly “monoxenous associates” (i.e., occurring on 1 host), this figure becoming 87% if those commensals occurring on 2 or 3 different hosts are included. The high degree of specificity of the relationships involving polychaetes may explain these proportions. However, as repeatedly mentioned, the often vague and accidental information on most commensal polychaetes may contribute to exaggeration of the monoxenous pattern. Therefore, only a few species that have been studied in detail could be mentioned as examples of real monoxenous associates. Among them, *Histriobdella homari* inhabiting branchial chambers of two species of Atlantic lobsters (*Homarus vulgaris* and *H. americanus*), *Adyte assimilis* associated with two related species of echinoids (*Echinus sculentus* and *E. acutus*), and *Haplosyllis chamaeleon* associated with the gorgonian *Paramunicea clavata*.

On the other hand, polyxenous polychaetes are usually associated with hosts that frequently belong to the same taxa (i.e. class, order or even family). For example, *Iphitime cuenoti* inhabits the branchial chambers of 11 species of Mediterranean and Northern Atlantic crabs, *Paradyte crinoidicola* is associated with 20 species of unstalked crinoids, and *Gastrolepidia clavigera* lives symbiotically with 13 species of tropical holothuroids from two families (Stichopodidae and Holothuridae). Usually, this kind of specificity may be related to strict morphological adaptations of symbionts. Accordingly, *I. cuenoti* has a more or less simplified jaw apparatus (see [Figs 12A, 12B](#)), *P. crinoidicola* is equipped with hooked modified ventral setae (see [Fig 10C](#)), and *G. clavigera* has ventral sucker-like lobes (see [Fig 13A](#)). A strict preference of commensals for a given host taxon may also be extendable to the family level, such as the nautiliniellids associated with bivalves, the iphitimids with crabs or the serpulids with haerematipic corals ([Table 1](#)). More commonly, however, commensals from a given polychaete family are associated with a taxonomically wide range of host groups (e.g. the families Hesionidae, Polynoidae and Syllidae, [Table 1](#)).

Polyxenous associations involving host species from very different taxonomic groups are less common among polychaetes, occurring mainly within hesionids and polynoids. The hesionid *Ophiodromus flexuosus* inhabits the ambulacral grooves of 5 starfish species, as well as the tubes of 2 polychaetes, 1 balanoglossid and 1 burrowing holothuroid. *Hololepidella nigropunctata* is associated with 10 ophiuroids, 4 asteroids, 1 echinoid, 1 sponge and 1 cnidarian. *Arctonoe pulchra* is associated with 4 asteroids, 2 holothuroids, 1 gastropod, 1 polyplacophoran and 1 polychaete. However, the most surprising polyxenous species is *Arctonoe vittata* from the North Pacific ocean. Its host list includes about 30 species from very different taxa: cnidarians, gastropod and polyplacophoran molluscs, polychaetes, asteroids, holothuroids and echinoids! ([Table 1](#)). It is interesting to note that the areas of distribution of hosts harbouring *A. vittata* overlap only partially and, also, that its host preferences differ from one geographical area to another (Davenport 1950, Britayev et al. 1977). For example, its preferred host in Vostok Bay and the south-west coast of Sakhalin Island (Sea of Japan) is the gastropod *Acmaea pallida*, whereas in Avacha Bay (Pacific coast of Kamchatka peninsula) the host is the starfish *Asterias rathbunae* (T.A. Britayev personal observations).

These polyxenous associates with a wide range of host species require special attention and may be of great taxonomical interest, as the possibility of sibling or pseudosibling species-complex being hidden under the same species name remains always open. Probably one of the most striking cases was exemplified in Pettibone (1993), a recent paper reviewing the formerly “widespread”, “polyxenous” scaleworm *Harmothoe lunulata* (delle Chiaje 1841). This species was associated with a huge number of hosts, including asteroids, ophiuroids, holothuroids, cnidarians, polychaetes, sipunculids and balanoglossids. As a result of Pettibone’s (1993) careful taxonomic study, the different commensal specimens of this species were transferred to 15 species belonging to 3 different genera: *Malmgreniella*, *Lepidonopsis* and *Wiltoniella* (plus one additional genus, *Paragattyana*, and several more non-commensal species). The final result was that the number of hosts harbouring each new commensal species was restricted to one or a few closely-related species, from geographically closer areas.

INTRA-HOST DISTRIBUTION PATTERNS OF COMMENSAL POLYCHAETES

Since the first specific studies by Palmer (1968) and Dimock (1974) on symbiotic polychaete distribution patterns, a lot of new information has been reported. Nowadays, it seems clear that most adult symbiotic polychaetes with known distributions occur alone on their hosts ([Table 2](#)). In other words, their symbiotic populations show regular distributions. This type of distribution not only characterises most commensal polynoids, nereids, pilargids and amphinomids, but also some hesionids, syllids and sphaerodorids. Occasionally, several individuals have been reported on the same host, these worms always being one adult and several juveniles. More often, however, the juvenile individuals of a given species with solitary adults display a random or even an aggregated distribution pattern (Dimock 1974, Britayev & Smurov 1985). The transition from random toward regular patterns of distribution necessarily implies the existence of mechanisms regulating the distribution of adult symbionts on their hosts. As direct observations and specific experiments have shown, several polynoids (e.g. *Arctonoe pulchra*, *A. vittata*, *Halosydna brevisetosa*, *Hololepidella nigropunctata*) and nereids (e.g. *Nereis fucata*) may show strong territorial behaviour, fighting against other conspecific specimens (Devaney 1967, Goerke 1971, Dimock 1974, Britayev 1991). However, we suggest that territorial behaviour may be generalised to most symbiotic polychaetes with regular distributions. Two possibilities arise from the negative intraspecific interactions generated by territorial behaviour: the death of one of the competitors or its relocation to another host, with the final result of the successive fights leading to the formation of regular patterns of distribution. Therefore, both territorial behaviour and intraspecific aggressiveness emerged as major factors controlling the appearance and maintenance of regular distributions within symbiotic polychaetes. However, there are some other possible factors which should not be excluded. For example, the possession of its own host-territory may allow a solitary commensal to exploit by itself the limited resources supplied by its host (i.e. safe place or food sources).

As most polychaetes are heterosexual, the isolation of single specimens will apparently prevent successful reproduction. Therefore, regular distributions must be associated with mechanisms raising the chance of commensal males and females being in close proximity during the reproductive period. Among them, we may mention: (1) high densities of available hosts allowing successful reproduction of commensals (which do not force the symbiont to develop any specific adaptation), (2) a synchronised gamete release by the commensals (which will make them independent of the host distribution), and/or (3) the formation of temporary host aggregations (i.e. linked to its own reproduction or feeding activity) synchronised with the reproductive period of the commensals (which probably implies the recognition of chemical cues linked to host reproduction which will trigger reproduction in commensals).

The occurrence of isolated heterosexual pairs on the same host individual may be considered as a particular solution of reproductive problems within regularly distributed symbionts. This type of distribution, more typical among symbiotic crustaceans (e.g. Huber 1987), has been reported for only 5 polychaete commensals. These are the syllid *Ambliosyllis cincinnata* (from sponges of the genus *Halichlona*, *Halichondria* and *Isodyctia*), the pilargid *Antonbruunia viridis* (inhabiting the mantle cavity of the bivalve *Lucinia fosteri*) and the scaleworms *Bathynoe cascadiensis* (associated with the brisingid starfish *Astrocles actinodetus* and *Astrolirus panamensis*), *Harmothoe hyalonemae* (living in atrial cavities of deep-water hexactinellid sponges of the genus *Hyalonema*) and *Gastrolepidia clavigera* (associated with tropical holothuroids) (Hartman & Boss 1965, Riser 1982, Ruff 1991, Martin et al. 1992, Britayev & Zamyshliak 1996). Although there is no information on the reproductive cycle of these species, this pattern of distribution seems clearly more favourable to reproductive success. Moreover, there is no indication that the species living in heterosexual pairs are not as aggressive as the species living alone, which strongly supports the existence of sex-specific recognition for the symbiotic species living in pairs. Among polychaetes, sex-specific recognition has been previously reported for aggressive species such as *Neanthes fucata* (Reish 1957).

Several species of commensal polychaetes aggregate on their hosts ([Table 3](#)), along with most parasitic boring polychaetes ([Table 10](#)). This seems to be valid for the symbiotic iphitimids, some histriobdellids, dorvilleids, syllids, serpulids, spirorbids, caobangids and spionids. Since the

formation of aggregations among symbiotic polychaetes has not been the subject of specific studies, we can hypothesise that this pattern may result either from a peculiar gregarious habit in the settling larvae (i.e. chemically mediated settlement cues), or from the existence of mechanisms allowing the symbionts to increase their number on the host after an initial infestation by only one or two founders. This second strategy may be accomplished either by short larval development without pelagic phase, viviparity or asexual reproduction.

The aggregated distribution of the serpulid *Spirobranchus giganteus* living on corals (Hunte et al. 1990a), as well as of the spirorbid *Circeis armoricana* and the spionid *Polydora commensalis* on the inner surface of host hermit crab's shells (Rzhavsky & Britayev 1988, Radashevsky 1989) may result from gregarious behaviour. In fact, aggregated distributions are common among tubicolous polychaetes and has been attributed to the attraction of settling larvae towards the tubes of conspecific adults (Eckelbarger 1978, Jensen & Morse 1984, Pawlik 1988, Marsden et al. 1990). A particular case of aggregated distribution in tubicolous polychaetes occurs in an undescribed species of *Vermiliopsis* from the Caribbean Madreporid coral *Stephanocenia michelini*. The worm tubes of this serpulid are surrounded by the coral tissues and, according to Humann (1992), the crowns are regularly distributed on the coral surface (Fig. 4A). We suggest that this special distribution may result from negative adult/larval interactions. In fact, the circulation generated by the crowns may very well prevent the settlement of larvae on the host surface areas controlled by resident worms. Therefore, settling larvae would only be able to start building their tubes at a given distance from all previously existing neighbours, this distance being almost always the same.

The dense populations of the small polydorid species of the genus *Polydorella* inhabiting the surface of cork-sponges (Fig. 2C) apparently resulted from their asexual reproductive cycles, allowing them to reach quickly very high densities of up to 130 individuals per cm² after the colonisation of a suitable host sponge by a single new larva (Tzetlin & Britayev 1985, Radashevsky 1996). However, at least one *Polydorella* species (*P. smurovi*) may also reproduce sexually, since cocoons with eggs and embryos at different developmental stages have been found inside the adult tubes. In spite of the absence of direct observations, we can hypothesise that pelagic larvae resulting from sexual reproduction may be responsible for long-distance dispersion. Therefore, the combination of both reproductive strategies may allow them to succeed in finding and quickly colonising the rare suitable host sponges. A detection of chemical cues from the host sponges by pelagic chemosensitive larvae may be involved in host location, as was suggested for the parasitic syllid *Branchiosyllis oculata* (Pawlik 1983).

In *Histriobdella homari*, the males impregnated the females hypodermically by means of specialised copulatory organs, allowing the spermatozoa to avoid the necessity of swimming to reach the mature eggs, which are directly fertilised in the body cavity of females (Jamieson et al. 1985). Then, the female attaches the eggs both to the ventral surface and egg masses of the host, the young worms being then released as minute adults without planktonic phase (Haswell 1913). Thus, the juveniles directly colonise the host infested by their own parents. This leads to a clustered distribution of the commensals and to high infestation intensities reaching more than 600 worms per host lobster (Simon 1967). The transference from one host to another is probably accomplished by direct migration of adults.

LOCATION OF COMMENSAL POLYCHAETES ON THEIR HOSTS

Most commensals are characterised by a defined location on the host surface or, less frequently, inside the hosts (Figs 2, 3, 4, 5, 6). Since hosts may be considered as commensal refuges, the symbionts are normally located in the most protected sites. For example, commensals of decapods are usually located inside the host's branchial chambers (e.g. most *Iphitime* species, *Ophryotrocha geryoncola*, *O. mediterranea*, *Histriobdella homari*), inside the shells inhabited by hermit crabs (e.g. *Iphitime paguri*, *Nereis fucata*, *Circeis paguri*) or under the tails of egg-bearing female crabs (e.g. *Iphitime hartmanae*). The commensals of tubicolous polychaetes, burrowing holothurians or ghost shrimps (e.g. species of *Harmothoe*, *Lepidastenia* or *Malmgreniella*) occur inside host tubes

or burrows. The numerous associates of starfishes, sea-urchins and brittle starfishes (among them, many scaleworms, hesionids and some syllids) prefer the more protected oral surface of their hosts. The commensals of bivalves or limpets often live inside the mantle cavity (e.g. *Parasyllidia humesi*, *Antonbruunia viridis*, *Harmothoe commensalis*, *Arctonoe vittata*), whereas a similar position has been reported for cirriped associates (e.g. *Hipponoe gaudichaudi*). Although rare, some commensals may live inside the host's body, e.g. the amphinomid *Bentoscolex cubanus* living in the intestine of the deep-water sea urchin *Archeopneustes hystrix* (Emson et al. 1993).

Some commensals have slow movements and, when disturbed, tend to keep themselves firmly attached to their hosts. For example, the syllid *Haplosyllis chamaeleon* living on the branches of the gorgonian *Paramunicea clavata* (Laubier 1960). The worm usually extends its body along the longitudinal axes of the host branches, preferably near zones with a high number of living polyps (mainly the apical parts). When disturbed, the polychaetes introduce their strong hooks into the coenochym and cannot be taken off without damage to the host. However, most commensal polychaetes are agile animals able to change their position according to different stimuli. For example, *Gastrolepidia clavigera* are usually located near anterior or posterior ends of their holothurian host's body, quickly hiding in the oral or cloacal openings when threatened (Britayev & Zamyshliak 1996). Most commensal locations are reported from animals extracted from their natural habitats, meaning that observed locations may not be those preferred by the symbionts. Only a few data on the location of commensals in natural conditions are available. The commensal syllid *Branchiosyllis exilis* occurs on the arms or disc of its ophiuroid host *Ophiocoma echinata* (Hendler & Meyer 1982). The polychaete was observed moving along the ventral arm plates, between the alternating rows of arm spines and tube feet. They have also been found partially or entirely hidden in the oral cavity of the ophiuroid. However, immediately after host collection, *B. exilis* occurred more frequently on the arms of the ophiuroid than on the disk. Conversely, *in situ* observations of the scaleworm *Arctonoe vittata* associated with starfish *Astherias rathbunae* indicated that the worm occurred more frequently on the oral surface of starfish, in the ambulacral grooves or even partially inside the oral cavity (Britayev et al. 1989). Nevertheless, it had been reported as more frequently inhabiting the oral disk (65%) than the arms of the starfish.

It should be pointed out that the locations of *Haplosyllis chamaeleon*, *Branchiosyllis exilis* and *Arctonoe vittata* on their respective hosts are not simply connected with the finding of shelter or physical protection. *H. chamaeleon* was observed with its anterior end inside the gastral cavity of the gorgonian polyps. The slow movements and sensibility of the polyps may favour this behaviour, allowing the worm to feed either on the preys inside the polyp's stomach or on the polyps themselves. Although some pigmented parts inside the worm's gut supported the last possibility, no damage was observed in the polyps (Laubier 1960). Thus, it is not likely that *H. chamaeleon* behaves as a commensal or cleaner than as a parasite. *B. exilis* generally lies on the proximal portion of the ventral surface of its host's arms, directly in the path of food boluses carried by the tube feet towards the ophiuroid mouth. As suggested by Hendler & Meyer (1982), such a location allows the commensals to gather food from the alimentary tract of its hosts. Similarly, the preferred location of *A. vittata* on the host's oral disk seems likely to be connected with food supply. Direct observations on *A. vittata* feeding behaviour in natural conditions demonstrated that the worms gather pieces of their hosts' preys by biting them off both from the everted starfish stomach or directly through the mouth opening (Britayev et al. 1989).

The location on the host may change during the life-history of symbionts. The adult specimens of *Hipponoe gaudichaudi* occur inside the branchial chambers of its goose-barnacle host, whereas the juveniles may be located between the mantle and the calcareous plates of the host or attached to the adult symbionts *H. gaudichaudi* (Figs 5D, 5E) (Britayev & Memmy 1989, Núñez et al. 1991). The characteristic position occupied by *Iphitime cuenoti* is at the extreme anterior dorsal end of the branchial cavity, where the individual worms lie with the ventral surface of body closely applied to the branchiostegal fold separating the viscera from branchiae (Comely & Ansell 1989). When more than one worm occurs in a single host crab, the largest individual generally occupies this position, while other individuals may be found in a similar position in the opposite branchial chamber, at another point on the walls of each chamber, or among the gills. Moreover, in the

largest worms, the body is generally coiled. The smallest worms are only found in the interlamellar gill spaces and, when growing, the majority moves out and became established in the roof of the branchial chamber (Comely & Ansell 1989).

We suggest that a low availability of optimum larval settlement sites on the host surface could be one of the reasons why the commensals alter their locations during their life-cycle. Other probable reasons are: (1) differential preferences of juveniles and adults, (2) inaccessibility to optimum sites for juveniles, as a consequence of the competition with conspecific adults or other symbiotic species. The influence of intraspecific interactions between commensals on their location was demonstrated for the scaleworm *Arctonoe vittata* (Britayev et al. 1989). Its preference for the ventrum of its host's starfish oral disk was apparently inhibited when two worms infested the same host. In fact, the two symbionts were never found together on the oral disk. Whenever one of them occupied the oral disk, the other was on one arm (69% of starfish), the preferred area (i.e. oral disk) being always occupied by the larger worm. Moreover, the location of the two symbionts separately on the arms was also frequent (31% of starfish).

The location of commensal polychaetes must necessarily be influenced by the presence of other symbionts on the same host. However, although it is well-known that some commensal polychaetes may share their hosts with symbionts from different taxonomic groups (see Dales 1957 for *Hesperonoe adventor* and the complex network of guests associated with the innkeeper *Urechis caupo*) (Fig 3A), this discussion has not yet been developed. Changes in the location of commensal species may also vary in accord with the morphology or behaviour of their different host species. The scaleworm *Malmgreniella macginitiei*, for example, has been reported in the burrows of its host shrimp *Callinassa californina*, inside the parchment-like tubes of its host polychaete *Axiiothella rubrocincta*, or on the arms of its host brittle starfish *Amphiodia urtica* (Pettibone 1993). Another species of the same genus, *M. andreapolis*, was found inside the burrows of host holothurians, as well as curved around the disk and mouth of host brittle starfish s.

A special comment should be reserved for those commensal polychaetes that are not "satisfied" by the shelter or the protective abilities of their hosts. These symbionts may either construct their own refuges on the host's surface or stimulate their hosts to build protective structures around them. Among them, the eunicid *Eunice floridana* and the scaleworms *Harmothoe melanicornis*, *Malmgreniella dicirra*, *Polynoe uschacovi* and several species of *Gorgonyapolynoe* live inside tunnels or gall-like cavities formed by coenenchymal walls of gorgonian or hydrocoral hosts (Figs 4B, 4C, 4D) whose formation seems to have been brought about by the presence of the commensals (Britayev 1981, Pettibone 1991a, b), the lumbrinerid *Lumbrineris flabellicola* associated with scleractinian corals lives in membranous transparent tubes attached to the side of the host (Zibrovius et al. 1975, Miura & Shirayama 1992) (Fig 4F) and *Eunice* sp. constructs a fragile tube attached to the length of the upper surface of its gastropod host *Cerithium vertagus* (Gibbs 1969) (Fig 5A).

CHARACTERISTICS OF THE INFESTATIONS BY COMMENSAL POLYCHAETES

The prevalences of infestations by commensal polychaetes are highly variable, ranging from very low values (e.g. 0.03% for *Iphitime sartoral* associated with *Portunus spinicarpus*) up to host populations being infested as a whole (e.g. *Liocarcinus corrugatus* infested by *Iphitime cuenoti*, and some host populations infested by *Acholoe astericola* or *Bentoscolex cubanus*) (Table 4). The prevalence has been seldom considered as characteristic at the species level. In *Sphaerodoridium commensalis*, for example, a low prevalence of 3.5% seems to be the normal condition for all known populations of the species (Lutzen 1961), whereas in *Acholoe astericola* the characteristic prevalence is as high as 75-100% (Barel & Kramers 1977). However, each population of a given commensal species is usually characterised by different prevalences. Although bathymetric, spatial and temporal (i.e. seasonal and annual) variability in infestation prevalence and intensity may be expected in commensal populations, the corresponding patterns have seldom been documented.

Changes in infestation prevalence with depth have been reported for the Mediterranean populations of *Iphitime cuenoti* inhabiting *Liocarcinus depurator* (Belloni & Mori 1985, Abelló et

al. 1988). Although host abundance increases above 100 m depth, the commensal appears to avoid this depth range, the prevalence of the infestation increasing with depth (Fig 7A). This seems to be closely related with the temperature, colder and more stable in deep waters (> 100 m deep). In fact, the prevalence of the commensal population infesting another Mediterranean host crab, *Macropipus tuberculatus*, was independent of depth, but this host never occurs deeper than 100 m. It is a common fact that species occurring both in the Mediterranean and the Atlantic tend to inhabit cooler waters in the latter (e.g. Laubier 1973). Accordingly, no relationship between depth and prevalence was observed for *Ophryotrocha mediterranea* infesting *Geryon longipes* (Martin et al. 1991). In this case, although the host crab occurs both in the Mediterranean and in the Atlantic, *O. mediterranea* appears to be endemic to the former, whereas in the latter, the ecological niche was occupied by *O. geryoncola*.

Hendler & Meyer (1982) reported spatial variability in infestation prevalence from the different populations of the brittle starfish *Ophiocoma echinata* harbouring the tropical syllid *Branchiosyllis exilis* along the Panamanian coast (Fig 7B), where the maximum prevalence occurs in late Autumn and in Winter. Moreover, near Galeta, on the Caribbean coast of Panama, the prevalence of *B. exilis* varied over time between 20 and 90% (Fig 7C). It was highest from November to March (i.e. the dry season) and lowest in the local rainy season. The hesionid *Ophiodromus pugettensis* infesting the starfish *Patiria miniata* at Dana Point (California) reached its highest (79-92%) and lowest (19-32%) prevalence in November-December and Summer (prior to the decrease of water temperature), respectively (Lande & Reish 1968) (Fig 7D). The prevalence of the sphaerodoridae *Sphaerodorum ophiurophoretus* infesting the brittle starfish *Amphipholis squamata* at Wimereux (English Channel coast of France) was maximal during early Spring (11.9%), decreased in May (6.6%) and totally disappeared in Summer (Alvà & Jangoux 1989). The prevalence of *Iphitime cuenoti* in the Scottish waters showed different seasonal pattern depending on the host (Comely & Ansell 1989). In *Liocarcinus puber* and *L. depurator*, the prevalence ranged between 70 and 100%, with no indication of seasonality. In *L. depurator*, however, there was an apparent prevalence fall during April, independently of the catch size. *Carcinus maenas* showed a low level of infestation which apparently varied seasonally, the maximum prevalence occurring in October (i.e. 14%). It was suggested that the decreasing prevalences of *B. exilis* linked to the rainy season resulted either from seasonal changes in salinity (and other environmental parameters) or from seasonal fluctuations in the mortality of the polychaetes because of the recurrent, low-tide emergence of the reef flat (Hendler & Meyer 1982). The marked seasonal pattern of *O. pugettensis* seemed to be connected with commensal reproductive dynamics (Lande & Reish 1968). The absence of clear seasonal pattern in *I. cuenoti* from some of their host crabs was attributed to the persistence of small worms throughout the year, whereas the well-defined seasonal peak in the host *Carcinus maenas* was clearly correlated with the peak season for the commensal spawning in October (Comely & Ansell 1989). Conversely, in *S. ophiurophoretos*, there was no further analysis of what caused the seasonal pattern.

With the exception of the impressive fidelity of the year-to-year counts of a regular seasonal trend demonstrated for the infestation prevalence in *Branchiosyllis exilis* (Fig 7C), the only known data on year-to-year variability are on *Arctonoe vittata* infesting the starfish *Asterias amurensis* (Britayev & Smurov 1985). These authors reported a progressive increase in infestation prevalence from 0% in 1975-76 to 8.4% in 1978 and to 79.1% in 1980.

An additional source of variability in the respective prevalences of commensal populations emerges from the association with different hosts, even if this occurs in the same locality. In these cases, the different prevalences are linked to the greater or lesser suitability of different host suitability. As pointed out by Dimock (1974), the infestation prevalence of the scaleworm *Arctonoe pulchra* on the coasts of Santa Barbara (California) was higher in the preferred host, the sea cucumber *Stichopus parvimensis*, than in the limpet *Megatoma crenulata*. Similarly, the infestation prevalences of *Arctonoe vittata* in Vostok Bay progressively increased from the starfish *Aphelasterias japonica* (2-5%) and *Asterias amurensis* (79.1%) to the limpet *Acmaea pallida* (94%), the latter being the preferred host for the scaleworm (Britayev & Smurov 1985). The prevalence of the infestation by *Iphitime cuenoti* in Scottish waters was also higher in the preferred hosts,

Liocarcinus corrugatus and *L. puber*, than in the non-preferred hosts (such as *L. depurator*, *Carcinus maenas* and *Hyas araneus*) (Comely & Ansell 1989).

Data on intensities of infestations by commensal polychaetes have been more widely reported than prevalences, ranging from 1 to 648 symbionts per host (Tables 2 and 3). However, the 1:1 associations are clearly dominant owing to the usually low symbiont densities or to the regular distribution pattern linked to intraspecific aggressive behaviour (see above). Moreover, the list of species characterised by an intensity of 1 individual per host (Table 2) should probably be larger than it is, as most species included in Table 3 are indeed characterised by a normal intensity of only one large adult worm per host with the occasional presence of one to several more juveniles. Among these species, we may mention those of the genera *Acholoe*, *Adyte*, *Branchiosyllis* and, probably, some others whose growth status was not indicated in the original descriptions.

Infestation intensities may be considered as more species-specific than prevalences. Nevertheless, they may also differ seasonally within the same population, as also occurs with the relative densities (or abundances). However, this variability has been seldom reported. The abundance of the commensal *Ophiodromus pugettensis* was maximum in winter (2.0 - 2.6 worms per host) and minimum in the middle of summer (0.26-0.44 worms per host) (Lande & Reish 1968) (Fig 8A). In *Arctonoe pulchra*, intensity and abundance reached maximum values in August for *Stichopus parvimensis* associates (7 and 3.97 worms per host, respectively) and in September for *Megatūra crenulata* associates (4 and 1.06 worms per host, respectively) (Dimock 1974). Although it was not clearly demonstrated, these maximum values were due to an increasing number of juvenile commensals. Thus, the seasonal pattern in *A. pulchra* seems to be related to the reproductive cycle of the species. In *Iphitime cuenoti*, seasonal peaks of infestation intensities apparently occurred in the host crabs *Carcinus maenas* (maximum of 5 worms) and *Liocarcinus puber* (maximum of 9 adults and 98 juveniles) in October and May, respectively (Comely & Ansell 1989). Both peaks were clearly related to the reproductive cycle of the symbiont. However, it was difficult to attribute the character of seasonal pattern to the trends shown during a given year, at least in *L. puber*. Comely & Ansell (1989) pointed out that, although they considered unlikely that any considerable numbers of juveniles were overlooked during their routine examinations of the gills, the peaks of intensity found during one year (1986) were not observed during the next (1987). In fact, this seems to indicate that the seasonal patterns are linked to the reproduction of the symbiont, which may vary from one year to another, as it occurs in virtually all marine organisms (either symbionts or free-living).

As occurred with prevalences, we may expect additional changes in intensity of infestation among commensal populations from a given locality that are associated with different hosts. An example of this variability was reported for the scaleworm *Arctonoe pulchra*, whose populations associated with the sea-cucumber *Stichopus parvimensis* and the gastropod *Megatūra crenulata* showed infestation intensities of 1 to 7 and 1 to 4 commensals per host, respectively (Dimock 1974). In this case, the differences in intensity are likely to be connected with the amount of living space available to the commensal polychaetes, which is clearly higher in the first host species than in the second. For *Iphitime cuenoti*, the incidence of intensities higher than 1 commensal per host was higher in the preferred host crabs (Comely & Ansell 1989).

RELATIONSHIPS BETWEEN HOST AND COMMENSAL POLYCHAETE CHARACTERISTICS

When reported, the relationship between size structure of commensal and host populations is, if anything, unclear (Martin et al. 1991, 1992, Emson et al. 1993, Rozbaczylo & Cañete 1993, Britayev & Zamyshliak 1996). This suggests that the life-histories of commensal polychaetes are usually independent of their hosts', the host tending to live longer than the symbiont. In many cases, this dynamic implies that the same host population may successively harbour different polychaete populations. More detailed studies focusing on population dynamics of symbiotic polychaetes and their hosts may well reveal the existence of positive correlation between the respective size structures, as occurs among other symbiotic animals (e.g. the pontoniin shrimp *Anchistus custos* associated with the host bivalve *Pinna bicolor* in Britayev & Fahrutdinov 1994).

The size of host may affect the prevalence of infestation, with the largest individuals more often showing the highest prevalence (Figs 8B, 8C, 8D). Examples of this trend are found in the associations between *Circeis paguri* and *Eupagurus bernhardus* (Al-Ogily & Knight-Jones 1981), *Branchiosyllis exilis* and *Ophiocoma echinata* (Hendler & Meyer 1982), *Arctonoe vittata* and *Asterias rathbunae* (Britayev et al. 1989), and *Gastrolepidia clavigera* and *Stichopus chloronotus* (Britayev & Zamyshliak 1996). Certainly, a similar pattern may be expected for many other associations. Many reasons may explain why large hosts are more favourable to symbionts. They are usually older and so have been exposed to planktonic larvae settlement or adult migration for a longer period than small hosts. Moreover, large hosts provide more room for symbionts. Accordingly, many examples of the existence of low host-size limits have been reported. Among them, starfish *A. rathbunae* with disc radii lower than 35 mm were not inhabited by *A. vittata*, whereas those with radii up to 90 mm harboured only 1 symbiont and the largest starfish were infested with 1-4 symbionts (Britayev et al. 1989). Also, the scaleworm *Harmothoe commensalis* was not present in shells of the clam *Gari solida* lower than 60 mm in length (Rozbaczylo & Cañete 1993). In the case of *Circeis paguri*, both small shells and hermit crabs are rarely colonised (Fig 8C). In fact, the few small shells that are colonised are not very suitable habitats for the symbionts within them, which are rarely or never reach breeding size, presumably because the space available is too small to provide enough food or to satisfy their respiratory needs (Al-Ogily & Knight-Jones 1981).

The associations involving sexually dimorphic hosts merit special mention. One of the clearest examples was of the association between the dorvilleid *Ophryotrocha mediterranea* and the deep-water crab *Geryon longipes* (Martin et al. 1991). The polychaete was not detected in any of the small female crabs examined, while the prevalence among the large male crabs reached up to 19%. Indeed, the carapace length of the smallest infested host male (41 mm) was similar to the maximum length of the female's carapace (Fig 8E). Thus, it was suggested that the symbionts need a minimum of vital space, which the branchial chambers of juvenile and female crabs do not satisfy. This concurs with the fact that the closely related dorvilleid *O. geryoncola* was detected in females of *Geryon* species that reached larger sizes than males (Gaston & Benner 1981, Pfannenstiel et al. 1982). The opposite situation was reported for *Capitella capitata* living as commensal with the pea-crab *Pinnixia littoralis* (who lives itself as a commensal of the mactrid bivalve *Schizothaesus capax*). The commensals are always associated with the female crabs and never with the males, although both sexes may share the same host bivalve (Clark 1956). The worms lived more often inside thin mucous tubes attached to the crab's carapace, but could also be found burrowing inside a mass of detritus accumulated on the basis formed by the tubes. The most obvious solution was that males were too small to provide a suitable area on which the large *Capitella* could settle and, also, to support the large bolus of detritus. This was unlikely, however, because young female crabs, smaller than full-sized males, did carry the worms. The alternative and more likely explanation, proposed by Clark (1956), was that the males were too active. They were able to leave their own host bivalve, which was never observed of any females crab. By moving, the males prevented the accumulation of detritus on which the worms were presumed to feed and this caused the absence of commensal worms on the male's carapace.

When several hosts may be infested by the same commensal species, we may also expect that the relative size of the different host species would affect the respective symbiotic populations. In *Iphitime cuenoti*, for example, the largest commensals are usually reported on those hosts which are also larger (e.g. *Liocarcinus corrugatus* and *L. puber*). Thus, the total size of the commensal may be a function of the size of its crab host. However, this is valid for the small host species of the genus *Macropodia* and *Inachus* but not for the large *Cancer pagurus*, suggesting that other factors may limit the success of the worm (e.g. moulting frequency or stage). The commensal iphitimids seems able to support moulting stress, as worms have been found inhabiting recently moulted soft crabs (Abelló et al. 1988, Comely & Ansell 1989). However, a high moulting frequency may significantly disturb the success of the infestation. Hartnoll (1962) and Comely & Ansell (1989) also suggested that the substrata inhabited by the different hosts or by different individuals of the same host may affect the success of the infestation.

Theoretically, we may expect that the host's population structure will influence the structure of the symbiont population. Nevertheless, the available data to illustrate this statement are very scarce. The relationships between host size and prevalence mentioned above, lead to the speculation that higher values of the infestation indexes will be positively correlated to the presence of large and more numerous hosts. A positive relationship between host population density and infestation characteristics was reported for the starfish *Asterias rathbunae* and its commensal *Arctonoe vittata* (Britayev et al. 1989). In Avatcha Bay, Pacific coast of Kamchatka, the highest infestation prevalence, mean intensity and abundance occurred in the area most densely populated by the host. The high number of intraspecific traumas reflected the frequency of intraspecific interactions resulting from the high density of commensals in the mentioned area (i.e. higher than in the neighbouring ones). This may probably be related to a high mobility of the commensals among hosts, affecting also the structure of the commensal populations.

In most cases, however, the mechanisms to explain how the population density of hosts influences the commensal population remain unclear. We may hypothesise that the accumulation of chemical cues released from dense host populations may attract a high number of settling larvae of the commensal polychaetes more effectively than less dense host populations. Thus, we may expect higher recruitment and more young worms associated with dense host populations. Nevertheless, the influence of other external factors, such as predation pressure, can not be discarded. In fact, predatory activity will probably decrease the fitness of commensals associated with less abundant host populations more significantly than those harboured by dense host populations.

ADAPTATIONS OF POLYCHAETES TO THE COMMENSAL MODE OF LIFE

Cryptic colouring in commensal polychaetes

The colour patterns of commensal polychaetes frequently differ from those of its free-living relatives, even if the latter belong to strictly the same species. For example, the only apparent morphological difference between free-living and commensal specimens of *Lepidonotus glaucus* is the degree of pigmentation (Hanley & Burke 1990). The specimens associated with the *Eunice* hosts were more darkly pigmented, often appearing almost black, when compared with free-living specimens. We may tentatively suggest that the dark colouring of the commensal *L. glaucus* is closely related to the dark colour of its host. In fact, one of the most peculiar features of commensal polychaetes (mainly ectocommensal) is their cryptic colouring masking them on the host's surface.

The fact that many commensal animals inhabiting crinoids and holothuroids (including polychaetes) resembled their hosts was pointed out by Potts (1915). Later, the similarity of symbiont worms' colouring to their hosts' was stressed by nearly all authors studying commensal associations. Thus, when describing the association of the scaleworm *Malmgreniella variegata* [as *Harmothoe lunulata*] with the ophiuroid *Ophionereis reticulata*, Millot (1953) noted that "worms matched the ophiuran very closely, being white, with a well defined repetitive black pattern borne on elytra". This matching was also reported and well illustrated by Pettibone (1993). Another remarkable similarity in colouring is that of the hesionid *Gyptis ophiocoma* with its ophiuroid host *Ophiocoma scolopendrina* (Storch & Niggemann 1967). Moreover, the effectiveness of the polychaete's camouflage is often heightened by their location on an appropriate site on the host surface. The segments of the syllid *Branchiosyllis exilis* each had a thin white border so that they displayed light striations on close examination. This pattern of pigmentation was reinforced by the location of polychaetes on the black and white banded arms of the ophiuroid host *Ophiocoma echinata*, between colonnades of black and white striped spines (Fig 6D), which made it difficult to distinguish the commensals (Hendler & Meyer 1982).

The colour pattern of commensals inhabiting several host species is usually appropriately similar to the corresponding host colouring. For example, the individuals of the scaleworm *Gastrolepidia clavigera* associated with the uniformly black sea cucumber *Stichopus chloronotus* are usually black, whereas those associated with the yellow to brown *Thelenota ananas* are light

brown, and those with the greenish-grey *Stichopus variegatus* are greenish-grey with brown spots (Britayev & Zamyshliak 1996). However, some exceptions to this general rule may be observed. Dark brown worms typical to *S. chloronotus* have been found on *S. variegatus*, probably because the scaleworm changed from one host to another (Britayev & Zamyshliak 1996). Gibbs (1969) noted similar changes between hosts by this scaleworm species.

In light of the above, we may certainly assume that *Gastrolepidia clavigera* is not able to change its colour in a short time interval, such as octopus or flatfish do. A dual question then arises: does the observed colour pattern result from the host influencing the developing symbiotic polychaetes? or does a commensal population consist of several “sub-populations”, genetically pre-adapted to each appropriate host species? With the exception of the experimental demonstration of the trophic origin of the colour pattern in the parasitic syllid *Branchiosyllis oculata* (Pawlik 1983), there are no specific studies on this particular aspect of the arrangement of symbiotic associations. However, the accidental observation of commensal specimens with unusual “hybrid” colouring inclined us towards the first question. Indeed, hybrid colouring may result from the regeneration of posterior sections of the body. In *Arctonoe vittata*, the colour of the posterior part was yellowish-white in accordance with the body colour of its current host, the limpet *Acmaea pallida*, whereas the anterior (i.e. old or original) half of the body was pink-brown, closely resembling the colouring of the worms associated to the starfish *Asterias amurensis* (T.A. Britayev personal observations). As relocation from one host to another has been demonstrated (see above), the logical sequence of events may be as follows. A symbiont inhabiting the initial starfish host is disturbed (either as a result of intraspecific aggressive behaviour or predator attack), losing the posterior part of the body (i.e. autotomised or bitten). Then it is obliged to relocate to a new host, the limpet in this case, with the subsequent regeneration of the posterior half being in accord with the colour of the new host. It should be pointed out that how these changes in colouring are accomplished has not yet been assessed. In fact, we may hypothesise that the changes may be produced by a substance (or substances) obtained by the polynoids from their hosts (i.e. by partly feeding on them or by incorporating some kind of secretion) but, also, that the substance stimulating the different colourings are obtained both by the hosts and the commensals by feeding on the same kind of food. These two hypotheses clearly had different consequences in the allocation of the involved relationships within parasitisms or commensalisms.

A comparable case of colour mimicry occurs in the relationship between the syllid *Haplosyllis chamaeleon* and its single known host, the gorgonian *Paramunicea clavata* (Laubier 1960). The colouring of the worms varied from pale yellowish to dark red, matching exactly the colours of its host. Although these colours actually occur on the same host colony, there are no evident relationships between the colour of the host branch and that of the attached polychaetes. Moreover, hybrid specimens showing all possible colour combinations may occur. Uniform colour patterns may indicate symbionts growing to their adult size on the same gorgonian branch, then moving to different parts of the colony without any preference for the colour of the branches. Hybrid forms may be the result of these displaced specimens being bitten or autotomised and then regenerating on a differently coloured branch.

Although all these examples support the idea of the influence of the host on the colouring of its commensal polychaetes, the question of how the mimicry is accomplished still remains open. Is there an intrinsic metabolic reaction of the symbiont to the different stimuli provided by the different hosts? or are the symbionts taking pigments directly from the hosts, i.e. feeding on it? If the second answer is correct, then the associations involved should be re-evaluated as being closer to parasitisms. However, without specific descriptions of the behaviour of symbiotic polychaetes and its effects on their hosts, we decided to include them within the commensalisms.

Morphological adaptations of commensal polychaetes

Forty years ago Clark (1956) noted that “Although some worms ... to be found in more or less intimate association with other animals, very little structural adaptations appear to have taken place to suit them for this mode of life”. However, after carefully re-analysing the significantly high

number of commensal species described since this classic paper, it becomes clear that most, or even all, commensals have more or less defined morphological features allowing us to distinguish them from their free-living relatives.

The symbiotic features of commensal polychaetes can be divided into two categories: those significantly adapted to the commensal mode of life, and those repeatedly connected with the commensal mode of life, but lacking any obvious adaptive significance. The first group includes structural adaptations such as: i) modifications permitting the attachment of the symbionts to their hosts, ii) modifications allowing the symbionts to reproduce without leaving their hosts and so prevent gamete losses, iii) modifications affecting the buccal equipment of symbionts, and iv) modifications enabling the symbionts to mimic their hosts. The best known modifications included in the second group are those of elytra and parapodia in scaleworms, but the eyes may also show interesting modifications. Moreover, it has also been pointed out that commensal polynoids are often larger than their free-living relatives. This modification, however, has been interpreted as a consequence of - instead of an adaptation to - the commensal mode of life. This fact was supposed to be due to a decreasing necessity of exercise in the commensals, and to a food supply being greater and more easily accessible to commensals than to free-living worms (Essenberg 1918).

The observation and correct interpretation of all morphologically evident commensal features (whether they have clearly adaptive significance or not) is important: in particular, whether these features enable symbiotic and free-living polychaetes to be distinguished, despite the specimens being found separately from their hosts. It should be pointed out that this situation is quite common when studying worm collections, which are based on trawl or dredge samples that often reach the polychaetologists already sorted.

Adaptive morphological modifications

Attachment structures are frequently related to the setal arrangement. Hooked setae apparently modified to facilitate the attachment have been reported for a wide number of species from many different families (viz. Iphitimidae, Polynoidae, Amphinomidae, Sphaerodoridae, Nautiliniellidae, Spintheridae, Syllidae) (Figs 9, 10, 11, 12). Some of them show remarkable coincidence in shape and, although not demonstrated, probably in functionality, too. In the case of polynoids, some species seem able to continually replace the hooked setae becoming blunt from wear by new pointed ones growing out from the basis of the parapodia (e.g. *Arctonoe fragilis*). This characteristic is not common to all polynoids but is an exception observed in a few species which are in a habit of attaching themselves to other organisms (Essenberg 1918).

Attachment structures other than those based on setae have been reported only twice: for the holothurian-associated scaleworm *Gastrolepidia clavigera* (Fig 13A) and for the highly modified species of the crustacean-associated family Histriobdellidae. The highly peculiar attaching structures of *G. clavigera* consist of semicircular, serially arranged, shield-like ventral lobes of the segments. These lobes considerably increased the area of contact between the commensal and the smooth, mucus-covered holothurian body. Moreover, when combined with a characteristic arching of the worm's body, they probably function like suckers (Gibbs 1971). Such an attaching organ, unique among polychaetes, is reminiscent of the small clam *Entovalva semperi* Oshima, which attaches itself to the burrowing sea cucumber *Protankyra bidentata* by means of a highly modified foot that functions like a suction cup (Dales 1957).

The attachment structure of the histriobdellids clearly differs from that of the scaleworm. The body of these commensal worms is so highly modified that they were initially considered as larval serpulids (van Beneden 1853), then as adult leeches (van Beneden 1958) and as Archiannelids (Hermans 1969). Although some differences may occur at the species level, the attachment structures are located on the distal end of two widened lateral expansions present on the posterior end of the body (Figs 13D, 13E) and consist on several adhesive glands. Modified reproductive structures are also present in this family. Indeed, the males are provided with a copulatory complex (Fig 13D) composed of a penis with one (*Stratiodrilus* spp.) or two (*Histriobdella*) projecting structures, a highly developed musculature, peniform external structure and several lateral or

median expansions or lips. Moreover, the males have also one or two lateral retractile or claspers. This complex organ enables the males to inject the sperm directly into the body cavity of females (Lang 1949, Jamieson et al. 1985), assuring the effectiveness of fertilisation in the limited space provided by the host.

Modifications of jaw apparatus have not been so often reported for commensals as for parasitic polychaetes (see the corresponding chapter). The mandibles of the histriobdellids closely resemble those of the eunicids (Mesnill & Caullery 1922), among which they are currently included (Fauchald 1977), and do not have any apparent adaptive modification. Although it was pointed out that they were not solid but hollow, the relationship of this characteristic with the symbiotic mode of life of these worms has not been defined. In addition, it is often very difficult to describe their exact composition as they vary from individual to individual (Lang 1949). *Stratiodrilus* species have denticulated bucal lips surrounding the mouth opening (Moyano et al. 1993). As these worms feed by grazing on the microflora that grow on the different surfaces of the host's body (Cannon & Jennings 1987), this mouth structure is likely to be related to its feeding mode. In fact, most of the jaws defined as highly specialised do not differ greatly in complexity and function from those of related free living-polychaetes (e.g. commensal *Ophryotrocha* spp. versus other dorvilleids). Moreover, the jaw apparatus may vary in size and appearance according to the size of the worms and the time of usage, such as in *O. geryoncola* (Pfannestiel et al. 1982). The mandibles of the iphitimids also resemble those of the free-living relatives (i.e. eunicids such as *Halla* spp.). However, evidences of tissue damage in their host crabs has never been reported, although all the species have mandibles well equipped for biting and chewing (Fig 12). In this case, commensal iphitimids are not notably simpler, their jaws being only modified in that the basal pair of maxillae (the only well-developed pair) are fused together to form a pair of pincers (Hartnoll 1962). Conversely, the single parasitic iphitimid, *Veneriservia pygoclava*, shows a highly simplified jaw apparatus (see Fig 12G). Additional variability was initially related to the fact that some species are sexually dimorphic (e.g. *Iphitime cuenoti*), with the males being significantly smaller than females (Hartnoll 1962, Abelló et al. 1988). More recently, however, it was demonstrated that individuals of *I. cuenoti* may have either small or large jaws (Figs 12A, 12B), independently of sex, and that those with small jaws were probably young sexually undifferentiated individuals (Comely & Ansell 1989).

Morphological adaptations also allow the commensal polychaetes to mimic the surface structure of their hosts. *Bathynoe cascadiensis*, a scaleworm associated with starfish, has unusually large elytra with numerous prominent nodular macrotubercles (Fig 13B). These tubercles are likely to be a specific adaptation for living with hosts from the order Forcipulata, a group characterised by having numerous knobs and spines and being heavily armed with large pedicellaria. By mimicking the spines and tube feet of starfish, it has been suggested that the camouflaged worms may protect themselves from being attacked and rejected by their own hosts (Ruff 1991). A spectacular example of mimicry has been demonstrated by the individuals of the scaleworm *Gastrolepidia clavigera* that are associated with the sea cucumber *Holothuria atra*. The holothurians are black, sometimes with tints of violet, and usually have white coral sand grains adhered to their surface so that they appear to be covered by a silvery-white "coat". The commensal worms are deep violet, almost black, with the elytra dark brown to black with bright white tubercles (Potts 1910, Gibbs 1969). Moreover, the distal part of antennae, palps, and tentacular and dorsal cirri are swollen and white. These white tubercles and appendages on the dorsal side of the worms exactly mimic the holothurian papillae with attached white sand grains (Britayev & Zamyshliak 1996). In the case of *Asterophilina carlae*, this uncoloured scaleworm is very conspicuous on the surface of its blue host starfish *Linkia laevigata*. However, the large swellings of the appendages and raised mounds of the posterior edge of each elytron of the polynoid (Fig 13C), as well as the elliptical outline of its body, perfectly mimic the host in that, often, the starfish has only a portion of each ambulacral groove open and this groove, through which the tube feet protrude, is elliptical in outline (Hanley 1989).

Non-obviously adaptive morphological modifications

Many commensal polychaetes have structural modifications of their external features which differentiate them from their free-living relatives, but lack an obvious adaptive significance. Often, the finding of some of these characteristics in newly described species allowed its commensal habit to be inferred without reliable observations of the specimens living with any host species (e.g. *Minusculiscama hughesi* and its maldanid hosts in Pettibone 1983). The most typical series of “commensal” trends are certainly found within the polynoids.

The elytra of many commensal scaleworms are small (leaving much of the dorsal surface uncovered), thin and smooth, and lack the ornamentations frequently found on free-living species. A good example of these small elytra occurs in the species of the genus *Lepidasthenia*: in *L. mossambica*, the elytra are very thin, whereas they are smaller in *L. microlepis* and so diminished in overall size as to be mere vestiges at the end of long elytophores in *L. stylolepis* (Figs 13H to 13J). Additionally, some polynoids (viz. species of the genus *Arctonoe*, *Bathynoe*, *Branchipolynoe*, *Disconatis*, *Gastrolepidia*, *Hololepidella*, *Lepidasthenia*, *Minusculiscama*) have very small notopodia (subbiramous parapodia) with a limited number of purely developed notosetae or even without setae (e.g. *Branchipolynoe pettiboneae* in Fig 10K). Although some of these modifications may occur in commensal polychaetes associated with bivalves (e.g. *Branchipolynoe symmytilida* in Pettibone 1984a), they appear more frequently as a result of sharing tubes or galleries with a host. Perhaps the protection afforded by the tube and the clean water circulated through the tube by the host diminish the need for elytra to form a defensive covering, the requirement for large elytra and the presence of notosetae to help keep the dorsal respiratory surface of the body clean. In fact, certain species (e.g. *Disconatis contubernalis*, *Lepidasthenia microlepis*) have the first pair of elytra much larger than the subsequent pairs. This may be closely related to the protective role of elytra, particularly if commensal habits include sticking its head out of the tube (Hanley & Burke 1988). A limitation of movement requirements may also be related to the decreasing importance of notosetae in the commensal tube-inhabitant scaleworms.

The scaleworm *Ophthalmonoe pettiboneae*, which lives inside the tubes of the large chaetopterid *Chaetopterus appendiculatus*, also show a very interesting modification. This commensal species has two pairs of eyes, with the anterior one being enlarged, directed anteriorly and with conspicuous lenses (Figs 13F, 13G). Both this orientation and structure of eyes are rather rare among polynoids, but are typical for tube-dwelling acoetids. Therefore, although this eye shape seems clearly to be an adaptation of the scaleworm to inhabiting tubes (Petersen & Britayev 1997), the relationship with its commensal mode of life is not clear.

Adaptive behaviour in commensal polychaetes

Although the behaviour of any commensal polychaete should undoubtedly be adapted to the symbiotic mode of life, very often this adaptive behaviour seems easy to deduce from the normal habits of the free-living polychaetes. Some typically symbiotic types of behaviour we expect in commensal polychaetes are: the co-ordination of movements with those of their host when feeding and moving, the finding of a new host (i.e. during recruitment or if they are moved out from their current host, either as a result of intra-specific competition or death of the host), the finding of a reliable way of attaching themselves to their hosts, and the selection of the most protected area in the host body. The last two types are closely connected with morphological adaptive modifications which have already been discussed in other sections. The first two require a more specific discussion. As mentioned in the introduction, commensal relationships are often known as “0+” associations. However, detailed behavioural studies strongly support the view that certain commensal associations are, in fact, “++” or mutualistic relationships, when the benefits are bilateral. This mutualistic behaviour also merits a specific discussion.

It should be pointed out that behavioural information often results from direct field or experimental observations of living associates. Consequently, it tends to be very rare.

Nevertheless, some interesting examples have been reported and will be discussed in the following sections.

Co-ordination of host/symbiont movements

Remarkable host/symbiont co-ordination in movements and feeding behaviour occurs between the reddish scaleworm *Hesperonoe adventor* and its host echiuroid *Urechis caupo*. The host constructs a large burrow in mud flats and feeds with the aid of a mucous bag, drawing water through the bag by peristaltic movements of the body. The commensal usually lives alongside the host ([Fig 3A](#)) and so is obliged to move back and forth along the wall of burrow to avoid the peristaltic swellings of the host. The commensal feeds on parts of the mucous bag formed by the host, but can reach the bag only when the host itself is eating it (Dales 1957).

The behaviour of *Hesperonoe adventor* closely resembles that of an undetermined species of polynoid (probably belonging to the genus *Malmgreniella sensu* Pettibone 1993) found associated with a tube-dwelling synaptid holothurian on the Catalan coast of the Mediterranean (D. Martin personal observations). The scaleworm was observed inside the host burrow, lying below the holothurian with its dorsum touching the ventral side of the host. The symbiont moved in order to avoid the host's peristaltic swellings, exactly as *H. adventor* does. In this case, however, there is not a clear trophic relationship between the deposit-feeding host and the probably carnivorous symbiont.

Nature and specificity of host recognition behaviour

The most widely studied aspect of host-commensal relationships among polychaetes is probably host recognition behaviour (viz. Davenport 1950, Davenport & Hickok 1951, Davenport 1953a, b, 1955, Bartel & Davenport 1956, Hickok & Davenport 1957, Davenport 1966a, b, Gerber & Stout 1968, Webster 1968, Dimock & Davenport 1971). In the well-known series of experiments using different models of choice-apparatus, most of these authors clearly demonstrated that all the symbiotic polychaetes studied were able to recognise their hosts and to respond to their presence or to some signals (i.e. the so-called host-factor) released from the host into the water (i.e. in absence of the hosts themselves). The known symbiotic polychaetes showing host recognition behaviour in experimental conditions include 14 species and 25 relationships ([Table 5](#)). Some commensal polychaetes (viz. some *Arctonoe* spp., *Ophiodromus puggetensis*, *Hesperonoe adventor* and *Hololepidella nigropunctata*) seemed able to detect their hosts from a distance. Other commensal worms did not show distant host recognition. *Acholoe astericola*, for example, seems only able to recognise its host starfish when adjacent to, or even touching, host's. As soon as its head contacts the host, the worm becomes active almost at once, fastening itself to the host either by climbing quickly to the aboral surface or into the ambulacral groove, or by wrapping itself entirely around the tip of the host arm (Davenport 1953a). *Haplosyllis chamaeleon* shows a similar specific response to its gorgonian host (Laubier 1960). When separated from the gorgonian, the polychaetes remain particularly immobile and coiled around themselves. Only after contacting a host branch, do they start to crawl and reach their habitual position on the branches.

The mechanism of host recognition appears highly specific in some commensal polychaetes, at least in experimental conditions. Commensal polychaetes seem able to recognise their host, to distinguish it from taxonomically related species, and to distinguish the original host species from alternative ones. *Arctonoe fragilis* was attracted by water from a tank occupied by its host starfish *Evasterias troschelii*, but not by water from a tank of another starfish of the genus *Pisaster*, with which the worm is not associated. Similarly, *Arctonoe pulchra*, was attracted by water coming from the sea cucumber *Stichopus* (i.e. the host), but not by water from *Cucumaria* (non-associated, but common in the same habitat) (Davenport 1950, Davenport & Hickok 1951).

The specificity of the response is highly variable depending on the different commensal polychaetes. *Acholoe astericola*, for example, may respond positively both to its host and to many other taxonomically related animals (see below). Conversely, *Arctonoe pulchra* showed undifferentiated liking for animals belonging to different taxonomic groups. Indeed, this

commensal repeatedly show preference for the arm of the choice-apparatus with water flowing from: starfish (*Dermasterias imbricata*), sea cucumbers (*Stichopus californicus*, *S. parvimensis*) and molluscs (*Megathura crenulata*), all of which were in fact their natural hosts. The specimens of *Arctonoe vittata* harboured by *Asterias amurensis* positively respond to chemical signals both from the original host and from its alternative host mollusc *Acmaea pallida*. However, the positive responses of worms associated with *A. pallida* were restricted to the host mollusc (Britayev 1991). The behaviour of *A. vittata* has clear implications for the population dynamics and life-cycle of the species (see Fig 14). In fact, recruitment may occur on both hosts. However, the symbionts (i.e. juveniles or adults) driven off the host starfish as a result of intraspecific competition will be able to relocate not only on other starfish but also on the host mollusc, whereas those worms initially associated with the mollusc have only one relocation possibility, i.e. another host mollusc.

Certain chemical cues released by or from the host to the surrounding water seem to hold the key of host recognition behaviour in polychaetes (Davenport & Hickok 1951). When the asteroid *Evasterias troschelii* was suspended in a bolting-silk bag in an aquarium and then carefully removed, the commensal *Arctonoe fragilis* was able to detect the signal released by the host. When the host starfish was suspended in an aquarium overnight in a dialysis bag, the commensal did not respond to the water outside. However, by splitting the bag with a razor the attractive cue was released and the commensal immediately responded. But it is not at all clear what this cue substance (or substances) is. It seems to be very labile, as the positive response of *A. fragilis* to the water in absence of the host was only maintained for between 15 and 30 minutes. Also, a temperature higher than 64 °C either alters or completely destroys the attractant, eliminating any response (Davenport 1953a).

The fact that, in some cases, commensal responded positively to several taxonomically close hosts suggests a possible biochemical similarity between them, with their cues having the same or very similar chemical composition. The specimens of *Acholoe astericola* originally associated with the starfish *Astropecten irregularis* at Plymouth positively respond not only to their original host but, to some extent, to other asteroids of the order Phanerozonia from the same area (e.g. *Astropecten*, *Luidia*, *Porania*, *Solaster*) and to certain spinulose starfish (*Asterina*, *Palmipes*, *Henricia*), but they did not ordinarily respond to forcipulate starfish (*Asterias*, *Marthasterias*, *Stichastrella*).

The scaleworm *Polynoe scolopendrina* showed a more specific response than *Acholoe astericola* when tested against a wide spectrum of terebellid polychaetes. Although certain reduced responses to two species of *Amphitrite* (not its normal hosts) were detected, the polynoid consistently responded only to its original host (i.e. *Eupolymnia nebulosa*). This commensal has two alternative hosts, the terebellid *Lanice conchilega* (described from deep water on the French coast) and the eunicid *Lysidice ninetta* (occurring also in the Plymouth area). Interestingly, however, the commensal polynoid responded strongly to *L. ninetta* and did not respond to *L. conchilega*. Accordingly, it was suggested that, although belonging to the same polychaete family, the attractants released by the hosts *E. nebulosa* and *L. conchilega* and recognised by the respective commensal populations, did not share the same chemical composition (Davenport 1953b).

Biochemical studies on the “host factor” based on disc electrophoresis with polyacrylamide gel revealed that seven protein fractions (five of them mucoproteins) were very likely responsible for the attraction of symbionts. These interesting studies were carried out on a copepod, *Sabelliphilus sarsi*, living in symbiosis with a sabellid polychaete, *Spirographis spallanzani* (Carton 1966a, b, 1967, 1968a, b). Apart from the studies mentioned above, there are no further studies on the nature of the “host-factor” and on the specificity of host recognition in polychaetes. This is certainly one of the most promising lines of research into symbiosis in polychaetes, particularly as many studies suggest the importance of host recognition behaviour. According to Carthy (1958), the difference between taste (contact chemoreception) and smell (distant chemoreception) in aquatic organisms is a question of threshold, smell receptors having a low, and taste receptors a high, threshold. In support of this, Gerber & Stout (1968) demonstrated that *Arctonoe vittata* (from the host *Diodora aspera*) apparently had two different chemoreceptors, one for distant reception (the antennae) the other for contact reception (the palps). However, these authors also demonstrated that the behaviour of the commensals indicated that the distant chemoreceptors did not function in

contact chemoreception, which strongly supported the existence of two different host factors involved in this particular relationship. Gerber & Stout (1968) also pointed out that “further work needs to be done to demonstrate the presence of two possible host factors and their chemical nature and to identify morphologically and physiologically the receptors involved”. Although recommended in 1968, this work has still not been done.

Several classical studies on host recognition behaviour have repeatedly been considered conflicting and obscure. The most representative is probably the study on *Harmothoe lunulata* and its hosts from Plymouth (Davenport 1953b). The scaleworms associated with the terebellid *Amphitrite johnstoni* unexpectedly demonstrated slight positive responses to the alternative hosts *Arenicola marina*, *Lanice conchilega* and *Golfingia elongata*, but not to species taxonomically related to the original host such as *Amphitrite edwardsi*. In fact, the recent taxonomic review on *H. lunulata* and related species (Pettibone 1993) enables light to be cast on Davenport’s conflicting observation. According to Pettibone (1993), the specimens of “*H. lunulata*” should probably be considered as belonging to different species. The population associated with *A. johnstoni* was transferred to *Malmgreniella andreapolis*, whereas those associated with the ophiuroid *Acrocnida brachiata* and the holothuroid *Leptosynapta galliennii* reallocated to *M. arenicola*. Moreover, the three hosts which triggered unexpected positive responses in Davenport’s “*H. lunulata*” associated with *A. johnstoni* (i.e. *A. marina*, *L. conchilega* and *G. elongata*) were reported as natural hosts of *M. arenicola* by Pettibone (1993). These observations seem to clarify the unexpected commensal responses, but pose new questions about the “nature of the host-factor” problem.

It has been demonstrated that the high frequency of commensals migrating from host to host (including other species than the original host) may result from intraspecific competition (Lande & Reish 1968, Palmer 1968, Dimock 1974, Britayev 1991). Therefore, the classic authors, working before these dates, could not fully assess the relevance of the host recognition behaviour they found. In 1966, Davenport wrote that “...during adulthood of the commensals, the chaemotaxis serves merely to keep the commensal on the surface of the hosts...under natural conditions an annelid... would seldom be forced to seek a new host when its own is damaged or dying. Such an event is probably too rare to be considered a factor in the evolution of the powerful chaemotactic response ...”. However, the fact that the spatial pattern formation in symbiotic polychaete populations strongly depends on intraspecific competition and resulting symbiont relocation revealed the significance of host recognition behaviour in life-cycles of symbionts.

Host-entering behaviour

The section above may suggest that chaemoreception is the dominant mechanism contributing to the maintenance of marine symbiotic partnerships. However, other kinds of stimuli produced by the hosts may trigger characteristic adaptive responses from commensal polychaetes. As pointed out by Gilpin-Brown (1969), the nereidid *Nereis fucata* seemed unable to discriminate between different species of hermit crabs. Thus, the peculiar association of *N. fucata* with hermit crabs seems to display non-chemically regulated behaviour. Surprisingly, this association has been studied by many authors (Rabaud 1939, Thorson 1949, Brightwell 1951, Gilpin-Brown 1969, Goerke 1971, Jensen & Bender 1973, Cram & Evans 1980) and, unusually, it has even been filmed (Goerke 1977a, b).

The most distinctive attribute of *Nereis fucata* is, probably, its intricate mode of entering the gastropod shell inhabited by the host. Settlement of this species occurs directly on the sea bottom, without any kind of host specificity. Both young recruits and adults that had moved out from their shells owing to the death or moulting of their hosts, are found inside tubes in the bottom sediments. When a hermit crab is placed in the vicinity of such pseudo “free-living” commensals in an experimental aquarium, the worms immediately begin to come out of their tubes. As the worms stretch out of their tubes, the anterior portion of their bodies rise up from the bottom and begin to wave about in a wide, sweeping movement. When the hermit crab enters the search area delimited by these sweeping movements and touches the worm head, the worm starts moving straight to the shell and quickly enters it. A similar reaction was experimentally triggered by bouncing an empty and carefully washed shell on the bottom or even by tapping the edge of the culture vessel with a

finger nail. All these experiments demonstrated that the characteristic searching behaviour of *N. fucata* was triggered by the perception of substrate vibrations. Presumably, this behaviour will also be present in natural commensal populations, starting as soon as substrate vibrations are perceived by the worms. This behaviour appears 4 months after settlement and is maintained during the whole life of the commensal. This fact was the main argument used to consider the association of this species and hermit crabs truly commensal (Gilpin-Brown 1969).

On contacting a host hermit crab, the individuals of *Nereis fucata* take up a position behind the shell, then crawl over it, usually along its sutures, before eventually reaching the aperture. The worm enters *via* the upper lip of the aperture and rapidly crawls inside the shell to adopt its habitual position (see [Fig 5G](#)). *N. fucata* is able to crawl on the smooth shell surface by secreting mucus from special glands located in its parapodia. These glands have not been reported in free-living nereidids, so constitute a differential character of this symbiotic species. Therefore, *N. fucata*'s characteristic adaptive behaviour is accompanied by a singular physiological adaptation.

Mutualistic behaviour

The fact that some commensal associations may probably be transferred to mutualistic interactions may be indicated both by specific behavioural response of hosts to the presence of symbionts and also by the absence of hostile host reaction. A typical example of host response was described in the association between the hesionid *Ophiodromus puggetensis spinapandens* and its echinoid host, the sand dollar *Clypeaster humilis* (Storch & Niggemann 1967). The commensal is usually found crawling among the spines on the oral side of the host. When the head appendages of the symbiont contact the host's spines, these start moving apart, which allows the commensal to go further on the host surface. During its movements, the worm directs its parapodia vertically downwards. Conversely, when different free-living species of polychaetes (*viz.* nereidids, syllids, chrysopetalids) were experimentally forced to touch the surface of the sea urchin and placed among the host's spines, the spines were motionless. This behaviour prevented any kind of worm movement and was reinforced by the pedicellaria attempting to snatch the intruders. Such very specific host behaviour closely resembled that of giant sea-anemones in their well-known association with clown fishes and crabs inhabiting their crowns. In these cases, the symbionts are tolerated by the host, whereas their free-living relatives are damaged or killed by the nematocysts, as soon as any contact with anemone tentacles occurs. Symbiont recognition may also occur in the associations between predator hosts and polychaetes, such as those involving hermit crabs and *Nereis fucata*. Adult *N. fucata* stretch from the inner surface of the shell and crawl out to take food from the pagurid's maxillipeds. Either owing to the worm's avoidance of the hermit crab's buccal equipment or to some chemical signal from the symbiont that is effectively recognised by the host, the fact is that the commensals are never attacked by the host. However, other polychaete species may perfectly well be preys of the hermit crab.

Symbiont recognition by hosts would be meaningless if the hosts derived no benefits from the association with their symbionts. Benefits for the host may include defence against predators or cleaning, which imply steps from a unidirectional towards a mutualistic relationship. The most evident benefit from the host's association with an aggressive inquiline, like a polynoid (Dimock 1974), is certainly assistance in fending off predators by biting them. This behaviour has been suggested in certain associations involving polynoids (*e.g.* *Harmothoe hyalonemae* in Martin *et al.* 1992), but was earlier demonstrated in the association between *Arctonoe vittata* and its host limpet *Diodora aspera* (Dimock & Dimock 1969). In this case, the symbiont aggressiveness towards the predatory starfish *Pisaster ochraceous* was not displayed by worms on their own, which strongly suggests that stimuli linked to the host (*i.e.* chemical or mechanical cues) may trigger the commensal's aggressive behaviour.

Hosts may also benefit from symbionts' cleaning activity, though this may bear no relation to symbiont aggressive behaviour. Benefits based on cleaning activity have been suggested for the associations between spionids and molluscs (*Polydora glycymerica* and *Glycymeris yessoensis* in Radashevsky 1993) or sponges (*Cliona viridis* and *Polydora rogeri* in Martin 1996). In these cases, the ability of the polydorids to manipulate relatively large particles may favour the filtering

activity of the hosts by cleaning the water around the bivalve's siphons or the sponge's inhalant papillae (see the section on boring symbiotic polychaetes). However, the so-called aggressive polynoids may also act as cleaning symbionts either by removing epi- or endobionts or by feeding on mucus or settled detritus. In bathyal muddy benthic environments, the Mediterranean hexactinellid sponges of the genus *Hyalonemae* were certainly suitable refuges likely to attract the existing vagile fauna. However, those sponges inhabited by the polynoid *Harmothoe hyalonemae* were never occupied by endobionts other than the commensal worms (Martin et al. 1992). In the association between the polynoid *Arctonoe vittata* and the starfish *Dermasterias imbricata*, the commensal may benefit the host by feeding on sea star mucus and settled detritus (Wagner et al. 1979). In fact, *D. imbricata* lacks pedicellariae, structures which are thought to function in part by keeping the aboral surface of other starfish free of epibionts and detritus. As pointed out by Wagner et al. (1979), most starfish hosts reported for *A. vittata* also lack pedicellariae. All these observations strongly suggest that *A. vittata* may be involved in a mutualistic, rather than a unidirectional, association with its host starfish. Moreover, the series of experiments carried out by Wagner et al. (1979) are the only demonstration of a host, *D. imbricata*, being attracted toward its commensal polynoid, *A. vittata*. Although this attraction was clear in the laboratory, its precise role in nature was not clear. Rather than acquire symbionts from a pool of free-living worms (*A. vittata* is considered an obligatory commensal), the host response more likely served to re-establish an existing association after the symbiont had become temporarily separated from its host. In fact, this suggestion coincides with the importance attributed to host-relocation behaviour in the life-cycle of symbiont *Arctonoe* species (Dimock 1974, Britayev 1991).

LIFE-CYCLES OF COMMENSAL POLYCHAETES

Little is known on the life-cycles of commensal polychaetes. The available data, however, allow us to surmise that, in fact, the life-cycle structure of most commensal species does not significantly differ from those of their free-living relatives. The well-known generic scheme of polychaetes' life-cycle, divided into planktonic larval and benthic adult phases may perfectly be applied to commensal polychaetes, with a single main difference: the symbiotic habits replace the free-living ones in the benthic phase. The tropical serpulid *Spirobranchus giganteus*, an obligate symbiont which builds its tubes on the surface of living haematypic corals, instead of bore or excavate the coral skeleton (Marsden 1987, Hunte et al. 1990a, b, Marsden et al. 1990), may well illustrate this point. *S. giganteus* is a dioecious species, which has external fertilisation and a planktonic larval phase of 9 to 12 days long. These planktonic larvae are attracted by certain coral species whereas they do not respond to certain others. Despite it was suggested that commensals' larval settlement should occur on the bottom, with a subsequent juvenile migration towards the respective hosts (Davenport 1966a), it seems more likely that host-recognition by settling larvae is a widespread trend among symbiotic polychaetes (parasites included, see the corresponding sections below). Moreover, the planktonic larvae of symbiotic polychaetes may also be attracted by their adult conspecifics, as it occurs in *S. giganteus*. In summary, the life-cycle of this species consists of a symbiotic adult stage with limited mobility and a free-living planktonic phase, which is in fact responsible for dispersion.

This scheme may vary depending on the species. For example, in the nereidid *Nereis fucata*, the life-cycle is complicated with an additional free-living benthic stage. The gravid heteronereis leave the hosts and spawn freely in the water column from late Spring to early Summer (Gilpin-Brown 1969, Goerke 1971). Unexpectedly, the planktotrophic larvae settle directly on the soft bottom, rather than on their hosts, and the juveniles live in tubes inside the bottom sediment during several months. During this phase, they feed on detritus and small benthic animals, exactly like their free-living related species. However, 4 months old juveniles start to develop the ability to recognise the substrate vibrations produced by the hermit crab shell bouncing on the bottom (Gilpin-Brown 1969). The development of the life-cycle is completed when a hermit crab reaches the area inhabited by the pseudo free-living juveniles and triggers their characteristic host-entering

behaviour (see the corresponding section above). Host-entering occurs more intensively in Spring, due to the increasing number of “emptied” host shells after the release of gravid heteroneris.

Some commensals tend to simplify their life-cycles by reducing, or even eliminating, the free-living pelagic stage. In these cases, the adult symbionts are the responsible for dispersal. Known examples of this strategy occur, for example, among the histriobdellids, which possess internal fertilisation and whose eggs directly develop inside cocoons attached to the host (e.g. *Histriobdella homari* in Haswell 1913). Conversely, other commensals tend to increase the complexity of their life-cycles by having an intermediate host (or hosts). The best known example of such complex life-cycle occurs probably in the scaleworm *Arctonoe vittata*. This species is also one of the most widely studied commensal species, whose behaviour, population ecology and reproductive biology has been reported in detail (Davenport 1950, Palmer 1968, Dimock & Dimock 1969, Wagner et al. 1979, Britayev & Smurov 1985, Britayev et al. 1989), allowing to reconstruct the main traits of its life-cycle (Britayev 1991). In the Northwest part of the Sea of Japan (Vostok Bay) this species is associated with several host from different taxa (i.e. the starfish *Asterias amurensis*, the limpet *Acmaea pallida* and, more accidentally, with the sea cucumber *Stichopus japonicus* and the starfish *Aphelasterias japonica*). The spawned eggs are poor in yolk so that the fertilisation gives rise to planktotrophic larvae. After a long pelagic phase, settlement occurs on all above-mentioned hosts, with the main flow of settling larvae being addressed to *A. amurensis*, and the low number of successfully settled larvae occurring on *A. pallida* (Fig 13). However, the later remain during the whole life on their host limpets, whereas the former may have diverse destinations: the initial starfish individual will be the definitive hosts for some of them, while some others will be forced to leave it and to relocate on other host-individuals (i. e. starfish of the same species, or of *A. japonica*, but also the limpets or the sea cucumbers). Undoubtedly, intraspecific competition plays the most important role in these relocation processes.

The limpets are probably more “suitable” hosts than the starfish for *A. vittata*. However, both the high infestation prevalence and the limited available space on the limpet tend to reduce juvenile’s survival. It should be taken into account that the species shows a strong intraspecific aggressive behaviour. However, as a result of the large surface of the host starfish, the amount of aggressive interactions between the symbionts from the same host individual may be significantly reduced. It is thus possible for recently settled juveniles to survive sharing the same host starfish with a large adult. However, if several young specimens settle on the same host, the number of negative interactions between them, as well as that of aggressive actions of the large adult (if present), became higher together with young’s growth (Britayev et al., 1989). The final result is that some symbionts (usually the smallest) are obliged to leave the host and move then to another one. In this case, the starfish *A. amurensis* may be regarded as an intermediate host, whereas, at least for some symbionts, *A. pallida* acts as the definitive one. In fact, we may speculate that the complex life-cycle of *Arctonoe vittata* has an additional interest in that it may probably illustrate how some symbiotic (i.e. parasitic) life-cycles including different hosts may have evolved as a result of symbionts’ intraspecific competition.

PARASITIC POLYCHAETES

Parasites are often specially adapted to facilitate their specialised way of life (Margalef 1980). Thus, a low degree or the lack of specialisation has been interpreted as a sign of an evolutionarily recent change to parasitic life (Clark 1956). A strict parasitic relationship often implies some degree of co-evolution. In fact, the hosts may even be able to support the presence of their parasites, the infested populations attaining a certain level of equilibrium in normal, non-stressed conditions (Margalef 1980). Endoparasitic relationships tend to be more strict than ectoparasitic relationships. Most ectoparasites are, indeed, haematophagous, dermatophagous or secretophagous. The endoparasites inhabit the tissues or the body cavities of the hosts. As we have included within the commensals those symbiotic polychaetes lacking clear parasitic characteristics, the following sections will refer to the polychaete species with known described morphological or behavioural parasitic trends.

TAXONOMICAL DISTRIBUTION OF PARASITIC POLYCHAETE SPECIES

81 polychaete species belonging to 13 different families are reported to be involved in 253 different parasitic relationships (Tables 6, 8 and 9; Fig 15A). Parasitic polychaetes are thus present in about 15% of known polychaete families and about 0.5% of known species, which is far from being the highest figure for the presence of commensals (see the above corresponding section).

Probably one of the most striking facts arising from the comparison between classic papers, such as those by Paris (1955) and Clark (1956), and the present review is that some of the typical examples of parasitic polychaetes have now been excluded from this category, and included in the commensals. Clearly this is due to increased knowledge of the characteristics of the involved associates. *Histiobdella homari* and *Ophryotrocha geryoncola*, together with species of the genus *Iphitime*, were reported as ectoparasites of the branchial chambers of crustaceans by the above classic authors. More recent studies, however, demonstrated that *H. homari* behave more as a cleaning symbiont than as a parasite (Jennings & Gelder 1976), whereas the relationships between crabs and *Iphitime* spp. (Hartnoll 1962, Pilger 1971, Abelló et al. 1988, Comely & Ansell 1989) and *Ophryotrocha* spp. (Gaston & Benner 1981, Martin et al. 1991) may be regarded as commensalisms. In fact, these worms feed on material captured or attracted by the host, and their presence did not negatively affect the gills of the host.

The highest number of polychaete species considered, to some degree, as parasites belong to the family Spionidae (38%) which are, in fact, boring species. This family also includes the highest number of relationships (52%), which suggests that most of the parasitic spionid species have a low degree of specificity. In other words, the same species may frequently bore (and infest) many different hosts. However, the symbiotic associations involving boring polychaete species (spionids, but also the so-called parasitic species of the families Caobangidae and Sabellidae) show very peculiar characteristics and their main trends will be analysed in separate sections.

Most of the polychaetes that have been reported, in principle, as real parasites are obligatory symbionts (45%), whereas only 30% are permanent parasites (Table 6). Parasitic polychaetes mainly belong to the family Oeonidae (about 24%). These worms are internal parasites and, with the exception of *Oligognathus bonelliae* (parasitic on the echiuroid *Bonellia viridis*) and *Pholadiphilia turnerae* (parasitic on the bivalve *Xyloredo ingolfia*), all their hosts are other polychaetes (Table 6). The parasitic oeonids apparently show a high degree of specificity: of the 19 known species, 16 are known to infest a single host. This trend may be explained, however, by their extreme rarity which gives rise to the fact that most species are only known from a single original record.

The syllids are the second most well represented family within the “non-boring” parasites (14%). Members of this family have been mainly reported from sponge hosts, the most representative parasitic syllid being the cosmopolitan species *Haplosyllis spongicola*. The remaining polychaete families include only one or two parasitic species. Among them, the highly specialised families Calamizidae (2 species) and Ichtyotomidae (1 species) are entirely parasitic.

MARINE TAXA HARBOURING PARASITIC POLYCHAETES

The parasitic polychaetes infest 186 different host species included in 16 groups of organisms (Table 6, 8 and 9; Fig 13B). With the exception of 3 fishes and 1 plant, all remaining host species are benthic invertebrates. Gastropod and bivalve molluscs showed the highest percentage of species harbouring parasitic polychaetes (29% and 23%, respectively). Thus, they are involved in most of the parasitic relationships (28% and 31%, respectively). With the exception of the oeonid *Pholadiphilia turnerae*, all parasitic polychaetes infesting gastropods and bivalves belong either to the caobangids or to the spionids. Similarly, the host cirripeds and bryozoans, a few of the host sponges and cnidarians, and the host seagrass are also infested by spionids.

The next most common host groups (each one representing about 16% of the host species) are the sponges and the polychaetes themselves. The former are mainly parasitised by syllids, particularly *Haplosyllis spongicola* and *Branchisyllis oculata*. The latter are infested by the parasitic oeononids (with the exception of *Pholadiphilia turnerae*), 2 calamizids, 1 iphitimid and 1 syllid. The host polychaete species belong to the families Aphroditidae, Eunicidae, Onuphidae, Terebellidae, Spionidae, Ampharetidae, Syllidae, Nereidae and Sabellidae.

SPECIFICITY AMONG PARASITIC POLYCHAETES

It is very difficult to analyse the degree of specificity among parasitic polychaetes. The analysis of the available data seems to point to a clear monoxenous pattern. More than half of the parasitic polychaete species (about 69%) infest a single host species, while the figure rises to 91% if those infesting 2 or 3 different host species are included. However, this monoxenous pattern is clearly biased by the virtual absence, in most cases, of data other than the original citation. As new data are reported, the host spectrum tends to increase. This may be the case of the oeononid *Labrorostratus parasiticus*. This species, with 6 known host polychaete species (up to 9 if we assume that the specimens described by San Martín & Sardá 1986 as *Labrorostratus* sp. are indeed *L. parasiticus*), is certainly the most frequently reported and the one with most recent citations. *L. parasiticus* is also the only oeononid known from more than one host polychaete. According to our interpretation, the latter may be a direct consequence of the former. A certain degree of specificity in the parasitic habits of *L. parasiticus* can be assumed, as all known hosts belong to the family Syllidae ([Table 6](#)).

Polyxenous relationships are mainly present within the syllids parasitising sponges (i.e. *Branchisyllis oculata* and *Haplosyllis spongicola*). However, the apparently polyxenous behaviour of *H. spongicola* (it has been reported from as many as 21 different host sponges) must be interpreted with care. The external morphology of this species is very well adapted to its life style and appears to be relatively simple. However, two different morphologies have been reported (viz. different arrangements of cirri, different shapes of setae) and are considered either as belonging to different subspecies, *H. spongicola spongicola* and *H. spongicola tentaculata* (Imajima 1966), as different growth stages of the same species (San Martín 1984) or, even, as different species, *H. spongicola* and *H. tentaculata* (Lee & Rho 1984). The existence of different colourings has been related to the colour of the host sponge (San Martín 1984, Magnino & Gaino in press). In light of the above, we suggest that the possible existence of a hidden sibling or pseudosibling species complex is still open for this species.

After the above-mentioned syllids, the number of host species parasitised by the same polychaete species sharply decreases: two species, *Ichthyotomus sanguinarius* and *Sphaerodorium flavus*, parasitise 3 host species, whereas only *Pholadiphilia turnerae* parasitises 2 host species. It must be pointed out, however, that these parasitic species closely resemble the behaviour of *Labrorostratus parasiticus* in that the taxonomic status of their respective hosts is always very close. All hosts are sponges for *H. spongicola*, fishes (species of conger) for *I. sanguinarius*, ophiuroids for *S. flavus* and pholadid bivalves for *P. turnerae*.

INFESTATION CHARACTERISTICS AND INTRA-HOST DISTRIBUTION PATTERNS OF PARASITIC POLYCHAETES

The known prevalences of infestation by non-boring parasitic polychaetes are extremely low: 0.2% within 28,604 hosts examined for *Labrorostratus luteus* (Uebelacker 1978), 0.05% within more than 6,000 hosts examined for *Labrorostratus* sp. (San Martín & Sardá 1986), and a maximum of 4% for *Arabella endonata* but with only 25 hosts examined (Emerson 1974). Probably, the infestation prevalence for *A. endonata* could not be accurately predicted from the small host sample examined and a decrease in prevalence could be expected with an increase in the amount of hosts examined. However, Emerson (1974) pointed out that several hundred of the host polychaete

Diopatra ornata from a population located in the vicinity of the type locality were examined and none of the specimens were infested.

Infestation intensities have been more often reported than prevalences (Table 7). A regular pattern of distribution seems to characterise most of the known parasitic relationships involving polychaetes, with each host harbouring only one single adult parasite. This statement can not be easily confirmed due to lack of information on the incidence of parasitic relationships involving polychaetes. However, the presence of one parasite in each host in the most frequently reported species, *Labrorostratus parasiticus*, supports the hypothesis of a regular distribution for all related species. The presence of two parasites on the same host specimen was reported for *Haplosyllis spongicola* on a eunicid host (as *H. cephalata* in Treadwell 1909), for *Ichthyotomus sanguinarius* (one male and one female, see Fig 20C) on an eel host (Eisig 1906, Fauvel 1923) and for *Calamyzas amphictenicola* (also one male and one female) on its ampharetid host (Franzén 1982).

Although less frequently, an aggregated distribution has also been reported for parasitic polychaetes (Table 7). The aggregates always seem to be connected to the reproduction of the involved species, with the exception of the parasitic syllids *Brachiosyllis oculata* and *Haplosyllis spongicola*. The highest known number of parasites (more than twenty thousand) inside a single host has been reported for *H. spongicola* (Bacescu 1971). However, *B. oculata*, *Proceraea* sp. and some of the endoparasitic oeononids also show numerous individuals inside a single host (Table 7). In *B. oculata*, the high densities were surprisingly supported by the host sponges with no apparent effect on them (Pawlik 1983). In *Proceraea* sp., the aggregated distribution occurs only within the juveniles, the mature adult phase being probably free-living (Britayev et al. unpubl.). In the oeononids *Notocirrus spiniferus* (Allen 1952) and *Arabella endonata* (Emerson 1974) the individuals were juveniles showing many different developmental stages. Amaral (1977) reported that two adult individuals of *Labrorostratus prolificus* showed traces of asexual reproduction (stolons) coexisting with their numerous juvenile stages. Conversely, there was not additional information about the several individuals of *Veneriservia pygoclava* found inside its aphroditid host.

LOCATION OF PARASITIC POLYCHAETES ON THEIR HOSTS

Most parasitic polychaetes are endoparasites (Fig 16), either inhabiting the tissues of their hosts (e.g. *Alciopina parasitica*, *Dorvillea sociabilis*, *Branchiosyllis exilis*, *Autolytus penetrans*, *Myrianida pinnigera*, *Typosyllis extenuata*), the peri-intestinal blood sinus (e.g. *Haematocleptes terebellidis*), the coelomic cavities (e.g. *Ophryotrocha puerilis*, *Veneriservia pygoclava*, *Oligognathus bonelliae*, most oeononids parasitising polychaetes), the aquiferous system (e.g. *Haplosyllis spongicola*), the hydrothecae (e.g. *Proceraea* sp.) or special galls formed by the host because of the presence of the parasite (e.g. *Ophiuricola cynips*). With the exception of *A. penetrans* and the last three species, no special morphological, structural or behavioural reactions to the presence of the parasites in their hosts has been described.

Wright & Woodwick (1977) described the blisters formed by the small syllid *Autolytus penetrans* on the hydrocorall *Allopora californica*. This worm apparently penetrated the surface of the host resulting in a hyperplasia of cellular and calcareous material which produce a characteristic vermiform mound. The blisters may be located almost anywhere on the living hydrocoral with no specific association with the coral polyps. This species was not originally described as parasite. In fact, there were no indications of any damage to the host - other than the blisters themselves - linked to the presence of the symbiont, but also any profit was suggested. Although this species does not actually bore, its blisters closely resemble those of the polydorids. In this case, however, the blister lining had cellular, instead of muddy, make up (Wright & Woodwick 1977).

The induction of special modifications in host sponges by *H. spongicola* apparently depends on the morphology of its hosts. If the sponge canals are larger than the parasite, it may be located inside these canals without inducing special modifications in the host (Bacescu 1971, Pansini & Daglio 1981, Tsurumi & Reiswig 1977, Magnino & Gaino in press). However, it may directly suck the sponge-bacteria tissues by inserting the pharynx through the canal walls, as was observed in the host reef bacteriosponge *Aplysina cauliformis* (Tsurumi & Reiswig 1977) (Fig 17B). Where

the canals are smaller than the parasite, *H. spongicola* directly penetrates into the sponge tissues, living inside them and often inducing malformations in the host sponge. The formation of a thick protective epithelial layer surrounding the zone inhabited by the worms has been mentioned for the sponge *Rhizaxinella pyrifera* (Uriz 1978) (Fig 17A) and *Aaptos* cf. *aaptos* (T.A. Britayev personal observations).

According to Ludwig (1905), the galls produced by *O. cynips* are rather large and partly protrude into the coelomic cavity of the host ophiuroid *Ophioglypha tumulosa*. In the host hydroid *Abietinaria turgida*, there is a single large mature adult *Proceraea* sp. per colony, inhabiting a thin hyaline tube attached to the axis of the host branches (Britayev et al. unpubl.). Conversely, a large number of juveniles of this parasite occurs inside modified hydrothecae from the same colony (Fig 17C, Table 7). The modified hydrotheca consist of a basal jug-like part (as in uninhabited ones) and a distal cylindrical part, which is the result of the polyp's response to the presence of the worm. Moreover, the presence of the parasite leads to morphological changes in the polyp, which lengthens its body during the initial stages of infestation (when the hydrothecae are shared with the parasite). At a further stage polyps are totally absent from the infested hydrothecae. Finally, the worms leave the hydrothecae and build mucous tubes attached to the stem or branches of the colony to continue their development until the adult stage being then able to leave the colony.

The oeonid *Pholadiphila turnerae* can be considered as an ectoparasite, as it inhabits the mantle (infrabranchial) cavity of the host bivalve (Dean 1992). The ectoparasitic polychaetes, however, tend to live more or less intimately attached to different parts of the host's body (see Fig 20). They may simply live on the host's surface (e.g. *Sphaerodorum flavus*), inside tubes attached to the host surface (e.g. the species of the genus *Procerastea*), attached to an external appendix (e.g. a parapodial cirrus in *Haplosyllis spongicola* as *H. cephalata*) or penetrating the host tissues (e.g. the body wall in *Asetocalamyzas laonicola* and *Parasitosyllis claparede*, the branchiae in *Calamyzas amphictenicola*, the fins in *Ichthyotomus sanguinarius*). *Branchiosyllis oculata* has been mentioned as living inside the canals of *Speciospongia vesparium* (Pearse 1932, Westinga & Hoetjes 1981), but has been more often found living (and feeding) on the external surface of the remaining sponge host species (see Table 6). It was found often embedded in a trench in the sponge ectosome (excavated by the setae), with their long dorsal cirri extending outward onto the sponge surface (Pawlik 1983). Moreover, *B. oculata* is morphologically adapted for dwelling on sponge surface and even takes on the colouring of some of its hosts. Thus, it can be considered a specialised ectoparasite.

RELATIONSHIPS BETWEEN HOST AND PARASITIC POLYCHAETE CHARACTERISTICS

It is commonly accepted, and is implicit in the definition of a parasitic relationship, that the parasitic organisms must be smaller than their hosts. Most parasitic associations involving polychaetes are so. However, some exceptions can be found within the oeonids. Some parasitic species are not smaller than their free-living relatives (e.g. *Notocirrus* spp., *Drilonereis* spp.), some other species are similarly sized or even larger than their hosts (Fig 16). In these cases, the species involved would probably be closer to a predator than to a real parasite. In the case of *Pholadiphila turnerae*, the fact that the mere presence of the large worm in the branchial cavity causes significant stress to the host, as it hinders water flow, was the basis for considering the relationship parasitic (Dean 1992).

The feeding activity of *Haplosyllis spongicola* apparently caused a decrease in the growth rate of host sponge *Verongula reisi* (Reiswig 1973). On the other hand, the *H. spongicola* population inhabiting another closely related host sponge, *Aplysina cauliformis*, was reproductively active at all times of the year, and was thus qualified as a "good" parasite (*sensu* Ricklefs 1990) by Tsurumi & Reiswig (1997). The same authors mentioned that there was no correlation between the timing of sexual reproduction in *H. spongicola* and *A. cauliformis*. However, because of its continuous grazing and removal of host biomass, the syllid certainly must have an impact, though of unknown significance, upon both sexual and asexual reproduction of the host sponge (Tsurumi & Reiswig 1997). In *Proceraea* sp., growth from late larva to juvenile is

accompanied by mouth and gut development but also by the disappearance of polyps from the infested hydrotheca. Moreover, juveniles from empty hydrothecae were observed inserting their heads into thecae openings from neighbouring polyps. Not surprisingly, pigment granules characteristic of the hydroid were observed in the polychaete intestine. All these observations strongly support that the polychaetes feed on the hydroid tissues, and so are real parasites (Britayev et al. unpubl.). As a consequence of the parasite's feeding activity that causes a significant reduction in the number of active polyps per colony, we suggest that considerable stress, affecting the overall well-being of the infested host, should be expected. A very close feeding habit was described for *Procerastea halleziana* living on the hydroid host *Tubularia indivisa*. The worm lives in hyaline tubes attached to the host branches and was observed to suck the contents of the gastro-vascular cavity of its host after piercing the basis of the hydroid polyps exteriorly (Caullery 1925). On the basis of this observation (and lack of specific information), we have considered all remaining species of *Procerastea* from hydroid hosts to be parasites (see [Table 6](#)).

ADAPTATIONS OF POLYCHAETES TO THE PARASITIC MODE OF LIFE

Morphological adaptations in parasitic polychaetes

As a general rule, endoparasites show a reduction or specialisation of locomotive appendages and mouth parts, and they are usually smaller than their free-living relatives (Clark 1956). However, endoparasitic polychaetes often undergo nothing but the most trivial changes. Unfortunately, several factors prevent the development of a satisfactory hypothesis: first, these parasites' rarity and second, the fact that we know practically nothing on their life-histories.

Reductions in the setal pattern of the endoparasitic oeononids ([Fig 18](#)) are seen in the species *Drilonereis benedicti* which has no emergent setae and in the two species of *Haematocleptes*, which possess several slender, distally pointed setae rather than the typical limbate setae of the oeononids. In *Drilogonathus capensis*, the setae are completely absent and only a single stout pointed aciculum, often projecting through the skin, is present on each parapodium. Moreover, study of the jaw apparatus of all endoparasitic oeononid species ([Fig 19](#)), shows that they tend to have smaller jaws. This tendency can be related to some extent to a more specialised parasitic mode of life. The mandibles are well-developed in the free-living oeononids, as well as in the parasitic *Notocirrus spiniferus*, *Arabella iricolor*, *A. endonata* and *Drilogonathus capensis*. Conversely, they are only small plates in *Labrorostratus*, *Haematocleptes* and *Oligonathus*, and are completely lacking in the parasitic species of *Drilonereis*. The free living oeononids, like the parasitic *Notocirrus* and *Arabella*, possess 5 pairs of well-developed maxillae whereas the parasitic *Drilonereis* possess 4. In the remaining parasitic genera, the maxillae consist of 3 pairs of unidentate hooks in *Oligonathus* while in *Drilogonathus*, *Labrorostratus* and *Haematocleptes* they are 2 pairs of small cuticular pieces. Free-living oeononids and both free-living and parasitic species of *Notocirrus* and *Drilonereis* possess a pair of long, slender maxillary carriers with a third carrier attached ventrally. The paired maxillary carriers show a different degree of fusion in *Labrorostratus* and *Haematocleptes* than in *Drilogonathus*, *Oligonathus* and the parasitic species of *Arabella*, with the third carrier retained in the former two genera and lost in the latter three. The maxillae and maxillary carriers of the single known species of *Drilogonathus*, *D. capensis*, were considered vestigial (Day 1960, 1967). However, they closely resembled those of the young *Notocirrus spiniferus* found living as parasite in *Diopatra cuprea*, which were considered incompletely developed (Pettibone 1957). Whether the jaw apparatus of *D. capensis* corresponds to a young developing specimen or to an adult with highly modified jaws is impossible to assess. However, the shape of the jaw apparatus and the size of the worm (3 mm long for only 60 segments) suggest that the single known specimen was not adult.

Besides the structural changes in the jaw apparatus that may be more or less subjectively related to a progressive adaptation to the endoparasitic mode of life, little is known on the possible sources of food for the endoparasitic oeononids and, thus, on the real significance of the above-mentioned smallness in jaws. Emerson (1974) mentioned that the *Diopatra ornata* females

harbouring *Arabella endonata* contained significantly fewer oocytes than the uninfested females. This author suggested that the gametes may represent the major food source for the later growth stages of the parasite, when it has a fully functional jaw apparatus and digestive tract, and that smaller or juvenile parasites lacking jaws could survive by either direct consumption of the coelomic fluid or absorption of dissolved nutrients from it. Moreover, gamete consumption by adults may also provide additional space within the coelomic cavity of the host for the parasites at the earlier stages.

Surprisingly, it is within the ectoparasitic polychaetes where we find the highest degree of structural and behavioural adaptations to their peculiar mode of life. An exception, however, are those temporary ectoparasites which are not at all modified, such as *Myrianida pinnigera* which feeds on the body fluids of ascidians, or the capitellids *Capitomastus lividus* and *Capitella ovincola* which parasitise the egg-masses of *Loligo* (Table 6).

The mouth parts of *Pholadiphila turnerae* are small, like those of the endoparasitic oeononids (Fig 19), with well-developed mandibles and 3 pairs of maxillar plates, which suggests reliance on the host for nutrition (Dean 1992). Although their maxillae are less modified than those of several endoparasitic oeononids, the slender, short (but not broad) maxillary carrier with indications of tripartite end (which strongly suggests fusion of the original priognat carrier) are believed to be the consequence of a parasitic lifestyle (Dean 1992). Possible food sources within the pholad mantle cavity may be the gill filaments, the mucous coat on these filaments or perhaps partly digested material within the pholad's food-storing caecum. The setal arrangement of *P. turnerae* is the same as in all oeononid species (free-living or endoparasitic). However, its acuminate setae and strong spines may be an adaptation to its parasitic mode of life, affording strong purchase against the body of its mollusc host. These setae are more highly developed than those seen in other parasitic oeononids, being more robust, more numerous and extending out much further from the parapodia which may be a consequence of the ectoparasitic habit of the species (Fig 18).

The ectoparasitic sphaerodorids of the species *Sphaerodorum flavus* feed on the epithelium of their host ophiuroids and, as its regeneration is not possible, they may even kill the hosts if the wounds are too big (Ockelman, personal communication). This association, together with that between *P. turnerae* and the pholadid mollusc and those of the temporary ectoparasites, are probably the simplest relationships developed by ectoparasitic polychaetes. Otherwise, there is a progressively increasing gradient in intimacy in host/parasite relationships.

Haplosyllis cephalata, which has been thought identical to *H. spongicola* (San Martín 1984), was found attached to a parapodial cirrus of the host eunicid, which had been swallowed and occupied most of the pharyngeal cavity of the parasite. However, no special modifications of the mouth, pharynx or pharyngeal cavity seem to be present in this species. *Asetocalamyzas laoncola* penetrates the body wall of the host terebellid using its large everted pharynx, which was distended after penetrating the host body (Tzetlin 1985), allowing the parasite to keep firmly attached to the host (Fig 20A). A more specialised pharynx can be found in *Parasitosyllis clapparede* (Potts 1912). The pharynx projects from the pharynx-sheath and resembles an elongated vase with a short stem, the rim of which is embedded in the host body while the stem communicates posteriorly with the proventriculum (Fig 20B). Except in this posterior region, the pharynx is enormously thickened and composed of at least four layers of chitin. Anteriorly, these chitinous layers run far into the host, bending round at right angles as they enter the host body. As they penetrate, these layers become thinner and thinner so that it is soon extremely difficult to distinguish between the tissues of parasite and host. The lumen of the pharynx is narrow anteriorly and there is a cushion muscle posteriorly. A narrow duct can be observed apparently communicating the pharynx with the proventriculum, which would serve for the passage of fluids absorbed from the host. The other known species of calamyzid, *Calamyzas amphictenicola*, possesses a buccal sucker and a specialised eversible pharynx with stylet-shaped sucker tube to penetrate the branchiae of its host ampharetid (Arwidsson 1932, Paris 1955, Fauvel 1959, Hartmann-Schröder 1971).

Certainly, the highest degree of specialisation occurs in the single known ichthyotomid species *Ichthyotomus sanguinarius* (Eisig 1906). Its peristomium, with the subterminal mouth, forms an oral cone that is capable of being protracted beyond the prostomium and retracted to form a cup-shaped oral sucker by which it fixes on the skin of the host fins (Fig 20C). The ventral cirri

have spinning glands opening at their tips, serving also to attach to the host. The muscular pharynx has a pair of articulating, scissorlike jaws, each formed by a distal spoonlike stylet provided with recurved teeth, a middle articulating joint and a bifurcated basal stem for muscle attachment (Fig 20D). When the oral cone is protracted, the stylets project from the opening, pierce the skin of the eel and attach firmly. In such a way, the worm cuts the blood capillaries of the host and uses its muscular pharynx to suck the host blood. The blood passes into dorsal and ventral haemophilic pharyngeal glands and into the gut, which is enlarged with diverticula extending into the parapodia. The modifications of this species are not only morphological but physiological. Effectively, like the mosquito, it has developed an anticoagulant to facilitate its feeding mode. Moreover, the circulatory apparatus and branchiae are absent. According to Eisig (1906), the fact that the eel's blood remains always liquid and constantly flows towards the gut diverticula may enable the tissues of the parasite to breathe.

Behavioural adaptations in parasitic polychaetes

Probably the only study reporting behavioural aspects of a parasitic polychaete is about *Branchiosyllis oculata* on different sponge hosts (Pawlik 1983) (Table 6). This author reported a series of data which define this species as a specialised parasite apparently well-adapted to living on the surface of its hosts. By means of a combined effect of parapodial muscular contractions and the claw-like hooks of the setae (Fig 20E), the worm may either keep itself firmly attached to the host tissues or advance across the sponge's surface. The long dorsal cirri appear to have a mechanosensory function. Touching the worm cirri produced a rapid reaction: a writhing backward motion (to dislodge setae) followed by a rapid forward advance. Hooked setae are also present in other parasitic syllids such as *Haplosyllis spongicola* (see Fig 11C) and the species of *Procerastea* (Figs 20F, 20G, 20H). Although *H. spongicola* may use its setae as *B. oculata* does (i.e. to move on and inside its host sponges), the species of *Procerastea* more probably use their setae to move back and forth along their tubes and to keep themselves attached to the branches of their host hydroids when feeding.

The colour of the gut contents and body of *B. oculata* on the sponges *Cinachyra alloclada*, *Speciospongia othella* and *Tedania ignis* was yellow, brownish-black and red, respectively, each the same colour as its sponge host. Worms from the remaining host species had uncoloured bodies with the gut contents varying from brown to grey. When transferring uncoloured worms to the red *T. ignis*, they were observed to have taken on red gut-contents a few hours after transplantation. This was considered a clear demonstration of the fact that the polychaete feeds on sponge tissue. In addition, transplanted autotomised worms regenerated their posterior setigers with pigmentation identical to that of *B. oculata* found on the surrogate sponges, while their anterior setigers did not show any detectable change in colour. This provided evidence that the polychaetes incorporate sponge pigments into their body tissues, although only the pigments of some species were incorporated. The worms having the same colour as the sponges they inhabit may have a distinct antipredatory advantage as the uncoloured worms were much more readily eaten by fishes under laboratory conditions.

Life-cycle and reproductive adaptations in parasitic polychaetes

It seems evident that a parasitic mode of life should lead to modifications in the life-cycle of parasites as they adapt to their particular mode of life. However, little is known on the developmental and reproductive cycles of parasitic polychaetes. In *Ichthyothomus sanguinarius* and *Calamyzas amphictenicola*, male and female individuals have been reported on the same host. The former has a hypertrophied genital apparatus (Eisig 1906), whereas the latter has aflagellate spermatozoa (Franzén 1982). There is not a clear relationship between the hypertrophy of the genital apparatus and the parasitic mode of life or the presence of heterosexual pairs. Conversely, the aflagellate spermatozoa have extremely low motility. In this case, the relationship of low motility

with male and female individuals always being found close together seems clear, as the spermatozoa do not need to swim to reach the eggs.

Fully mature specimens carrying eggs or sperm have not been reported for the solitary endoparasitic oeononids such as *Labrorostratus parasiticus*, while some specimens were reported as free-living among algae. On the basis of this slender evidence Caullery & Mesnil (1916) suggested that infestation took place when the parasites were extremely young, that adults left the host as they approached sexual maturity and that they spawned outside it. If this theory is general among solitary endoparasitic oeononids, it would explain the retention by some of them of characteristics of free-living species of the family (Clark 1956). According to this author, however, what is more inexplicable and puzzling than the lack of morphological specialisation, is how the endoparasitic habit was ever evolved in these worms, particularly if there is no substantial reduction in size.

Occasionally, however, the size of endoparasitic oeononids is much smaller than that of their hosts. In these cases, the existence of endoparasitic juvenile stages, very abundant in a single host, together with the presence of asexually reproductive adults inside the host body (Amaral 1977) suggest two different strategies of dispersion. In the first case, we may assume an adult free-living reproductive phase. Then, the initial infestation would be accomplished by larvae (probably pelagic), whereas the host infestation would progress as a result of successive cycles of asexual multiplication of the parasites inside it. The final step in the infestation would be the release of adults that would reach maturity as free-living forms. In the second case, we may assume an absence of the sexual reproductive phase. Although the infestation inside the host could progress the same as in the first strategy, the infestation of new hosts would be undertaken by direct migration of the stolons released from the first infested host after entirely consuming the available host resources. This second strategy involves a more contagious distribution of both host and parasite populations. In theory, the two strategies could coexist in the same species. The asexual phase would lead to the infestation of hosts from the same population while the sexual phase would allow the colonisation of new host populations. Unfortunately, the low incidence of these parasites and poor knowledge of their life-histories do not permit satisfactory general extrapolations.

In the case of the parasitic syllid *Proceraea* sp., a first approach to the initial infestation phases suggested that the infestation may occur through planktonic larvae reaching the colony and subsequently penetrating the hydrothecae. However, three different reasons lead Britayev et al. (unpubl.) to discard this strategy: 1) the penetration of the well-defended thecae by the delicate larvae of the worm seems very difficult, 2) that the larvae have no ciliary cover but a small apical tuft strongly suggests the absence of a pelagic larval phase, and 3) there is only one parasite per host hydrothecae. Therefore, these authors suggested that the female *Proceraea* sp. (*Sacconereis*) take care of their offspring by directly laying their eggs inside the hydrothecae. Thus, both a reliable shelter and fresh food are provided for the initial developmental stages of the parasite. This behaviour closely resembles that of the ichneumonid insects that lay their eggs inside the body of other insects and keep them alive to supply their larvae with fresh food. This, in turn, leads to the observed clustered distribution of commensals among the host colonies and also favours the presence of a high number of commensals infesting each host colony. Accordingly, swimming fertilised females are probably responsible for commensal dispersion from one host colony to another.

In *Branchiosyllis oculata*, the fact that adult worms removed from the host sponges had little capacity to relocate their original host or to locate a new sponge suggested that sponge selection and colonisation was carried out solely by larvae (possible swimming or crawling) (Pawlik 1983). However, all adults were morphologically identical and were able to survive after being experimentally relocated to different host sponges. Thus, it appeared unlikely that recruitable larvae were more specifically adapted to particular sponge species. The same author also pointed out that the differential densities on some host species (particularly high in *Tedania ignis*, intermediate in the coloured species and lower in the colourless species) may result from the combination of two factors: (1) differential recruitment as a result of simple differences of density or accessibility of the host species, or chemical cues and corresponding chemosensitive larvae; (2) differential mortality linked either to worms' colour mimicry, to physical (spicules) or chemical defences of hosts (whether these defences are transferable or not to the worms) or to the inaccessibility of the host to

the potential predators. Differences in infestation intensity within the polychromatic host *Tethya actinia* may indicate that whatever controls host pigmentation may also have a direct effect on *B. oculata* larval recruitment and/or adult survival.

From the two examples reported above, it seems clear enough that an accurate study of a given parasitic relationship (from an ecological, behavioural or even morphological point of view) provide pointers towards a reliable hypothesis on the life-cycle of the symbiont. However, unfortunately, these studies are few and far between.

SYMBIOTIC BORING POLYCHAETES

Usually, boring polychaetes did not show special adaptations other than those allowing them to bore into other organisms with more or less hard structures (mainly of a calcareous nature). The association between them and the bored organisms often appeared to be fortuitous, as the worms might be found boring either into living organisms or non-living substrates. 48 species of polychaetes, belonging to the families Spionidae, Sabellidae, and Cirratulidae have been reported as borers of other living marine organisms ([Tables 8](#) and [9](#)). Some interactions between these boring worms and their hosts, however, seemed to be negative, which lead to the species being labelled as “parasitic” borers. They are pests that drain the energy by causing the host to work harder to keep them away from the interior of the shell, but they are often uninterested in the hosts as such. The host suffers, but is not attacked directly: it just is stressed by a mud-eating worms that are “looking for a home”. This may reflect an old-fashioned view of a “parasitic” association. Hence, although we decided to mention these associations in the present review, we realised that some of the cannot be certainly considered as a real symbionts and, thus, they have been included them in the present specific section. In other cases, there were either no negative interactions described or the nature of the interactions was assessed by behavioural observations and some benefits were suggested or even demonstrated, enabling classification of the worms as “commensal” borers. There are a few quantitative studies on infestations by boring polychaetes: the known data on intensities and prevalences re summarised in [Table 10](#). The two types of interactions involving boring polychaetes (i.e. parasitic and commensalistic) will be reviewed in the following three sections.

Parasitic boring polychaetes

The most common parasitic boring polychaetes are, certainly, the spionids ([Table 8](#)). Among them, the species of *Polydora* and related genera are the only one able to bore (Blake 1969, 1980, 1996, Blake & Evans 1973). However, little is known concerning the initial steps of their establishment in the calcareous habitats (but see Hopkins 1958), and the physical (linked to the modified setae of the 5th setiger) or chemical (a not-yet identified acidic substance) mechanisms of burrow expansion are still a matter of controversy (Haigler 1969, Blake & Evans 1973, Zottoli & Carriker 1974, Sato-Okoshi & Okoshi 1993).

We also know little about how the polydorids interact with their hosts and most polydorids that live in molluscs do not really harm their hosts. However, other worms may make different kinds of burrows (viz. U-shaped, branched, cylindrical) ([Fig 21](#)), which may be lined with a variety of parchment-like secretions or with mud or sand grains. When reaching the inner walls of the shells, however, this boring activity often leads the mollusc hosts to react by producing “mud-blisters”, probably the most damaging effect of polydorids. The mud-blisters are masses of mud accumulated on the inner surface of the shell by the recently settled worms ([Figs 21D, 21E](#)). The hosts react by first secreting over the mud a roof of conchiolin and then a layer of nacreous material. The mud-filled chambers formed are occupied by the worms which communicate with the exterior *via* pairs of tubes either at or close to the periphery of the shell. Although it is difficult to evaluate the expenditure of metabolic energy linked to this extraordinary secretion of protective layers (and,

thus, to determine to what extent the life of the mollusc might be affected), the mollusc host may suffer a certain degree of distress (Kent 1979). Additionally, mud-blisters may be so numerous that they lead to the hosts' death. In fact, all this boring activity weakens the shells (Kent 1981) and so makes them less resistant to diseases, other parasites and predators.

The presence of blisters was also reported on the hydrocoral *Allopora californica*. In this case, however, the blisters were formed by the syllid *Autolytus penetrans*, which apparently penetrated the surface of the host resulting in a hyperplasia of cellular and calcareous material (Wright & Woodward 1977). However, *A. penetrans* does not actually bore. Although its blisters closely resemble those of the polydorids, they were lined with cells instead of mud. In spite of blisters, there were no indications of any other damage to the coral linked to the presence of the syllid. Therefore, *A. penetrans* was not originally described as parasite. However, two points allowed us to include this relationship among parasitisms (see [Table 6](#)): (a) no apparent profits were reported for the host and (b) the behaviour of the symbiont closely resembles that of a cysticole parasite.

The boring polydorids have been often considered as parasitic organisms from an anthropogenic rather than ecological point of view. As soon as they infest species of molluscs that are cultivated or harvested as a fishery resource (viz. mussels, pearl oysters, edible oysters, scallops), they are immediately viewed as pests (e.g. Haswell 1885, Houlbert & Galaine 1916, Lunz 1940, 1941, Korrington 1951, Landers 1967, Blake & Evans 1973, Tkachuk 1988). However, the polydorids may, although rarely, cause the demise of the cultivated host populations so affect commercial profit. A decrease of mollusc growth-rates linked to the presence of polydorid species has seldom been reported (but see Imajima & Sato 1984 and Mori et al. 1985). However, they may damage the appearance of the shell, making it less attractive to potential consumers and so lowering the market value of the mollusc. In most cases, the shell damage caused by boring species may be linked to their gregarious habits, leading to the presence of large numbers of individuals on the same host ([Table 10](#)).

The boring polydorids may also inhabit other organisms with calcareous structures. In some cases, the interactions with their hosts (e.g. cirriped crustaceans, serpulid polychaetes) closely resembles the interactions established with molluscs ([Table 9](#)). They simply bore into the calcareous parts of these hosts and no further information about the interactions between host and polydorids is available (Radashevsky 1993). Similarly, *Polydora armata* was reported as symbiont with the madreporid *Leptastrea purpurea* by Okuda (1937), but there was no additional information. *Polydora alloporeis* inhabits deep burrows in the coenosteum of the hydrocoral *Allopora californica*, forming large colonies without apparently damaging the host (Light 1970a). Each *P. alloporeis* burrow has two distinctive openings and the worms may be seen in living material with the palpi projecting from one of the openings and the pygidium just visible below the lip of the other.

Probably the most remarkable associations with non-mollusc hosts are, however, those between *Polydora armata* and *P. hoplura* and the bryozoans *Holoporella sardonica*, *Porella concina*, *Schizoporella armata* and *S. auriculata* (Laubier 1958, 1959). The bryozoans are infested throughout their basallayer (usually dead) fixed to the substratum, the worms entering the colony using the existing crevices or breaks. In *H. sardonica*, *P. armata* excavates a dense complex of galleries, some of them reaching the outer surface of the colony. At the beginning, the openings are only made of silt and mucus. Then, the bryozoan builds a thin calcareous layer (about 2 mm high and 0.25 mm in diameter) surrounding the worm tubes ([Fig 22A](#)). In *P. concina*, the initial infestation steps are the same, but there is no trace of galleries inside the colony. The special structures surrounding the polychaete tubes are, in this case, composed of host zooids ([Fig 22B](#)). The tube heights are similar but wider (about 1 mm wide). At the end of these formations, a thin calcareous zone (probably a growing zone) resembles that in *H. sardonica* ([Figs 22A, 22B](#)). In *S. armata* the two types of calcareous formations (with and without zooids) may be found. *Polydora hoplura* was only found infesting *Schizoporella auriculata*. In this case, the calcareous formations surrounding the worm tubes are made of zooids, reaching about 6 mm high. The formations are conical with 4-5 mm at the basis and 0.5-1 mm at the top. A thin calcareous layer of no more than 0.1 mm forms the border of the cones. The infestation of the bryozoan colonies by the polydorids

occurs in two phases. The first one (initial penetration of the colonies) does not differ from the normal excavating habits of the species. The second phase is characterised by a stimulation of the bryozoan to build the calcareous formations. These two points strongly suggest that these relationships may be considered specific parasitisms (closer to cysticole behaviour). Besides that, we may speculate on a possible cleaning behaviour of the worm, which could benefit the host and so lead to reallocate these relationships between the commensalisms (see *Polydora glycymerica* and *Dipolydora rogeri* on the next section).

Parasitic polydorids were also reported from non-calcareous organisms ([Table 9](#)). *Polydora cornuta* forms cysts in the eelgrass *Zostera marina* (Michaelis 1978). Any sponge with a substantial, firm body appears to be a suitable habitat for the hermaphroditic species *Boccardia androgyna* (Read 1975). The worm inhabits U-shaped mud-lined tubes within the sponges and a large mud-filled cavity may be formed if the sponge species has soft tissue with little spongine material. Finally, *Polydora wobberi* causes structural damage to the colony of the gorgonian *Lophogorgia* sp. (Light 1970b). The worm lives in U-shaped burrows along short branches which arise from the bases of the coelenterate colonies. The burrows open to the exterior at the tips of short stubby branches of the gorgonian which are about 20-30 cm in length (the longer uninfested branches may reach 70 cm in length). The final result is that the woody central stems of the gorgonian are entirely missing in infested branches. However, it seems not to seriously affect the overall well-being of the host.

A situation similar to that of the shell-boring polydorids was described for the sabellids *Pseudopotamilla reniformis* boring in *Placopecten magellanicus* (Blake 1969) and *Pseudofabricia* sp. in *Haliotis rufescens* (Oakes & Fields 1996). *P. reniformis* inhabits large ridges on the inside of the shell, which appear to be the response of the scallop to occasional penetration of the inside of the shell by the worm. The inside of the ridges is filled by mud and worm tubes. The large size of *P. reniformis* and the possibility of high infestation intensities ([Table 10](#)) qualifies this worm as a potential menace to the scallop. The very small specimens of *Pseudofabricia* sp. form cylindrical burrows at the outer part of the abalone shell's edge. As the result of their activity, the shell becomes very weak and porous, which prevents the abalone from enlarging its shell horizontally. Even a heavy infestation by *Pseudofabricia* sp. is generally not life-threatening for the host. It is, however, a very serious problem for the commercial exploitation of abalones, significantly decreasing their growth rate and hence causing additional costs and reducing profits.

The species of the fresh-water caobangid polychaetes (reviewed by Jones 1974), which are currently included within the family Sabellidae (Fitzhugh 1989, Fauchald & Rouse 1997) are exclusive inhabitants of mollusc shells ([Table 9](#)). Little is known of the life-history of the *Caobangia* species since most of them are known only from dried specimens in museums. The worms bore into shells of both gastropods and bivalve molluscs in Asian rivers. The adult burrows are restricted to the collumellar area of the snails (i.e. the thicker calcareous region of the shell), although encapsulated metamorphosing larvae were encountered all over the shell. The bore holes, mainly located in the apex of the snail shell, weaken this portion, which causes a truncated profile ([Figs 23A, 23B](#)). The burrows, lined with a thin secreted membrane, never connect with one another and are teardrop-shaped. In the case of boring bivalve shells, the worms were distributed throughout the available surface.

Cirratulids of the genus *Dodecaceria* are well-known boring polychaetes ([Table 9](#)). Although some of them may be pests in bivalves of commercial value such as *Placopecten magellanicus*, they are not particularly specific (or, perhaps, not specific at all). They bore into virtually any kind of calcareous substrata (e.g. live or dead mollusc or barnacle shells, encrusting coralline algae) without showing any apparent preference for a given species. Moreover, some species of this genus cannot be considered as strict borers. *D. fewkesi*, for example, forms its own free tubes, whereas *D. concharum* also occurs as a cryptofaunal nestler (i.e. it is commonly found between the internal ribs of dead barnacle shells in *Laminaria* holdfasts and occurs in protected cracks and crevices in shells). *D. concharum* may also be able to build a tube of sorts, but it seems that it is more probably creating just a smooth lining in already built burrows. In fact, Evans (1969) found North American populations of *D. concharum* to be "a secondary borer (i.e. occupying and adapting vacant burrows of primary borers, but unable to make a burrow of its own), whereas

Gibson & Clark (1976: 659) found that “in the laboratory ... adults or asexually produced individuals of *D. caulleryi* [= *D. concharum*] fail to make burrows in pieces of smooth rock or smooth *Lithothamnion*. Small holes made in the surface with a needle were sometimes temporarily occupied but a definitive burrow was never made in them”. Moreover, it was pointed out that worms in a dish with detritus will make a kind of tube and secrete a calcium layer sticking it together and corresponding to the lining of the tube (Gibson & Clark 1976, M.E. Petersen personal communication). In fact, the impact of borers or nestlers with some boring ability such as the species of *Dodecaceria*, would probably be higher on molluscs with exposed shells (e.g. scallops or oysters) than on those which are normally buried in the substratum (e.g. *Arctica islandica*). It should be mentioned that, in Danish waters, *D. concharum* occurs in shells of *A. islandica* previously excavated by the sponges of the genus *Cliona*. Usually, these are shells of dead molluscs, but probably *D. concharum* also occurs in live ones, if they are not buried in the sediment and have been attacked by *Cliona* spp. first (M. E. Petersen personal communication). However, this association has not been attributed to a worm / sponge symbiosis, but to the fact that shells that are older and partly decalcified by the sponge (i.e. “softer”) are probably easier to excavate than fresh ones. The behaviour of some *Dodecaceria* species as “secondary borers” may also contribute to explain their occurrence on sponge-excavated calcareous substrates. In the Mediterranean, specimens of *Dodecaceria* sp. have also been observed inhabiting calcareous substrates (i.e. encrusting coralline algae) previously excavated by *Cliona viridis* (D. Martin personal observations).

COMMENSAL BORING POLYCHAETES

One of the best known commensal borers is the spionid *Polydora commensalis*, which bores into snail shells occupied by numerous species of hermit-crabs ([Table 9](#)). Studies on its boring activity revealed that larvae mainly settle on the inner surface of the shells near the outer edge (Radashevsky 1989). Growing worms relocate themselves on the columella, enlarging their tubes along the columella toward the shell apex. As a consequence, all tube openings of *P. commensalis* are located along the columellar side (near the inner lip) of the opening of the shell occupied by the host hermit crabs. Occasionally, the worms excavate shallow channels along the columella, and some tubes can be found in the umbilicus of the shell. The tubes of large gravid females may even reach the top of the columella. The tubes are coiled within the sediment that fills the apex of the infested shell. Occasionally, the worm tubes are covered by a thin arched calcareous “roof” of unknown origin, covering the galleries on the inner surface of the hermit host’s shell (Radashevsky 1989). Each host shell is usually inhabited by one large female and several smaller males and juveniles, whose tube openings are characteristically non-visible externally. Besides that, simultaneous hermaphroditism has also been reported for *P. commensalis* and, in the case of death of the female, the remaining largest individual becomes a female (Radashevsky 1989). The worms have been observed feeding either by removing suspended particles from the branchial (respiratory) current of the hermit crabs or by removing particles attached to the setae on the legs of the hermit crabs (Dauer 1991). When feeding as suspension feeders, worms held the frontal surface of their palps directly in the branchial current of the crab, and constantly contacted the legs of its host with the abfrontal and lateral surfaces of the palps (which are very short).

Polydora glycymerica may be also considered as a specialised commensal borer (Radashevsky 1993). The inner walls of the long and wide U-shaped burrow are lined with silt, its two openings being located at the posterior end of the shell, in the region of the mollusc siphons. This position is closely related to the feeding mode: projecting out of the burrow, the worms expose their palps and catch suspended particles from the water current produced by the mollusc. Similar behaviour may be assumed for *Boccardia acus*, whose burrows are also U-shaped and usually follow the curve of the host’s shell growth lines. The borings are not lined with sand apart from a sand-grain partition at the short, U-shaped external chimneys. As the host cockle lies buried just beneath the sediment surface, the worm extends out through the external chimneys around the bivalve siphons (Read 1975). This is the easiest way to contact with the water column just over the

sediment, but also the closeness of the siphons may allow the worm to feed on the water current produced by the host.

A particularly curious relationship occurs between *Polydora rogeri* and the boring sponge *Cliona celata* (Martin 1996). Both organisms bore into calcareous algae, but the sponge may develop at different growth stages, progressively overgrowing the calcareous excavated substrate (Rosell & Uriz 1991). At the papillate stage of growth, only the papillae of the sponge protrude from the calcareous substrate and the tops of the polychaete tubes were observed protruding from the surface of the algae. The external part of the polydorid tube was formed by fine sediment grains embedded in an organic matrix, whereas the linear internal parts were only formed by the organic matrix. Internal tubes passed through the calcareous algae and the sponge body (choanosome) until an appropriate portion of an aquiferous canal of the sponge was reached. Then, the tubes disappeared, being replaced by the sponge canals (Figs 24A, 24B). In encrusting and massive sponge specimens with almost no trace of visible calcareous substrate within the sponge surface, the anterior ends of the polychaete tubes were also observed directly protruding from the sponge surface. The polychaetes tend to place the openings of their tubes near the inhalant papillae of the sponge. Thus, their feeding activity can be favoured by the inhalant flow originated by the filtering activity of the host. Moreover, the sponge offers physical protection to the worm when the calcareous algae have completely disappeared (i.e. massive stage). The ability of the polychaetes to manipulate relatively large particles (either to feed or to build its tubes) may favour the filtering activity of the sponge by cleaning the area around the inhalant papillae, thus preventing the collapse of their orifices. Moreover, the polychaetes do not disturb the normal progress of the host through successive growth stages and the aquiferous canal occupied by the polydorid does not collapse. If the canal belongs to the exhalant system, water flow would contribute to the discharge of worm faeces, while faeces **would** be used as food by the sponge if the canal belongs to the inhalant system. In light of the above, the association between *P. rogeri* and *C. viridis* was tentatively considered as a mutualism (Martin 1996).

SPECIFICITY IN THE SYMBIOTIC RELATIONSHIPS INVOLVING BORING POLYCHAETES

The analysis of the available data (Tables 8 and 9) on the specificity of the relationships between boring polychaetes and their hosts seems to display a generic monoxenous pattern. About 37% of the polychaetes infest a single host species, this figure becoming 63% if borers infesting 2 or 3 host species are included. It must be pointed out, however, that some species are reported on 10 to 19 different hosts and are, thus, clearly polyxenous. On the other hand, studies enabling the exact degree of specificity to be assessed are virtually lacking, although stimulating (but inconclusive) hypotheses may be found throughout the literature. It should be taken into account that more than half (53%) parasitic boring polychaetes are facultative symbionts, boring also into non-living substrata (Tables 8 and 9). Often, the appraisal of their interactions is tentative, as in the case of defining caobangids s parasites. There are no studies on the possible costs to the hosts arising from the infestation of these worms (other than the weakening of the shell); additionally, only one species of *Caobangia* was reported on a single host (probably the single specimen known), while the remaining were reported on 2 to 9 different hosts (Table 8). In fact, in the rivers, snails and bivalves are the most common and, often, the only available sources of calcareous substrates for these worms. However, the caobangids have also been found boring into empty shells of dead molluscs. Although there are no real observations, it was assumed that they might bore into non-living substrates such as calcareous limestone outcrops which, it was though, could serve as population reservoirs allowing the infestation of new molluscs.

Among "parasitic" *Polydora* species, there are a few observations suggesting a certain degree of specificity in the relationships with their hosts. Ramberg & Schram (1982) observed that the shells of the gastropod *Littorina littorea* smaller than 10 mm were never infested by *P. ciliata*. As the gastropod host did not become mature until it reached this size, it was suggested that larvae of *Polydora ciliata* may be guided to the snail by some substance which the snails secrete into the water. However, this was not supported by data. The existence of chemical cues in the interaction

between the polydorids infesting bryozoans was suggested by Laubier (1959) on the basis of two facts: i) the worm seems to control the height of the calcareous formations induced in the host colony, this height being always the same (on average); ii) even in colonies where the polydorids can not be currently found, the calcareous formations remain open, the bryozoan apparently being unable to close them. Finally, the special configuration of the prostomium (markedly projected forward), the presence of interbranchial septa and the reduced pygidium led Light (1970b) to suggest that *Polydora wobberi* could be a highly specialised parasitic borer.

Within the commensal boring polychaetes, little is known about the specificity of the relationships. *Polydora commensalis*, for example, is known to be associated with as many as 9 different species of hermit crabs (Table 9). This is habitually related to a lack of specificity. However, adult *P. commensalis* have never been found free-living and, although it was demonstrated that the species can be experimentally induced to burrow in shells that can never be occupied by hermit crabs (i.e. bivalve shells) this has never been reported in natural conditions. Conversely, the association of *Polydora glycymeris* and the burrowing bivalve *Glycymeris yessoensis* may be considered as a rare example of a high degree of specificity within commensal boring polydorids. Despite the intensive research carried out on this species, it was always found in the shells of *G. yessoensis*, with the exception of a very few localised cases where it was boring into the shell of another clam, *Anadara broughtoni* (Radashevsky 1989).

Food availability, sheltering or avoidance of stagnation were suggested as factors cementing the relationship between *Polydora commensalis* and the host hermit crabs (Hatfield 1965). When the host leaves an infested shell, the worms then have nutrient granules in the stomach wall to ensure their survival. Although these absences are necessarily temporary, they imply that the shell could be re-occupied by a different host individual or even by a different hermit crab species. Since the polydorids are, in principle, sedentary, and their feeding mode always incurs the added risk of being attacked by the host, we may assume that the crabs are able to recognise the worms as associates, such as in other polychaetes commensal with hermit crabs (e.g. *Nereis fucata*, Gilpin-Brown 1969). There are no studies on this particular aspect of the relationship, but some very interesting questions arise from the possibility of a chemically mediated recognition: Are the possible hosts “genetically” adapted to recognise the presence of the symbionts? Have the symbionts developed behavioural adaptations to solve the problem of host exchange (e.g. a delay in the start of feeding activity at the beginning of each new host occupancy, till the recognition of the commensal and the “permission” to feed)? Is the behaviour of the symbiont the same, independently of the re-occupation of the shell by the same or a different host species? Additional questions re posed by the fact that shells covered by the hydroid *Hydractinia echinata* were more heavily infested by *P. commensalis* (Andrews 1891a, b): May the hydroid be a third associated symbiont? How could the presence of the hydroid favour that of the worm? All these questions remain open, making the symbiotic relationships involving *P. commensalis* a very interesting subject for further research.

The relationship between *Polydora rogeri* and its host sponge *Cliona viridis* was considered endemic to the NW Mediterranean, as it was only known from the type locality (Martin 1996). *C. viridis* is a widely distributed species (Rosell & Uriz 1991, Rosell 1996) but the presence of its associated worm had not been previously reported. On the other hand, *Polydora armata*, the species most closely resembling *P. rogeri*, is a cosmopolitan polydorid which was reported to bore in calcareous algae from the same area in the NW Mediterranean. These algae were, however, non-excavated by *C. viridis* (Martin 1987). The behaviour of *P. rogeri* inhabiting calcareous algae excavated by papillate specimens of *C. viridis* appears not to differ greatly from that of other coralline-boring species of *Polydora*. The main difference, and indeed that characterising the association and supporting its specificity, is that the symbiotic association is still maintained when the sponge progresses to the encrusting and massive stages, with almost no trace of visible calcareous matrix. The association between *P. rogeri* and *C. viridis* has only been considered from a descriptive point of view, based on dead specimens. Further morphological and experimental studies are required before its exact nature may be assessed. Morphological aspects that might be addressed are, for example, both the cellular organisation and the aquiferous system structure of the sponge around the worm tubes. Experiments could also usefully analyse the substratum

preferences (excavated calcareous algae versus others) during larval settlement of polychaetes, or assess the possible differences in growth rates (from alpha to gamma stages) of infested and non-infested sponges.

THE WAY FORWARD

Over the last forty years, the information on symbiotic polychaetes has grown enormously. This review has attempted to give an overview of the current state of knowledge. What is clear, from this review, is that the relationships involving symbiotic polychaetes are often remarkably complex and this may be true no matter the approach we use to analyse them (i.e. taxonomical, biological, physiological, ecological, behavioural). Our understanding of the interactions between the symbiotic polychaetes and their hosts is still pitifully inadequate. In this final section, therefore, we shall conclude by suggesting avenues of further research which, in the next few years, could help to redress this shortfall.

One of the most troublesome facts dealing with many symbiotic polychaetes is their rarity. We cannot change this and, unfortunately, we will still leave the acquisition of new information on many species (either already known or not yet described) to chance. This may be the case of the parasitic oeonids, which are known, for the most part, only from the original descriptions. In fact, there are many interesting hypothesis arising from the comparison of all trends that characterise each known relationship involving the parasitic oeonids. These hypotheses are necessarily open and cannot be convincingly refuted or validated if no new data on the relationships are reported. However, a few additional information, more than a single mention, may provide relevant data. The host-specificity (i.e. it always infests syllids) characterising *Labrorostratus parasiticus* may be a good example.

The rarity of parasites also difficulties the evaluation of their role in natural communities. We may expect, however, that changes in the environmental conditions affecting a given community would lead to an increase of the number of parasites, so that they would significantly affect the natural "economy" of biocoenosis. In fact, symbionts has been often regarded as "curiosities of the nature", but the few known studies on the biology and behavioural trends of some target species clearly demonstrated their significance in the economy of marine communities (e.g. cleaners such as *Histiobdella homari* or *Arctonoe vittata*, defenders such as *Arctonoe vittata* or *Spirobranchus giganteus*). A different concept of "economy" comes from an anthropomorphic point of view. In this case, the species boring on shells of commercially exploited organisms may play a relevant role. Although these species are common in "healthy" cultures, the possibility of unpredictable outbreaks of their number, followed by harming commercial farms, might not be excluded (e.g. the undescribed boring sabellid in Oakes & Fields 1996). Besides that, the impact of borers on their host populations may significantly contribute to regulate the number of the latter, subsequently leading to community perturbations.

Most symbiotic polychaetes are known from dead specimens and their quality of symbionts has been either proposed after directly finding them on their respective hosts or inferred from some widely accepted "symbiotic attributes". As a consequence, we often know little about the nature of most associations. Although, in practice, it is difficult to obtain unequivocal demonstrations of all factors affecting a given interaction, the few known examples of symbiotic associations whose nature has been studied in deep revealed a more complex network of relationships than expected, these associations being apparently more bi-directional than unidirectional (e.g. Dimock & Dimock 1969, Wargner et al. 1979, Britayev 1991, Radashevsky 1993, Martin 1996). A significant step forward would be, therefore, to look at the nature of the associations on the basis of direct observations of living organisms (i.e. *in situ* or under experimentally controlled situations). This approach may provide information, for example, on host/symbiont colour matching. In fact, the source of this colour matching is also a matter of controversy by itself. Whether a symbiont acquire its host's colour by feeding on the host or as a response to any stimuli coming from the host will substantially contribute to make a decision on the exact nature of a given association. A closely related matter of study, which is also relevant to assess the nature of a given association may be,

thus, the type of trophic relationship established between a host and its symbiont(s). We may also pinpoint that, often, a symbiont is not alone on its host. A very interesting direction for further research will be, thus, to study the interactions (i.e. competition, predator-prey) between different symbionts (i.e. from the same or from different species) co-inhabiting on the same host individual (i.e. the association as a "microcosm"). A major problem may be that, often, it is difficult to obtain enough living partners to undertake experimental essays, but also, that the experimentally observed trends must be completed with the inference of their functional role in natural symbiotic populations.

Today, biologists have a number of new and interesting tools at their disposal and new and exciting techniques are being developed continually (in particular, we are all aware of the potential of electron microscopy or molecular biology). It is certain that such tools and techniques will be employed to great benefit in the area of polychaete symbiotic relationships. These approaches should not, however, be pursued to the exclusion of more established techniques because these still have a valuable contribution to make. Faunistic and systematic studies based on classical morphological characters are still fundamental in localising and describing new associations. The elegant review on symbiotic polynoids by Pettibone (1993) may be a good example of this. Moreover, it should be taken into account that remote areas, such as bathyal bottoms (e.g. Kirkegaard & Billet 1980, Martin et al. 1982, Emson et al. 1993), cold-seep sites (e.g. Miura 1988, Miura & Laubier 1990) or hydrothermal vents (e.g. Pettibone 1984a, b, Miura & Hashimoto 1991, Miura & Ohta 1991) are becoming more and more accessible to scientists. The limiting conditions of these environments are probably connected with the diversity of new symbiotic associations found there. The functionality of these associations, as well as the development of both host and symbiont life-cycles, are interesting fields still open to further research.

Although the polychaetes are probably one of the most widely studied group of marine benthic organisms, the basic information on descriptive ecology (e.g. spatial distribution, bathymetric distribution, seasonality, population structure and dynamics) is still lacking for most known symbiotic polychaetes and, consequently, for the ecological unit formed by the host/symbiont partnership. Symbiotic associations involving polychaetes may serve as useful models to study biological interactions among marine organisms. The associations could be analysed as elementary "biocoenosis", which included a reduced number of species and relationships. In that way, the biotic interactions (intra- and interspecific) could be studied and analysed with a less expenses. Moreover, symbiotic associations are "natural" sample units to study distribution patterns (Palmer, 1968). As all (or, at least, most) commensals are found on the hosts, each host is the basic habitat unit for a given commensal. Therefore, changes or variations in the commensal's distribution are likely to be of ecological interest. The symbionts may serve as a convenient model of distribution, being then possible to generalise on the basis of the main trends described from the association.

Finally, despite several examples where chemically mediated host-symbiont relationships are known to exist because behavioural responses of both partners have been demonstrated, there are no-one where any details of their chemical nature are understood. In this respect, polychaete physiology lags behind that of almost all other invertebrate groups. The habitat restrictions imposed to a symbiont by its intimate association with its host is probably at the basis of most suggested roles of chemical cues in symbiotic associations. The first, classical role is the host-recognition behaviour by adult symbiotic polychaetes, which is involved in the specificity of the response of the symbionts to their hosts. The few studies on this subject are now considered as classic papers but, in fact, the origin of the host-factors, its chemical nature, the way of reaching the symbiont and how the symbionts detect them are basically unknown for most symbiotic associations involving polychaetes. Among other roles, chemical cues may be also involved in: 1) location of host during larval settlement, 2) sex-specific recognition when heterosexual pairs of symbiont inhabit the same host individual, 3) hosts' reproduction triggering symbionts' reproduction, and 4) symbiont recognition by hosts. Molecular tools such as the biochemical and chromatographic techniques, which are employed in purification and structural analysis of chemicals have advanced significantly, so the identification of the substance (or substances) involved in the maintaining and regulation of symbiotic associations are today easier than ever. Chemical characterisation of cues may be a way to clarify the different patterns of symbiont specificity (i.e. if the host shared or

differed in the nature of the attractants). But we cannot forget the possibility of hidden sibling species-complex, being involved in non-specific relationships. Once the existence of this problem has been demonstrated is the way then open for analysis using a variety of modern techniques. Fine morphological studies using electron microscopy, molecular techniques such as protein electrophoresis and RNA/DNA sequencing may provide answers to questions on sibling species involved in symbiotic associations.

Certainly, we are not providing a complete list of shortcomings connected with the study of symbiotic associations involving polychaetes in this necessarily brief, conclusive section. A good final epilogue would probably be that, no matter the scientific field used to approach the symbiotic polychaetes, there are so many open questions that the efforts devoted will be always rewarded.

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REFERENCES

- Abelló, P. 1985. *Iphitime cuenoti* (Polychaeta: Iphitimidae), commensale des crabes en Méditerranée. *Rapports de la Commission Internationale pour l'Exploration de la Mer Méditerranéenne* **29**, 5 only.
- Abelló, P., Sardá, R. & Masalles, D. 1988. Infestation of some Mediterranean Brachyuran crabs by the Polychaete *Iphitime cuenoti*. *Cahiers de Biologie Marine* **29**, 149-162.
- Abelló, P., Villanueva, R. & Gili, J.M. 1990. Epibiosis in deep-sea crab populations as indicator of biological and behavioural characteristics of the host. *Journal of the Marine biological Association of the United Kingdom* **70**, 687-695.
- Achari, G.P. Kumaraswamy 1974[1977]. On the polychaete *Gattyana deludens* Fauvel Associated with the hermit crab *Diogenes diogenes* Herbst and *D. custos* Fabricius. *Journal of the Marine Biological Association of India* **16**, 839-843.
- Addicot, J.F. 1984. Mutualistic interactions in population and community processes. In *A new ecology. Novel approaches to interactive systems*, P.W. Preece, C.N. Slobodchikoff & W.S. Gaud (eds.), New York: Willey-Interscience Publ. (John Willey and Sons), pp. 438-453.
- Ajeska, R.A. & Nybakken, J. 1976. On *Halosydna brevisetosa* commensal with *Melibe leonina*?? *The Veliger* **19**, 19-26.
- Al-Ogily, S.M. & Knight-Jones, E.W. 1981. *Circeis paguri* the spirorbid Polychaete associated with the hermit crab *Eupagurus bernhardus*. *Journal of the Marine biological Association of the United Kingdom* **61**, 821-826.
- Allen, E.J. 1915. Polychaeta of Plymouth and the South Devon coast including a list of the Archiannelida. *Journal of the Marine biological Association of the United Kingdom* **10**, 592-646.
- Allen, E.J. 1921. Regeneration and reproduction of the syllid *Procerastea*. *Philosophical Transactions of the Royal Society of London* **211**, 131-177.
- Allen, M.J. 1952. An example of Parasitism among Polychaetes. *Nature* **169**, 197 only.
- Alós, C. 1988. Anélidos poliquetos de Cabo de Creus (Alt Empordà). Doctoral Thesis, Universitat de Barcelona.
- Alós, C. 1989. Adiciones a la fauna de Anélidos Poliquetos de la península Ibérica: familia Syllidae. *Cahiers de Biologie Marine* **30**, 329-337.
- Alós, C., Campoy, A. & Pereira, F. 1982. Contribución al conocimiento de los Anélidos Poliquetos endobiontes de Esponjas. *Actas Simposium Ibérico de Estudio del Bentos Marino* **3**, 139-159.
- Alvà, V. & Jangoux, M. 1989. Sur les symbioses entre Polychètes et Ophiures avec la description d'un nouveau cas de commensalisme. In *Echinodermes: Actuels et Fossiles. Actes du VIe Séminaire International sur les Echinodermes*, M.B. Régis, A. Segui, C. Frasson, P. Escoubet & A. Riva (eds.), Aix-Marseille III: CERAM; Faculté des Sciences et Techniques de Saint-Jérôme; Foundation Océanographique Ricard, pp. 185-192.
- Amaral, A.C.Z. 1977. Um poliqueto endoparasita, *Labrorostratus prolificus* sp. nov. em Nereídeo. *Boletim do Instituto Oceanográfico, Sao Paulo* **26**, 285-292.
- Amoureux, L., Josef, G. & O'Connor, B. 1980. Annélides Polychètes de l'éponge *Fasciospongia cavernosa* Schmidt. *Cahiers de Biologie Marine* **21**, 387-392.
- Andrews, E.A. 1891a. A commensal annelid. *American Naturalist* **24**, 25-35.
- Andrews, E.A. 1891b. Report upon the Annelida Polychaeta of Beaufort, North Carolina. *Proceedings of the United States National Museum* **14**, 277-302.
- Arvanitidis, C. & Koukouras, A. 1994. Polychaete fauna associated with the coral *Cladocora caespitosa* (L.) in the eastern Mediterranean. *Mémoires du Muséum national d'Histoire natural (zoologie), Paris* **162**, 347-353.
- Arwidsson, I. 1933. *Calamyzas amphictenicola*, ein ektoparasitischer Verwandter der Sylliden. *Zoologiska Bidrag fran Uppsala* **14**, 153-218.
- Augener, H. 1914. Polychaeta II, Sedentaria. *Fauna Südwest-Australia* **5**, 1-170.
- Augener, H. 1922. Results of Dr. E. Mjöberg's Swedish scientific expeditions to Australia 1910-13. 33. Polychaeten. *Kungliga Svenska vetenskapsakademiens handlinga* **63**, 1-49.
- Bacescu, M. 1971. Les Spongiaires: un des plus intéressants biotopes benthiques marins. *Rapports de la Commission Internationale pour l'Exploration de la Mer Méditerranéenne* **20**, 239-241.
- Bailey-Brock, J.H. 1985. Polychaetes from Fijian coral reefs. *Pacific Science* **39**, 195-220.
- Barel, C.D.N. & Kramers, P.G.N. 1977. A survey of the echinoderm associates of the North-East Atlantic area. *Zoologische Verhandelingen. Leiden* **156**, 1-159.

- Bartel, A.H. & Davenport, D. 1956. A technique for the investigation of chemical responses in aquatic animals. *British Journal of Animal Behaviour* **4**, 117-119.
- Beauchamp, P. de & Zachs, I. 1913. Esquisse d'une monographie bionomique de la plage de Terrénès. *Mémoires de la Société de Zoologie Française* **26**, 197-237.
- Bellan, G. 1959. Repartition biogéographique et bionomique de quelques annélides polychètes de la Méditerranée et du proche océan. *Recueil des Travaux de la Station Marine d'Endoume* **Bull. 17 Fasc. 29**, 127-172.
- Bellan, G. 1964. Contribution à l'étude systématique, bionomique et écologique des Annélides Polychètes de la Méditerranée. *Recueil des Travaux de la Station Marine d'Endoume* **Bull. 33 Fasc. 49**, 1-371.
- Belloni, S. & Mori, M. 1985. Presenza di *Iphitime cuenoti* (Annelida: Iphitimidae) in Mar Ligure. *Nova Thalassia* **7**, 402.
- Ben-Eliahu, M.N. 1975b. Polychaete cryptofauna from rims of similar intertidal vermetid reefs on the Mediterranean coast of Israel and in the Gulf of Elat: Nereidae (Polychaeta Errantia). *Israel Journal of Zoology* **24**, 177-191.
- Ben-Eliahu, M.N. 1975a. Polychaete cryptofauna from rims of similar intertidal vermetid reefs on the Mediterranean coast of Israel and in the Gulf of Elat: Sabellidae (Polychaeta Sedentaria). *Israel Journal of Zoology* **24**, 54-70.
- Ben-Eliahu, M.N. 1976. Polychaete cryptofauna from rims of similar intertidal vermetid reefs on the Mediterranean coast of Israel and in the Gulf of Elat: Serpulidae (Polychaeta Sedentaria). *Israel Journal of Zoology* **25**, 103-119.
- Beneden, P.J.van 1853. Note sur une larve d'annelide d'une forme toute particulière, rapportée avec doute aux serpules. *Bulletin de l'Académie Royale de Bruxelles* **20**, 69-72.
- Beneden, P.J.van 1858. Histoire naturelle d'un animal nouveau désigné sous le nom d'*Histriobdella*. *Bulletin de l'Académie Royale de Bruxelles* **5**, 270-302.
- Beneden, P.J.van 1869. Le commensalisme dans le Règne Animal. *Proceedings of the Royal Irish Academy* **28**, 621-636.
- Berkeley, E. 1924. On a new case of commensalism between echinoderm and annelid. *Canadian Field Naturalist* **38**, 193 only.
- Berkeley, E. & Berkeley, C. 1941. On a collection of Polychaeta from Southern California. *Bulletin of the Southern California Academy of Sciences* **40**, 16-60.
- Berkeley, E. & Berkeley, C. 1942. North Pacific Polychaeta, chiefly from the west coast of Vancouver Island, Alaska and Bering Sea. *Canadian Journal of Science* **20**, 183-208.
- Berkeley, E. & Berkeley, C. 1948. *Canadian Pacific Fauna*. Toronto: Fisheries Research Board of Canada.
- Berkeley, E. & Berkeley, C. 1950. Notes on Polychaeta from the coast of western Canada. IV. Polychaeta Sedentaria. *Annals and Magazine of Natural History* **3**, 50-69.
- Blake, J.A. 1969. Systematics and ecology of shell-boring polychaetes from New England. *American Zoologist* **9**, 813-820.
- Blake, J.A. 1971. Revision of the genus *Polydora* from the East coast of North America. *Smithsonian Contributions to Zoology* **75**, 1-32.
- Blake, J.A. 1980. *Polydora* and *Boccardia* species (Polychaeta: Spionidae) from western Mexico, chiefly from calcareous habitats. *Proceedings of the Biological Society of Washington* **93**, 947-962.
- Blake, J.A. 1983. Polychaetes of the family Spionidae from South America, Antarctica, and adjacent seas and islands. In *Biology of the Antarctic Seas XIV. Antarctic Research Series. Vol. 39 (3)*, L. Kornicker (ed.), Washington D.C.: American Geophysical Union, pp. 205-288.
- Blake, J.A. 1990. A new genus and species of Polychaeta commensal with a deep-sea thyasirid clam. *Proceedings of the Biological Society of Washington* **103**, 681-686.
- Blake, J.A. 1993. New genera and species of deep-sea polychaetes of the family Nautiliniellidae from the Gulf of Mexico and the Eastern Pacific. *Proceedings of the Biological Society of Washington* **106**, 147-157.
- Blake, J.A. 1994. Introduction to the Annelida. In *Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel. The Annelida part 1*, J.A. Blake, B. Hilbig & P.H. Scott (eds.), Santa Barbara, California: Santa Barbara Museum of Natural History, pp. 39-113.
- Blake, J.A. 1996. Family Spionidae Grube, 1850. Including a review of the genera and species from California and a revision of the genus *Polydora* Bosc, 1802. In *Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel. The Annelida part 3*, J.A.

- Blake, B. Hilbig & P.H. Scott (eds.), Santa Barbara, California: Santa Barbara Museum of Natural History, pp. 81-224.
- Blake, J.A. & Evans, J.W. 1973. *Polydora* and related genera as borers in mollusc shells and other calcareous substrates. *The Veliger* **15**, 235-249.
- Blake, J.A. & Kudenov, J.D. 1978. The spionidae (Polychaeta) from Southeastern Australia and adjacent areas with a revision of the genera. *Memories of the national Museum of Victoria* **39**, 171-280.
- Blake, J.A. & Woodwick, K.H. 1971. New species of *Polydora* (Polychaeta: Spionidae) from the coast of California. *Bulletin of the Southern California Academy of Sciences* **70**, 72-79.
- Boucher, D.H., James, S. & Keeler, K.H. 1982. The ecology of mutualism. *Annual Review of Ecology and Systematics* **13**, 315-347.
- Brettey, J. & Campbell, A. 1985. Occurrence of *Histriobdella homari* (Annelida: Polychaeta) on the american lobster in the Canadian maritimes. *Canadian Journal of Zoology* **63**, 392-395.
- Brightwell, L.R. 1951. Some experiments with the common hermit crab (*Eupagurus bernhardus* Linn.) and transparent univalve shells. *Proceedings of the Zoological Society of London* **121**, 279-283.
- Britayev, T.A. 1981. Two new species of commensal polynoids (Polychaeta: Polynoidae) and bibliography on polychaetes, symbionts of Coelenterata. [In Russian]. *Zoologicheski Zhurnal* **60**, 817-824.
- Britayev, T.A. 1989. The symbiotic Polychaetes: Morphology, Ecology and Distribution. In *Symbiosis among marine animals*, V.A. Sveshnicov (ed.), Moscow: A.N. Severtzov Institute, Russian Academy of Sciences, pp. 60-74.
- Britayev, T.A. 1991. Life cycle of the symbiotic scaleworm *Arctonoe vittata* (Polychaeta: Polynoidae). *Ophelia Suppl.* **5**, 305-312.
- Britayev, T.A. 1993. *Pilargis berkeleyae* (Polychaeta, Pilargidae) as a commensal of a sedentary polychaete *Chaetopterus cautus* (Chaetopteridae). [In Russian]. *Zoologicheski Zhurnal* **72**, 147-151.
- Britayev, T.A. & Fahrutdinov, R.R. 1994. Pontonin shrimps associated with molluscs at the coast of South Vietnam. [In Russian]. In *Hydrobionts of South Vietnam*, D.S. Pavlov & J.N. Sbikin (eds.), Moscow: Nauka, pp. 128-145.
- Britayev, T.A. & Memmy, M.P. 1989. Symbiotic association between the pelagic polychaete *Hipponoe gaudichaudi* (Polychaeta, Amphinomidae) and goose barnacles (Cirripedia, Lepadomorpha). [In Russian]. *Zoologicheski Zhurnal* **68**, 30-35.
- Britayev, T.A. & Smurov, A.V. 1985. The structure of a population of symbionts and related biological features, *Arctonoe vittata* (Polychaeta, Polynoidae) taken as an example. [In Russian]. *Zhurnal obschey Biologii* **46**, 355-366.
- Britayev, T.A. & Zamyshliak, E.A. 1996. Association of the commensal scaleworm *Gastrolepidia clavigera* (Polychaeta: Polynoidae) with holothurians near the coast of South Vietnam. *Ophelia* **45**, 175-190.
- Britayev, T.A., Ivashchenko, N.I. & Litvinov, E.G. 1977. Peculiarities of the commensal complex in the polychaete *Arctonoe vittata*. [In Russian]. *Biologiya Morya* **1978**, 76-78.
- Britayev, T.A., Smurov, A.V., Adrianov, A.V., Bazhin, A.G. & Rhzavsky, A.V. 1989. Ecology of symbiotic Polychaete *Arctonoe vittata* according to the peculiarity of starfish *Asterias ratbunae* ecology. [In Russian]. In *Symbiosis among marine animals*, V.A. Sveshnicov (ed.), Moscow: A.N. Severtzov Institute, Russian Academy of Sciences, pp. 102-127.
- Buzhinskaya, G.N. 1967. On the ecology of the Polychaetous Annelids of the Possjet Bay (the Sea of Japan). [In Russian]. *Issledovaniya Fauni Moorei* **5**, 78-124.
- Buzhinskaya, G.N. 1971. New and interesting species of polychaete worms of the Possjet Bay of the Sea of Japan. [In Russian]. *Issledovaniya Fauni Moorei* **8**, 123-145.
- Buzhinskaya, G.N., Obut, A.M. & Potin, V.V. 1980. Errantiate polychaetes (Polychaeta, Errantia) of the coral reefs and islands of the Indian and Pacific oceans (based on the material of the "KALLISTO" expedition of 1974, 1975) [In Russian]. In *Biology of Coral Reefs*, Moscow: USSR Academy of Sciences; Inst. Mar. Biol. Far E. Sci. Centre, pp. 225-256.
- Campoy, A. 1982. Fauna de España. Fauna de Anélidos Poliquetos de la Península Ibérica. *Publicaciones de la Universidad de Navarra. Serie Zoológica* **7**, 1-400.
- Cañete, J.I., Gallardo, V.A., Enríquez, S. & Baltazar, M. 1993. *Harmothoe brevipalpa* Begström, 1916 (Polynoidae), poliqueto asociado a los tubos de dos especies de poliquetos frente a la Bahía de Concepción, Chile. *Boletín de la Sociedad de Biología de Concepción, Chile* **64**, 43-46.
- Cannon, L.R.G. & Jennings, J.B. 1987. Occurrence and nutritional relationships of four

- ectosymbiotes of the freshwater crayfishes *Cherax dispar* Riek and *Cherax punctatus* Clark (Crustacea: Decapoda) in Queensland. *Australian Journal of Marine and Freshwater Research* **38**, 419-427.
- Carrasco, F.D. 1974. Spionidae (Polychaeta) provenientes de la Bahía de Concepción y lugares adyacentes. *Boletín de la Sociedad de Biología de Concepción, Chile* **48**, 185-201.
- Carthy, J.D. 1958. *An introduction to the behaviour in invertebrates*. London: George Allen & Unwin.
- Carton, Y. 1966b. Specificite parasitaire de *Sabelliphilus sarsi*, parasite de *Spirographis spallanzani*. 1. Intérêt de son étude dans la taxonomie de divers sabellidae. *Archives de Zoologie Expérimentale et Générale* **107**, 428-442.
- Carton, Y. 1966a. Etude du comportement et de la specificite parasitaire de *Sabelliphilus sarsi* Claparède, copepode parasite de *Spirographis spallanzani* Viviani. *Bulletin du Museum National d'Histoire Naturelle Paris* **37**, 807-817.
- Carton, Y. 1967. Specificite parasitaire de *Sabelliphilus sarsi*, parasite de *Spirographis spallanzani*. 2. Reactions histologiques des hôtes lors des contaminations expérimentales. *Archives de Zoologie Expérimentale et Générale* **108**, 387-411.
- Carton, Y. 1968b. Specificite parasitaire de *Sabelliphilus sarsi*, parasite de *Spirographis spallanzani*. 4. Etude biochimique des hotes et de leurs secretions. *Archives de Zoologie Expérimentale et Générale* **109**, 269-286.
- Carton, Y. 1968a. Specificite parasitaire de *Sabelliphilus sarsi*, parasite de *Spirographis spallanzani*. 3. Mise en evidence d'une attraction biochimique du Copepode par l'Annelide. *Archives de Zoologie Expérimentale et Générale* **109**, 123-144.
- Caullery, M. 1914. *Labidognathus parasiticus* n. g. n. sp. Cas nouveau d'endoparasitisme évolutif chez les Euniciens. *Compte Rendu de la Société de Biologie de Paris* **77**, 490-493.
- Caullery, M. 1925. Schizogenese et schizogamie de *Procerastea halleziana* Malaquin. Parasitism de ce Syllidien sur les Tubulaires. *Bulletin de la Société Zoologique de France* **50**, 204-208.
- Caullery, M. & Mesnil, F. 1916. Notes biologiques sur les mares à *Lithothamnion* de la Hague. 1. Presentation d'un *Labrorostratus parasiticus* S.J., parasite interne d'*Odonthosyllis ctenostoma* Clap. *Bulletin de la Société Zoologique de France* **40**, 160-161.
- Cazaux, C. 1968. Etude morphologique du developpement larvaire d'annelides polychetes (Basin d'Arcachon). I. Aphroditidae, Chrysopetalidae. *Archives de Zoologie Expérimentale et Générale* **109**, 477-543.
- Clark, R.B. 1956. *Capitella capitata* as a commensal, with a bibliography of parasitism and commensalism in the polychetes. *Annals and Magazine of Natural History* **12**, 433-448.
- Comely, A. & Ansell, A.D. 1988. Invertebrate associates with the sea-urchin *Echinus sculentus* L. from the Scottish West Coast. *Ophelia* **28**, 111-137.
- Comely, C.A. & Ansell, A.D. 1989. The occurrence of the Eunicid polychaetes *Iphitime cuenoti* Fauvel and *I. paguri* Fage & Legendre in crabs from the Scottish West coast. *Ophelia* **31**, 59-76.
- Cordero, E.H. 1927. Un nuevo Arquianélido, *Stratiadrilus platensis*, n. sp., que habita sobre *Aegla laevis* (Latr.). Nota preliminar. *Physis, Revista Soc. Argentina ciencias naturales* **8**, 574-578.
- Cram, A. & Evans, S.M. 1980. Shell entry behaviour in the commensal ragworm *Nereis fucata*. *Marine Behaviour and Physiology* **7**, 57-64.
- Cuenot, L. 1912. Contribution a la faune du Bassin d'Arcachon. Echinodermes. *Bulletin de la Station Biologique d'Arcachon* **14**, 17-1227.
- Dales, R.P. 1957. Interrelations of organisms. A. Commensalism. In *Treatise on marine ecology and palaeoecology* (Ed. J.W. Hedgpeth). *Memorials of the Geological Society of America* **67**, 391-412.
- Dauer, D.M. 1974. Polychaete fauna associated with Gulf of Mexico sponges. *Florida Scientist* **36**, 192-196.
- Dauer, D.M. 1991. Functional morphology and feeding behavior of *Polydora commensalis* (Polychaeta: Spionidae). *Ophelia Suppl.* **5**, 607-614.
- Davenport, D. 1950. Studies in the physiology of commensalism. I. The polynoid genus *Arctonoë*. *Biological Bulletin of the marine biological Laboratory, Woods Hole* **98**, 81-93.
- Davenport, D. 1953b. Studies in the physiology of commensalism. IV. The polynoid genera *Polynoe*, *Lepidasthenia* and *Harmothoe*. *Journal of the Marine biological Association of the United Kingdom* **32**, 273-288.
- Davenport, D. 1953a. Studies in the physiology of commensalism. III. The polynoid genera *Acholoe*, *Gattyana*, and *Lepidasthenia*. *Journal of the Marine biological Association of the United Kingdom* **32**, 161-173.

- Davenport, D. 1954. Notes on the early stages of the commensal polynoid *Acholoe astericola* (delle Chiaje). *Journal of the Marine biological Association of the United Kingdom* **33**, 123-127.
- Davenport, D. 1955. Specificity and behaviour in symbiosis. *Quarterly Review of Biology* **30**, 29-46.
- Davenport, D. 1966b. The experimental analysis of behaviour in symbioses. In *Symbiosis. I. Associations of Microorganisms, Plants and Marine Organisms*, S.M. Henry (ed.), New York: Academic Press, pp. 381-429.
- Davenport, D. 1966a. Echinoderms and the control of behavior in associations. In *Physiology of Echinodermata*, R.A. Boolootian (ed.), New York: Academic Press/John Wiley and Sons, pp. 145-156.
- Davenport, D. & Hickok, J.F. 1951. Studies in the physiology of commensalism. 2. The polynoid genera *Arctonoe* and *Halosydna*. *Biological Bulletin of the marine biological Laboratory, Woods Hole* **100**, 71-83.
- Davenport, D. & Hickok, J.F. 1957. Notes on the early stages of the facultative commensal *Podarke pugettensis* (Polychaeta, Hesionidae). *Annals and Magazine of Natural History* **10**, 625-631.
- Davenport, D., Camougis, G. & Hickok, J.F. 1960. Analysis of the behaviour of commensals in host-factor. I. A hesionid polychaete and pinnotherid crab. *Animal Behaviour* **8**, 209-218.
- Day, J.H. 1960. The Polychaete fauna of South Africa. Part 5. Errant species dredged off Cape coasts. *Annales of the South African Museum* **45**, 261-373.
- Day, J.H. 1962. Polychaeta from several localities in the western Indian Ocean. *Proceedings of the Zoological Society of London* **139**, 627-656.
- Day, J.H. 1967. A monograph on the Polychaetes of Southern Africa. Part 1. Errantia. *Trustees of the British Museum (Natural History)* **656**, 1-656.
- Day, J.H. 1973. Polychaeta collected by U.D. Gaikwad at Ratnagiri, south of Bombay. *Zoological Journal of the Linnean Society* **52**, 337-361.
- Dean, H.K. 1992. A new arabellid polychaete living in the mantle cavity of deep-sea wood boring bivalves (family Pholadidae). *Proceedings of the Biological Society of Washington* **105**, 224-232.
- Desportes, I., Laubier, L. & Theodorides, J. 1977. Présence d'*Ophriotrocha geryoncola* (Esmark) (Polychète, Dorvilleidae) en Méditerranée Occidentale. *Vie et Milieu* **27**, 131-133.
- Devaney, D.M. 1967. An ectocommensal polynoid associated with Indo-pacific echinoderms, primarily ophiuroids. *Occasional Papers of the Bernice Pauahi Bishop Museum* **23**, 287-304.
- Devaney, D.M. 1974. Shallow water Echinoderms from British Honduras, with a description of a new species of *Ophiocoma* (Ophiuroidea). *Bulletin of Marine Science* **24**, 122-164.
- DeVantier, L.M., Reichelt, R.E. & Bradbury, R.H. 1985. Does *Spirobranchus giganteus* protect host *Porites* from predation by *Acanthaster planci*: predator pressure as a mechanism of coevolution? *Marine Biology* **32**, 307-310.
- Dimock Jr, R.V. 1974. Intraspecific aggression and the distribution of a symbiotic polychaete on its host. In *Symbiosis in the sea*, W.B. Vernberg (ed.), Columbia: University of South Carolina Press, pp. 29-44.
- Dimock Jr, R.V. & Davenport, D. 1971. Behavioral specificity and the induction of host recognition in a symbiotic polychaete. *Biological Bulletin of the marine biological Laboratory, Woods Hole* **141**, 472-484.
- Dimock Jr, R.V. & Dimock, J.G. 1969. A possible "defense" response in a commensal polychaete. *The Veliger* **12**, 65-68.
- Ditlevsen, H. 1917. *Annelids. I.* Copenhagen: H. Hagerup.
- Eckelbarger, K.J. 1978. Metamorphosis and settlement in the Sabellariidae. In *Settlement and metamorphosis of marine invertebrate larvae*, F.S. Chia & M.E. Rice (eds.), New York: Elsevier, pp. 127-144.
- Eisig, H. 1906. *Ichthyotomus sanguinarius*, eine auf Aalen schmarotzende Annelide. *Fauna und Flora des Golfes von Neapel* **28**, 1-300.
- Emerson, R.R. 1974. A new species of polychaetous annelid (Arabellidae) parasitic in *Diopatra ornata* (Onuphidae) from Southern California. *Bulletin of the Southern California Academy of Sciences* **73**, 1-4.
- Emson, R.H., Young, C.M. & Paterson, G.L.J. 1993. A fire worm with a sheltered life: studies of *Benthoscolex cubanus* Hartman (Amphinomidae), an internal associate of the bathyal sea-urchin *Archeopneustes hystrix* (A. Agassiz, 1880). *Journal of Natural History* **27**, 1010-1028.
- Essenberg, C. 1918. The factors controlling the distribution of the Polynoidae of the Pacific coast of North America. *University of California Publications in Zoology* **18**, 171-238.
- Estcourt, I.N. 1967. Burrowing polychaete worms from a New Zealand estuary. *Transactions of the*

- Royal Society of New Zealand* **9**, 65-78.
- Euders, H.E. 1905. Notes on the commensals found in the tube of *Chaetopterus pergamentaceus*. *American Naturalist* **34**, 1-3.
- Fage, L. 1936. Sur l'association d'un annélide polychète *Lumbriconereis flabellicola* n. sp. et d'un madrépore *Flabellum pavoninum distinctum* E. et H. *Comptes Rendues du XIIe Congrès International de Zoologie* **1**, 941-945.
- Fage, L. & Legendre, R. 1925. Sur une Annélide Polychète (*Iphitime cuenoti* Fauv.) commensale des crabes. *Bulletin de la Société Zoologique de France* **50**, 219-225.
- Fage, L. & Legendre, R. 1933. Les anélides polychètes du genre *Iphitime*. A propos d'une espèce nouvelle commensale des pagures, *Iphitime paguri*. *Bulletin de la Société Zoologique de France* **58**, 299-305.
- Fauchald, K. 1970. Polychaetous annelids of the families Eunicidae, Lumbrineridae, Iphitimidae, Arbellidae, Lysaretidae and Dorvilleidae from western Mexico. *Allan Hancock Monographs in marine Biology* **5**, 1-335.
- Fauchald, K. 1977. Polychaete worms, definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County Science Service* **28**, 1-190.
- Fauchald, K. 1992. A review of the genus *Eunice* (Polychaeta: Eunicidae) based upon type material. *Smithsonian Contributions to Zoology* **523**, 1-422.
- Fauchald, K. & Jumars, P.A. 1979. The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology: An Annual Review* **17**, 193-284.
- Fauvel, P. 1913. Quatrième note préliminaire sur les Polychètes provenant des campagnes de l'“Hirondelle” et de la “Princesse-Alice”, ou déposées dans le Musée Océanographique de Monaco. *Bulletin de l'Institut Océanographique (Foundation Albert 1er, Prince de Monaco)* **270**, 1-80.
- Fauvel, P. 1914. Un Eunicien énigmatique *Iphitime cuenoti* n. sp. *Archives de Zoologie Expérimentale et Générale* **53**, 34-37.
- Fauvel, P. 1923. Faune de France. Polychètes Errantes. *Faune de France* **5**, 1-488.
- Fauvel, P. 1959. Classe des Annélides Polychètes. Annelida Polychaeta (Grube, 1851). In *Traité de Zoologie. Anatomie, Systématique, Biologie*, P.P. Grassé (ed.), Paris: Masson et Cie, pp. 13-196.
- Fox, R.S. & Ruppert, E.E. 1985. Shallow-water marine benthic macroinvertebrates of South Carolina, species identification, community composition and symbiotic associations. *The Belle W. Baruch Library in Marine Sciences* **14**, 1-130.
- Franzén, Å. 1982. Ultrastructure of the biflagellate spermatozoon of *Tomopteris helgolandica* Greef, 1879 (Annelida, Polychaeta). *Gamete Research* **6**, 29-37.
- Frith, D.W. 1976. Animals associated with sponges at North Hayling, Hampshire. *Zoological Journal of the Linnean Society* **58**, 353-362.
- Fuehr, I.M. 1971. A new histriobdellid on a marine isopod from South Africa. *South African Journal of Science* **67**, 325-326.
- Gaikwad, U.D. 1993. Some ecological observations on commensal behaviour of polychaetes, *Loimia medusa* and *Lepidasthenia tubicola*. *Journal of Ecobiology* **5**, 143-145.
- Gallardo, V.A. 1967. Polychaeta from the bay of Nha Trang, South Viet Nam. *Scientific Researches on the Marine Invertebrates of South China Sea and the Gulf of Thailand, 1959-1961. NAGA report* **4**, 35-279.
- Ganapati, P. & Radhakrishna, Y. 1962. Inquilinism between a new hesionid polychaete and a holothuria *Molpadia* sp. *Current Science* **31**, 382-383.
- Gardiner, S.L. 1976. Errant Polychaete Annelids from North Carolina. *The Journal of the Elisha Mitchell Scientific Society* **91**, 77-220.
- Gaston, G.R. & Benner, D.A. 1981. On Dorvilleidae and Iphitimidae (Annelida: Polychaeta) with a redescription of *Eteonopsis geryoncola* and a new host record. *Proceedings of the Biological Society of Washington* **94**, 76-87.
- George, J.D. & Hartmann-Schroeder, G. 1985. *Polychaetes: British Amphinomida, Spintherida and Eunicida. Synopses of the British Fauna (New Series). Vol. 32*. London: Linnean Society of London and Estuarine and Brackish-Water Sciences Association.
- Gerber, H.S. & Stout, J.F. 1968. Sensory basis of the symbiotic relationship of *Arctonoe vittata* (Grube) (Polychaeta, Polynoidae) to the keyhole limpet *Diodora aspera*. *Physiological Zoology* **41**, 169-179.
- Gibbs, P.E. 1969. Aspects of polychaete ecology with particular reference to commensalism. *Philosophical Transactions of the Royal Society of London* **255**, 443-458.
- Gibbs, P.E. 1971. The polychaete fauna of the Solomon Islands. *Bulletin of the British Museum of*

- Natural History* **21**, 101-211.
- Gilpin-Brown, J.B. 1969. Host-adoption in the commensal polychaete *Nereis fucata*. *Journal of the Marine biological Association of the United Kingdom* **49**, 121-127.
- Glasby, C.J. 1994. A new genus and species of polychaete *Bollandia antipathicola* (Nereidoidea, Syllidae), from black coral. *Proceedings of the Biological Society of Washington* **107**, 615-621.
- Goerke, H. 1971. *Nereis fucata* (Polychaeta, Nereidae) als kommensale von *Eupagurus bernhardus* (Crustacea, Decapoda) Entwicklung einer population und verhalten der art. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven* **13**, 79-81.
- Goerke, H. 1977b. *Nereis fucata* (Nereidae) - kommensalismus: Nahrungserwerb. *Publikationen zu wissenschaftlichen filmen* **59**, 3-11.
- Goerke, H. 1977a. *Nereis fucata* (Nereidae) - Kommensalismus: Eindringen in das Gehäuse von *Eupagurus bernhardus*. Film E 1891 des IWF, Gottingen 1977. *Publikationen zu wissenschaftlichen filmen* **58**, 3-12.
- Gravier, C. 1900. Sur le commensalisme de l'*Eunice harasii* Audouin et M.-Edwards et de l'*Ostrea edulis* L. *Bulletin du Museum National d'Histoire Naturelle Paris* **6**, 415-417.
- Gravier, C. 1905b. Sur les genres *Lepidasthenia* Malmgren et *Lepidametria* Webster. *Bulletin du Museum National d'Histoire Naturelle Paris* **11**, 181-184.
- Gravier, C. 1905a. Sur un Polynoidien (*Lepidasthenia digueti* n. sp.) commensal d'un *Balanoglossus*. *Comptes Rendues de l'Academie des Sciences de Paris* **140**, 875-878.
- Gravier, C. 1918. Note sur une Actinie (*Thoractis*) et un Annélide Polychète (*Hermadion fauveli*) commensaux d'une éponge silicieuse (*Sarcostegia oculata*). *Bulletin de l'Institut Océanographique (Foundation Albert 1er, Prince de Monaco)* **334**, 1-20.
- Guille, A. 1965. Contribution a l'étude de la systématique et l'écologie d'*Ophiotrix quinquemaculata* d. Ch. *Vie et Milieu* **15**, 243-308.
- Haigler, S.A. 1969. Boring mechanism of *Polydora websteri* inhabiting *Crassostrea virginica*. *American Zoologist* **9**, 821-828.
- Hamond, R. 1966. The Polychaeta of the coast of Norfolk. *Cahiers de Biologie Marine* **7**, 383-436.
- Hanley, J.R. 1984. A new host and locality records of the commensal *Adyte crinoidicola* (Polychaeta, Polynoidae). *The Beagle, Records of the Northern territory Museum of Arts and Sciences* **1**, 87-92.
- Hanley, J.R. 1989. Revision of the scaleworm genera *Arctonoe* Chamberlin and *Gastrolepidia* Schmarda (Polychaeta, Polynoidae) with the erection of a new subfamily, Arctonoinae. *The Beagle, Records of the Northern territory Museum of Arts and Sciences* **6**, 1-34.
- Hanley, J.R. 1992. Checklist of scaleworms (Polychaeta: Polynoidae) from Hong Kong. In *The marine flora and fauna of Hong Kong and southern China III. Proceedings of the Fourth International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 11-29 April 1989*, B. Morton (ed.), Hong Kong: Hong Kong University Press, pp. 361-369.
- Hanley, J.R. 1993. Scaleworms (Polychaeta: Polynoidae) of Rottnest Island, Western Australia. In *Proceedings of the Fifth International Marine Biological Workshop: The Marine Flora and Fauna of Rottnest Island, Western Australia*, F.E. Wells, D.I. Walker, H. Kirkman & R. Lethbridge (eds.), Perth: Western Australian Museum, pp. 305-320.
- Hanley, J.R. & Burke, M. 1988. A new genus and species of commensal scaleworm (Polychaeta, Polynoidae). *The Beagle, Records of the Northern territory Museum of Arts and Sciences* **5**, 5-15.
- Hanley, J.R. & Burke, M. 1989. A new genus and species of commensal scaleworm (Polychaeta, Polynoidae) from Broome, Western Australia. *The Beagle, Records of the Northern territory Museum of Arts and Sciences* **6**, 97-103.
- Hanley, J.R. & Burke, M. 1990. Scaleworms (Polychaeta: Polynoidae) of Albany, Western Australia. In *Proceedings of the Third International Marine Biological Workshop: The Marine Fauna of Albany, Western Australia*, F.E. Wells, D.I. Walker, H. Kirkman & R. Lethbridge (eds.), Perth: Western Australia Museum, pp. 203-236.
- Hanley, J.R. & Burke, M. 1991a. A new genus and species of scaleworm (Polychaeta, Polynoidae) from the Cascade Plateau, Tasman Sea. *The Beagle, Records of the Northern territory Museum of Arts and Sciences* **8**, 97-102.
- Hanley, J.R. & Burke, M. 1991b. Polychaeta Polynoidae: Scaleworms of the Chesterfield Islands and Fairway Reefs, Coral Sea. In *Résultats des Campagnes MUSORSTOM, Vol. 8*, A. Crosnier (ed.), *Mémoires du Muséum national d'Histoire naturel*, (A) **151**, 9-82.
- Harrington, N.R. 1897. On nereids commensal with hermit crabs. *Transactions of the New York Academy of Science* **16**, 214-221.

- Harrison, L. 1928. On the genus *Stratiodrilus* (Archiannelida: Histriobdella) with a description of a new species from Madagascar. *Records of The Australian Museum* **16**, 116-121.
- Hartman, O. 1941. New species of polychaetous annelids from Southern California. *Allan Hancock Pacific Expedition* **7**, 159-171.
- Hartman, O. 1942. The polychaetous Annelida. Report on the scientific results of the Atlantis Expedition to the West Indies under the joint auspices of the University of Havana and Harvard University. *Memorias de la Sociedad Cubana de Historia Natural* **16**, 89-104.
- Hartman, O. 1948. The polychaetous annelids of Alaska. *Pacific Science* **2**, 1-58.
- Hartman, O. 1951. The littoral marine Annelids of the Gulf of Mexico. *Publications of the Institute of Marine Sciences* **2**, 7-124.
- Hartman, O. 1952. *Iphitime* and *Ceratocephala* (Polychaetous annelids) from California. *Bulletin of the Southern California Academy of Sciences* **51**, 9-20.
- Hartman, O. 1954. Marine annelids from the northern Marshall Islands. *United States Geological Survey Professional Papers* **260 Q**, 615-644.
- Hartman, O. 1966. Polychaetous annelids of the Hawaiian Islands. *Occasional Papers of the Bernice Pauahi Bishop Museum* **23**, 163-252.
- Hartman, O. 1968. *Atlas of the errantiate polychaetous annelids from California*. Los Angeles: Allan Hancock Foundation, University of Southern California.
- Hartman, O. & Boss, K.J. 1965. *Antonbruunia viridis*, a new inquiline annelid with dwarf males, inhabiting a new species of pelecypod, *Lucinia fosteri* in the Mozambique channel. *Annals and Magazine of Natural History* **13**, 177-186.
- Hartman, O. & Fauchald, K. 1971. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic Areas. Part II. *Allan Hancock Monographies in Marine Biology* **6**, 1-327.
- Hartmann-Schröder, G. 1960. Polychaeten aus dem Roten Meer. *Kieler Meeresforschungen* **16**, 69-125.
- Hartmann-Schröder, G. 1971. Annelida, Borstenwürmer, Polychaeta. In *Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Maermalen und nach ihrer Lebensweise*, M. Dahl & F. Peus (eds.), Jena: Gustav Fischer Verlag, pp. 1-594.
- Hartmann-Schröder, G. 1978. Einige Sylliden-Arten (Polychaeta) von Hawaii und aus dem Karibischen Meer. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* **75**, 49-61.
- Hartmann-Schröder, G. 1981. *Hololepidella alba* n. sp. (Polynoidae: Polychaeta), a commensal with the crown-of-thorns starfish from Mactan, Cebu. *The Philippine Scientist* **18**, 10-14.
- Hartmann-Schröder, G. 1983. Zur Kenntnis einiger Foraminiferengehäuse bewohnender Polychaeten aus dem Nordostatlantik. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* **80**, 169-176.
- Hartmann-Schröder, G. 1984. Zwie neue kommensalische Polychaeten der Gattung *Hololepidella* Willey (Polynoidae) von der Philippinen. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* **81**, 63-70.
- Hartmann-Schröder, G. 1985. *Polynoe caeciliae* Fauvel (Polynoidae), ein mit Korallen assoziierter Polychaet. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* **82**, 31-35.
- Hartmann-Schröder, G. 1989. *Polynoe thouarellicola* n. sp. aus der Antarktis, assoziiert mit Hornkorallen, und Wiederbeschreibung von *Polynoe antarctica* Kinberg, 1858 (Polychaeta, Polynoidae). *Zoologische Anzeiger* **3/4**, 205-221.
- Hartmann-Schröder, G. 1991. *Syllis onkylochaeta* sp.n., ein korallenfressender Polychaet (Syllidae) aus dem Korallenaquarium des Löbbecke-Museums. *Helgoländer Meeresuntersuchungen* **45**, 59-63.
- Hartmann-Schröder, G. 1992. Drei neue Polychaeten-arten der familien Polynoidae und Syllidae von Neu-Kaledonien, assoziiert mit einer verkalteten Hydrozoe. *Helgoländer Meeresuntersuchungen* **46**, 93-101.
- Hartmann-Schröder, G. 1993. *Haplosyllis xeniaecola*, ein neuer Polychaet (Syllidae) von der Molukken (Indonesien). *Helgoländer Meeresuntersuchungen* **47**, 305-310.
- Hartnoll, R.G. 1962. *Iphitime cuenoti* Fauvel (Eunicidae), a polychaete new to Brithish waters. *Annals and Magazine of Natural History* **5**, 93-96.
- Haswell, W.A. 1885. On a destructive parasite of the rock-oyster (*Polydora ciliata* and *P. polybranchia* n. sp.). *Proceedings of the Linnean Society of New South Wales* **10**, 273-275.
- Haswell, W.A. 1900. On a new Histriobdellid. *Quarterly Journal of Microscopical Science* **43**, 299-335.

- Haswell, W.A. 1913. Notes on the Histriobdellidae. *Quarterly Journal of Microscopical Science* **59**, 197-226.
- Hatfield, P.A. 1965. *Polydora commensalis* Andrews - Larval developpement and observations on adults. *Biological Bulletin of the marine biological Laboratory, Woods Hole* **128**, 356-368.
- Hendler, G. & Meyer, D.L. 1982. An association of a polychaete, *Branchiosyllis exilis*, with an ophiuroid, *Ophiocoma echinata*, in Panama. *Bulletin of Marine Science* **32**, 736-744.
- Henry S.M. (ed.) 1966. *Symbiosis. I. Associations of Microorganisms, Plants and Marine Organisms*. New York & London: Academic Press.
- Hermans, C.O. 1969. The systematic position of the Archiannelida. *Systematics and Zoology* **18**, 85-102.
- Hickok, J.F. & Davenport, D. 1957. Further studies in the behavior of commensal polychaetes. *Biological Bulletin of the marine biological Laboratory, Woods Hole* **113**, 397-406.
- Hilbig, B. 1994. 9. Family Hesionidae Sars, 1862. In *Taxonomic atlas of the benthic fauna of the Santa Barbara Basin and western Santa Barbara Channel. Vol. 4 - The Annelida part 1. Oligochaeta and Polychaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae)*, J.A. Blake & B. Hilbig (eds.), Santa Barbara: Santa Barbara Museum of Natural History, pp. 243-269.
- Hopkins, S.H. 1958. The planktonic larvae of *Polydora websteri* Hartman (Annelida, Polychaeta) and their settling on oysters. *Bulletin of Marine Science of the Gulf and Caribbean* **8**, 268-277.
- Hornell, J. 1891. Report on the polychaetous annelids of the L.M.B.C. district. *Proceedings and Transactions of the Liverpool Biological Society* **5**, 223-268.
- Horst, R. 1915. On new and little-known species of Polynoinae from the Netherland's East-Indies. *Zoologische Mededeelingen Leiden* **1**, 2-20.
- Houlbert, C. & Galaine, C. 1916. Sur le chambrage des huiters et l'infection possible desc chambers parle fait d'une Annelide tubicole parasite de la coquille (*Sclerocheilus*). *Comptes Rendues de l'Academie des Sciences de Paris* **162**, 54-56.
- Hove, H.A. ten 1970. Serpulinae (Polychaeta) from the Caribbean. 1. The genus *Spirobranchus*. *Studies on the Fauna of Curaçao and Caribbean Islands* **32**, 14-19.
- Hove, H.A. ten 1989. Serpulinae (Polychaeta) from the Caribbean: IV *Pseudovermilia madracicola* sp.n., a symbiont of corals. *Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen* **123**, 135-144.
- Hove, H.A. ten 1994. Serpulidae (Annelida: Polychaeta) from the Seychelles and Amirante Islands. In *Oceanic reefs of the Seychelles. Cruise reports Neth. Indian Ocean Programm II*, J. van der Land (ed.), Leiden: National Natural Museum of Leiden, pp. 107-116.
- Humann, P. 1992. *Reef creature identification. Florida, Caribbean, Bahamas*. Orlando: Vaughan Press.
- Hunte, W., Colin, B.E. & Marsden, J.R. 1990a. Habitat selection in the tropical polychaete *Spirobranchus giganteus*. 1. Distribution on corals. *Marine Biology* **104**, 87-92.
- Hunte, W., Marsden, J.R. & Conlin, B.E. 1990b. Habitat selection in the tropical polychaete *Spirobranchus giganteus*. III. Effects of coral species on body size and body proportions. *Marine Biology* **104**, 101-107.
- Imajima, M. 1966. The Syllidae (polychaetous annelids) from Japan. IV. Syllinae. *Publications of the Seto Marine Biological Laboratory* **14**, 219-252.
- Imajima, M. & Hartman, O. 1964. The Polychaetous Annelids from Japan. Pt. I. *Allan Hancock Foundation Special Publication* **26**, 1-237.
- Imajima, M. & Sato, W. 1984. A new species of *Polydora* (Polychaeta: Spionidae) collected from Abashiri Bay, Hokkaido. *Bulletin of the National Science Museum of Tokyo, Series A* **10**, 57-62.
- Izuka, A. 1912. The errantiate Polychaeta of Japan. *Journal of the College of Science, Imperial University of Tokyo* **30**, 1-262.
- Jamieson, B.G.M., Afzelius, B.A. & Franzén, Å. 1985. Ultrastructure of the acentriolar, aflagellate spermatozoa and the eggs of *Histriobdella homari* and *Stratiodrilus novaehollandiae* (Histriobdellidae, Polychaeta). *Journal of Submicroscopical Cytology* **17**, 363-372.
- Jangoux, M. 1987. Diseases of Echinodermata. III. Agents Metazoans (Annelida to Pisces). *Diseases in Aquatic Organisms* **3**, 59-83.
- Jennings, J.B. & Gelder, S.R. 1976. Observations on the feeding mechanism, diet and digestive physiology of *Histriobdella homari* van Beneden 1858: An aberrant polychaete symbiotic with North American and European lobsters. *Biological Bulletin of the marine biological Laboratory, Woods Hole* **151**, 489-517.
- Jensen, K. & Bender, K. 1973. Invertebrates associated with snail shells inhabited by *Pagurus bernhardus* (L.) (Decapoda). *Ophelia* **10**, 185-192.

- Jensen, R.A. & Morse, D.E. 1984. Intraspecific facilitation of larval recruitment: gregarious settlement of the polychaete *Phragmatopoma californica* (Fewkes). *Journal of Experimental Marine Biology and Ecology* **54**, 677-684.
- Jones, M.L. 1974. On the Caobangidae, a new family of Polychaeta, with redescription of *Caobangia billeti* Giard. *Smithsonian Contributions to Zoology* **175**, 1-55.
- Jones, S. 1964. Notes on animal associations. The starfish *Pentaceros hedemanni* and the hesionid polychaete *Podarke angustifrons*. *Journal of the Marine Biological Association of India* **6**, 249-250.
- Kent, R.M.L. 1979. The influence of heavy infestations of *Polydora ciliata* on the flesh content of *Mytilus edulis*. *Journal of the Marine biological Association of the United Kingdom* **59**, 289-297.
- Kent, R.M.L. 1981. The effect of *Polydora ciliata* on the strength of *Mytilus edulis*. *Journal du Conseil Permanent International pour l'Exploration de la Mer* **39**, 252-255.
- Kirkegaard, J.B. 1977. A new species of *Iphitime* (Polychaeta: Iphitimidae) living under the tail of *Hyas* (Crustacea: Decapoda) in the oslo fjord. In *Essays of Polychaetous annelids in memory of Dr. Olga Hartman*, D.J. Reish & K. Fauchald (eds.), Los Angeles: Allan Hancock Foundation, University of Southern California Press, pp. 199-209.
- Kirkegaard, J.B. & Billett, D. 1980. *Eunoe laetmogonensis*, a new species of polynoid worm, commensal with the bathyal holothurian *Laetmogone violacea*, in the North-East Atlantic. *Steenstrupia* **6**, 101-109.
- Koch, H. 1846. Einige Worte zur Entwicklungsgeschichte von Eunice, mit einem Nachwort von A. Koelliker. *Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft für die Gesamten Naturwissenschaften* **8**, 1-31.
- Korringa, P. 1951. The shell of *Ostrea edulis* as a habitat: observations on the epifauna of oysters living in the Oosterchelde, Holland, with some notes on polychaete worms occurring there in other habitats. *Archives néerlandaises de zoologie* **10**, 32-152.
- Koukouras, A., Russo, A., Voultsiadou-Koukoura, E., Dounas, C. & Chintiroglou, C. 1992. Relationship of sponge macrofauna with the morphology of their hosts in the North Aegean sea. *Internationale Revue der gesamten Hydrobiologie* **77**, 609-619.
- Koukouras, A., Russo, A., Voultsiadou-Koukoura, E., Arvanitidis, C. & Stefanidou, D. 1996. Macrofauna associated with sponge species of different morphology. *P.S.Z.N. I: Marine Ecology* **17**, 569-582.
- Kudenov, J.D. 1975. The occurrence of the Polynoid *Harmothoe cf lunulata* from the tube of the Maldanid *Axiiothella rubrocincta* (Polychaeta). *Research Notes of the Pacific Marine Station of California* **34**, 42-43.
- Lande, R. & Reish, D.J. 1968. Seasonal occurrence of the commensal polychaetous annelid *Ophryodromus pugettensis* on the starfish *Patiria miniata*. *Bulletin of the Southern California Academy of Sciences* **67**, 104-111.
- Landers, W.S. 1967. Infestation of the hard clam, *Mercenaria mercenaria*, by the boring polychaete worm, *Polydora ciliata*. *Proceedings of the National Shellfisheries Association* **57**, 63-66.
- Lang, K. 1949. A contribution to the morphology of *Stratiodrilus platensis* Cordero (Histiobdellidae). *Arkiv för Zoologi* **42A**, 1-30.
- Laubier, L. 1958. Contribution à la faunistique de coralligène. I. Quelques particularités biologiques de *Polydora armata* Langerhans. *Vie et Milieu* **9**, 412-415.
- Laubier, L. 1959. Contribution à la faunistique de coralligène. III. Deux spionidiens inquilins sur des bryozoaires chilostomides. *Vie et Milieu* **10**, 347-349.
- Laubier, L. 1960. Une nouvelle sous-espèce de Syllidien: *Haplosyllis depressa* Augener ssp. nov. *chamaeleon*, ectoparasite sur l'octocoralliaire *Muricea chamaeleon* Von Koch. *Vie et Milieu* **11**, 75-87.
- Laubier, L. 1973. Découverte d'une annélide polychète de l'Atlantique boréal dans l'étage bathyal de Méditerranée occidentale. *Vie et Milieu* **23**, 255-261.
- Lee, J.-W. & Rho, B.-J. 1994. Systematic studies on Syllidae (Annelida, Polychaeta) from the South Sea and the East Sea in Korea. *The Korean Journal of Systematic Zoology* **10**, 131-144.
- Light, W.J. 1970b. A new spionid (Annelida: Polychaeta) from the Gulf of California. *Bulletin of the Southern California Academy of Sciences* **69**, 74-79.
- Light, W.J. 1970a. *Polydora alloporis*, new species, a commensal spionid (Annelida, Polychaeta) from a Hydrocoral off Central California. *Proceedings of the California Academy of Sciences (Fourth Series)* **37**, 459-472.
- López, E., San Martín, G. & Jiménez, M. 1996. Syllinae (Syllidae, Annelida, Polychaeta) from Chafarinas Islands (Alborán Sea, W. Mediterranean). *Miscel.lània Zoològica* **19**, 105-118.

- Ludwig, H. 1905. Ein endoparasitischer Chaetopod in einer Tiefsee Ophiure. *Zoologische Anzeiger* **29**, 397-399.
- Lunz, G.R. 1940. The annelid worm *Polydora* as an oyster pest. *Science* **92**, 310.
- Lunz, G.R. 1941. *Polydora*, a pest in South Carolina oysters. *The Journal of the Elisha Mitchell Scientific Society* **57**, 273-283.
- Lützen, J. 1961. Sur une nouvelle espèce de Polychète, *Sphaerodoridium commensalis* n. gen., n. spec. (Polychaeta Errantia, famille des Sphaerodoridae) vivant en commensal de *Terebellides stroemi* Sars. *Cahiers de Biologie Marine* **2**, 409-416.
- MacNae, W. & Kalk, M. 1962. The fauna and flora of sand flats at Inhaca Island, Mocambique. *Journal of Animal Ecology* **31**, 93-128.
- Magnino, G. & Gaino, E. Submitted. *Haplosyllis spongicola* (Polychaeta, Syllidae) associated with two species of sponges from East Africa (Tanzania, Indian Ocean). *P.S.Z.N. I: Marine Ecology*.
- Marenzeller, E. 1874. Zur Kenntnis der adriatischen Anneliden. *Sitzungsberichte der Kaiserliche Akademie der Wissenschaften Wien, Mathematisch-Naturwissenschaftliche Klasse* **69**, 407-478.
- Marenzeller, E. 1902. Süd-japanische Anneliden. III. *Denskschriften der Akademie der Wissenschaften Wien, Mathematisch-naturwissenschaftliche Klasse* **72**, 563-582.
- Marenzeller, E. 1904. Steinkorallen. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee- Expedition auf dem Dampfer 'Valdivia' 1898-1899* **7**, 261-318.
- Marenzeller, E. 1895. *Phalacrostemma cidariophilum*, eine neue Gattung und Art der Hermelliden. *Anzeiger, Akademie der Wissenschaften, Wien (mathematische naturwissenschaften Klasse)* **32**, 191-192.
- Margalef, R. 1980. *Ecología*. Barcelona: Ediciones Omega S.A.
- Margolis, L., Esch, G.W., Holmes, J.C., Kuris, A.M. & Schad, G.A. 1982. The use of ecological terms in parasitology (report of a committee of the American Society of Parasitologists). *Journal of Parasitology* **68**, 131-133.
- Marsden, J.R. 1987. Coral preference behaviour by planktotrophic larvae of *Spirobranchus giganteus corniculatus* (Serpulidae: Polychaeta). *Coral Reefs* **6**, 71-74.
- Marsden, J.R. 1992. Reproductive isolation in two forms of the serpulid polychaete, *Spirobranchus polycerus* (Schmarda) in Barbados. *Bulletin of Marine Science* **51**, 14-19.
- Marsden, J.R., Conlin, B.E. & Hunte, W. 1990. Habitat selection in the tropical polychaete *Spirobranchus giganteus*. II. Larval preferences for corals. *Marine Biology* **104**, 93-99.
- Martin, D. 1987. La comunidad de Anélidos Poliquetos de las concreciones de algas calcáreas del litoral Catalán. Caracterización de las especies. *Publicaciones del Departamento de Zoología de Barcelona* **13**, 45-54.
- Martin, D. 1996. A new species of *Polydora* (Polychaeta, Spionidae) associated with the excavating sponge *Cliona viridis* (Porifera, Hadromerida) in the North Western Mediterranean sea. *Ophelia* **45**, 159-174.
- Martin, D. & Alvà, V. 1988. *Sphaerodorum ophiurophoretos* n. sp., une nouvelle espèce de Sphaerodoridae (Annelida, Polychaeta) commensal sur *Amphipholis squamata* (Echinodermata, Ophiuridae). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* **58**, 45-49.
- Martin, D., Abelló, P. & Cartes, J. 1991. A new species of *Ophryotrocha* (Polychaeta: Dorvilleidae) commensal in *Geryon longipes* (Crustacea: Brachyura) from the Western Mediterranean Sea. *Journal of Natural History* **25**, 1-14.
- Martin, D., Rosell, D. & Uriz, M.J. 1992. *Harmothoe hyalonemae* sp. nov. (Polychaeta, Polynoidae), an exclusive inhabitant of different Atlanto-Mediterranean species of *Hyalonema* (Porifera, Hexactinellida). *Ophelia* **35**, 169-185.
- McGinitie, G.E. & McGinitie, N. 1949. *Natural history of marine animals*. New York: McGraw-Hill.
- McIntosh, W.C. 1900. *A monograph of the British Annelida. II. Polychaeta, Amphinomidae to Sigalionidae*. London: Ray Society.
- Mesnil, F. & Caullery, M. 1922. L'appareil maxillaire d'*Histriobdella homari*; affinités des Histiobdellides avec les Euniciens. *Comptes Rendues de l'Academie des Sciences de Paris* **174**, 913-917.
- Mettam, C. 1980. On the feeding habits of Aphrodita aculeata and commensal polynoids. On the Feeding Habits of Aphrodita aculeata and Commensal Polynoids, a Short Note. *Journal of the Marine biological Association of the United Kingdom* **60**, 833-834.
- Michaelis, H. 1978. Zur morphologie und oekologie von *Polydora ciliata* und *Polydora ligni* (Polychaeta, Spionidae). *Helgoländer Meeresuntersuchungen* **31**, 102-116.
- Millot, N. 1953. A remarkable association between *Ophionereis reticulata* (Say) and *Harmothoe lunulata* (Delle Chiage). *Bulletin of Marine Science* **3**, 96-99.

- Miura, T. 1988. A new species of the genus *Protomystides* (Annelida, Polychaeta) associated with a vestimentiferan worm from the Hatsushima cold-seep site. *Proceedings of the Japanese Society of Systematics and Zoology* **38**, 10-14.
- Miura, T. & Hashimoto, J. 1991. Two new branchiate scale-worms (Polynoidae: Polychaeta) from the hydrothermal vent of the Okinawa Trough and the volcanic seamount off Chichijima Island. *Proceedings of the Biological Society of Washington* **104**, 166-174.
- Miura, T. & Hashimoto, J. 1993. *Mytilidiphila*, a new genus of nautiliniellid polychaetes living in the mantle cavity of deep-sea mytilid bivalves collected from the Okinawa Trough. *Zoological Science* **10**, 169-174.
- Miura, T. & Laubier, L. 1989. *Nautilina calyptogenica*, a new genus and species of parasitic polychaete on a vesicomid bivalve from the Japan Trench, representative of a new family Nautilinidae. *Zoological Science* **6**, 387-390.
- Miura, T. & Laubier, L. 1990. Nautiliniellid polychaetes collected from the Hatsushima Cold-seep site in Sagami Bay, with descriptions of new genera and species. *Zoological Science* **7**, 319-325.
- Miura, T. & Ohta, S. 1991. Two polychaete species from the deep-sea hydrothermal vent in the Middle Okinawa Trough. *Zoological Science* **8**, 383-387.
- Miura, T. & Shirayama, Y. 1992. *Lumbrineris flabellicola* (Fage, 1936), a Lumbrinerid Polychaete associated with a Japanese haermatypic coral. *Benthos Research* **43**, 23-27.
- Mohammad, M.-B.M. 1972. Infestation of the pearl oyster *Pinctada margaritifera* (Linné) by a new species of *Polydora* in Kuwait, Arabian sea. *Hydrobiologia* **39**, 463-477.
- Monticelli, F.S. 1892. Notizia preliminare intorno ad alcuni inquilini degli Holothuroidea del Golfo di Napoli. *Monitore di Zoologia Italiani* **3**, 248-256.
- Moore, J.P. 1905. New species of polychaetes from the North Pacific, chiefly from Alaskan waters. *Proceedings of the Academy of Natural Sciences of Philadelphia* **57**, 525-554.
- Moore, J.P. 1908. Some polychaetous annelids of the North Pacific of North America. *Proceedings of the Academy of Natural Sciences of Philadelphia* **60**, 321-364.
- Moore, J.P. 1910. The polychaetous annelids dredged by the U.S.S. 'Albatross' off the coast of southern California in 1904. II. Polynoidae, Aphroditidae and Segaleonidae. *Proceedings of the Academy of Natural Sciences of Philadelphia* **62**, 328-402.
- Moore, P.G. & Gorzula, S.J. 1973. A note on the commensal eunicean *Ipitime paguri* Fage and Legendre (Polychaeta) in the Firth of Clyde. *Journal of Natural History* **7**, 161-164.
- Morgado, E.H. & Amaral, A.C.Z. 1981. Anelídeos poliquetos associados a um briozoário. III. Polynoidae. *Boletim do Instituto Oceanográfico, Sao Paulo* **30**, 91-96.
- Morgado, E.H. & Amaral, A.C.Z. 1981a. Anelidos poliquetos associados a um briozoario I. Euniceidae, Lumbrineridae, Lysaretidae e Dorvilleidae. *Iheringia* **60**, 33-54.
- Morgado, E.H. & Amaral, A.C.Z. 1981b. Anelídeos poliquetos associados a um briozoário. II. Palmyridae. *Boletim do Instituto Oceanográfico, Sao Paulo* **30**, 87-89.
- Morgado, E.H. & Amaral, A.C.Z. 1984. Anelídeos poliquetos associados ao briozoário *Schizoporella unicornis* (Johnston). IV. Phyllodocidae e Hesionidae. *Revista Brasileira de Biologia Curitiba* **2**, 49-54.
- Morgado, E.H. & Amaral, A.C.Z. 1985. Anelídeos poliquetos associados ao briozoário *Schizoporella unicornis* (Johnston). V. Syllidae. *Revista Brasileira de Biologia* **3**, 219-227.
- Mori, K., Sato, W., Nomura, T. & Imajima, M. 1985. Infestation of the Japanese scallop *Pecten (Patinopecten) yessoensis* by the boring polychaetes, *Polydora* on the Okhotsk Sea coasts of Hokkaido, especially Abashiri waters. *Bulletin of the Japanese Society of Scientific Fisheries* **51**, 27-41.
- Mori, M. & Belloni, S. 1985. Distribution, abundance and infestation of *Ophryotrocha geryonicola* (Annelida: Dorvilleidae) in *Geryon longipes* (Crustacea: Decapoda: Geryonidae) of Ligurian bathyal bottoms. *Oebalia* **11**, 277-287.
- Moyano, H.I.G., Carrasco, F.D. & Gacitua, S. 1993. On Chilean species of the genus *Stratiodrillus* Haswell, 1900 (Polychaeta, Histiobdellidae). *Boletín de la Sociedad de Biología de Concepción, Chile* **64**, 147-157.
- Newell, G.E. 1954. The marine fauna of Whitstable. *Annals and Magazine of Natural History* **7**, 321-350.
- Núñez, J., Brito, M.C. & Ocaña, O. 1991. Anelídeos poliquetos de Canarias: familia Amphinomidae. *Cahiers de Biologie Marine* **32**, 469-476.
- Oakes, F.R. & Fields, R.C. 1996. Infestation of *Haliotis refescens* shells by a sabellid polychaete. *Aquaculture* **140**, 139-143.
- Okuda, S. 1934. On a tubicolous polychaete living in commensal with a pycnogonid. *Annotations on*

- Zoology, Japan* **14**, 437-439.
- Okuda, S. 1936a. Description of two polychaetous annelids found in burrows of an apodous holothurian. *Annotations on Zoology, Japan* **15**, 410-415.
- Okuda, S. 1936b. Japanese commensal polynoids. *Annotations on Zoology, Japan* **15**, 561-571.
- Okuda, S. 1937. Spioniform polychaetes from Japan. *Journal of the Faculty of Science, Hokkaido Imperial University, Series 6, Zoology* **5**, 217-254.
- Okuda, S. 1950. Notes on some commensal polychaetes from Japan. *Annotations on Zoology, Japan* **24**, 49-53.
- Orton, J.H. 1923. Some new commensals from the Plymouth District. *Nature* **112**, 861.
- Orton, J.H. & Smith, C. 1935. Experiments with *Amphitrite* and its commensals. *Annals and Magazine of Natural History ser. 10* **16**, 644-645.
- Overstreet, R.M. 1983. Metazoan symbionts of crustaceans. In *The Biology of Crustacea*, A.J. Provenzano Jr. (ed.), New York-London: Academic Press, pp. 155-250.
- Paiva, P.C. & Nonato, E.F. 1991. On the genus *Iphitime* (Polychaeta: Iphitimidae) and description of *Iphitime sartorae* sp. nov. a commensal of brachyuran crabs. *Ophelia* **34**, 209-215.
- Palmer, J.B. 1968. An analysis of the distribution of a commensal polynoid on its hosts. Ph.D. Thesis, University of Oregon.
- Pansini, M. & Daglio, S. 1980-1981. Osservazioni sull'inquinamento di Policheti erranti in alcune demosponge del litorale ligure. *Bollettino del Museo del Istituto de Biologia dell'Universita di Genova* **48-49**, 55-60.
- Paris, J. 1955. Commensalisme et parasitisme chez les annélides polychètes. *Vie et Milieu* **6**, 525-536.
- Pascual, M., Núñez, J. & San Martín, G. 1996. *Exogone* (Polychaeta: Syllidae: Exoginae) endobiontics of sponges from the Canary and Madeira Islands with description of two new species. *Ophelia* **45**, 67-80.
- Pawlik, J.R. 1983. A sponge-eating worm from Bermuda: *Branchiosyllis oculata* (Polychaeta, Syllidae). *P.S.Z.N. I: Marine Ecology* **4**, 65-79.
- Pawlik, J.R. 1988. Larval settlement and metamorphosis of sabellariid polychaetes, with special reference to *Phragmatopoma lapidosa*, a reef-building species, and *Sabellaria floridensis*, a non-gregarious species. *Bulletin of Marine Science* **43**, 41-60.
- Pearse, A.S. 1932. Inhabitants of certain sponges at Dry Tortugas. *Carnegie Institut of Washington, Papers of Torugas Laboratory* **28**, 117-124.
- Pérès, J.-M. 1949. Sur un cas nouveau de parasitisme chez les Polychètes. *Bulletin de l'Institut Océanographique (Foundation Albert 1er, Prince de Monaco)* **46 number 945**, 1-4.
- Petersen, M.E. & Britayev, T.A. 1997. A new genus and species of polynoid scaleworm commensal with *Chaetopterus appendiculatus* Grube from the Banda Sea (Annelida: Polychaeta), with a review of commensals of Chaetopteridae. *Bulletin of Marine Science* **60**, 261-276.
- Pettibone, M.H. 1953. *Some scale-bearing polychaetes of Puget Sound and adjacent waters*. Seattle: University of Washington Press.
- Pettibone, M.H. 1954. Marine polychaete worms from Point Barrow, Alaska, with additional records from the North Atlantic and North Pacific. *Proceedings of the United States National Museum* **103**, 203-356.
- Pettibone, M.H. 1955. New species of polychaete worms of the family Polynoidae from east coast of North America. *Journal of the Washington Academy of Sciences* **45**, 119-126.
- Pettibone, M.H. 1956. Some polychaete worms of the families Hesionidae, Syllidae, and Nereidae from the coast of North America, West Indies, and Gulf of Mexico. *Journal of the Washington Academy of Sciences* **46**, 281-294.
- Pettibone, M.H. 1957. Endoparasitic polychaetous annelids of the family Arabellidae with descriptions of new species. *Biological Bulletin of the marine biological Laboratory, Woods Hole* **113**, 170-187.
- Pettibone, M.H. 1961. New species of polychaete worms from the Atlantic ocean, with a revision of the Dorvilleidae. *Proceedings of the Biological Society of Washington* **74**, 167-186.
- Pettibone, M.H. 1963. *Marine polychaete worms of the New England region. 1. Families Aphroditidae through Trochochaetidae*. Washington: Smithsonian Institution.
- Pettibone, M.H. 1969a. Review of some species referred to *Scalissetosus* McIntosh (Polychaeta, Polynoidae). *Proceedings of the Biological Society of Washington* **82**, 1-30.
- Pettibone, M.H. 1969b. Remarks on the North Pacific *Harmothoe tenebricosa* Moore (Polychaeta, Polynoidae) and its association with asteroids (Echinodermata, Asteroidea). *Proceedings of the Biological Society of Washington* **82**, 31-42.
- Pettibone, M.H. 1969c. The genera *Polyeunoa* McIntosh, *Hololepidella* Willei, and three new genera

- (Polychaeta, Polynoidae). *Proceedings of the Biological Society of Washington* **82**, 43-62.
- Pettibone, M.H. 1969d. *Australaugenira pottsi*, new name for *Polynoe longicirrus* Potts, from the Maldive Islands (Polychaeta: Polynoidae). *Proceedings of the Biological Society of Washington* **82**, 519-524.
- Pettibone, M.H. 1969e. Revision of the Aphroditoid Polychaetes of the Family Eulephthidae Chamberlin (= Eulepidinae Darboux; = Pareulepididae Hartman). *Smithsonian Contributions to Zoology* **41**, 1-44.
- Pettibone, M.H. 1970. Polychaeta Errantia of the Siboga Expedition. Part IV. Some additional polychaetes of the Polynoidae, Hesionidae, Nereidae, Goniadidae, Eunicidae, and Onuphidae, selected as new species by the late Dr. Hermann Augener with remarks on other related species. In *Siboga-Expeditie Uitkomsten op Zoologisch, Botanisch, Oceanographisch en Geologisch gebied verzameld in Nederlandsch Oost-Indië 1899-1900*, M. Weber, L.F.de Beaufort & J.H. Stock (eds.), Leiden: E.J. Brill, pp. 199-270.
- Pettibone, M.H. 1975. Review of the genus *Hermenia* with a description of a new species (Polychaeta: Polynoidae: Lepidonotinae). *Proceedings of the Biological Society of Washington* **88**, 233-248.
- Pettibone, M.H. 1977. Review of *Halosydropsis* and related genera (Polychaeta: Polynoidae: Lepidonotinae). In *Essays on Polychaetous annelids in memory of Dr. Olga Hartman*, D.J. Reish & K. Fauchald (eds.), Los Angeles: University of South California Press, pp. 39-62.
- Pettibone, M.H. 1982. Annelida. Polychaeta. In *Synopsis and classification of living organisms*, S.P. Parker (ed.), New York: McGraw-Hill Book Company, pp. 3-43.
- Pettibone, M.H. 1983. *Minusculisquama hughesi*, a new genus and species of scale-worm (Polychaeta: Polynoidae) from Eastern Canada. *Proceedings of the Biological Society of Washington* **96**, 400-406.
- Pettibone, M.H. 1984a. A new scale-worm commensal with deep-sea mussels on the Galapagos hydrothermal vent (Polychaeta: Polynoidae). *Proceedings of the Biological Society of Washington* **97**, 226-239.
- Pettibone, M.H. 1984b. Two new species of *Lepidonotopodium* (Polychaeta: Polynoidae: Lepidonotopodinae) from hydrothermal vents off the Galapagos and East Pacific Rise at 21°N. *Proceedings of the Biological Society of Washington* **97**, 849-863.
- Pettibone, M.H. 1986a. A new scale worm commensal with deep-sea mussels in the seep-sites at the Florida Escarpment in the Eastern Gulf of Mexico (Polychaeta: Polynoidae: Branchipolynoidae). *Proceedings of the Biological Society of Washington* **99**, 444-451.
- Pettibone, M.H. 1986b. Review of the Iphioninae (Polychaeta: Polynoidae) and revision of *Iphione cimex* Quatrefages, *Gattyana deludens* Fauvel, and *Harmothoe iphionelloides* Johnson (Harmothoinae). *Smithsonian Contributions to Zoology* **428**, 1-43.
- Pettibone, M.H. 1989a. A new species of *Benhamipolynoe* (Polychaeta: Polynoidae: Lepidasteniinae) from Australia, associated with the unattached stylasterid coral *Conopora adeta*. *Proceedings of the Biological Society of Washington* **102**, 300-304.
- Pettibone, M.H. 1989b. Revision of the Aphroditoid Polychaetes of the family Acoetidae Kinberg (= Polyodontidae Augener) and reestablishment of *Acoetes* Audouin and Milne-Edwards, 1832, and *Euarche* Ehlers, 1887. *Smithsonian Contributions to Zoology* **464**, 1-138.
- Pettibone, M.H. 1990. New species and new records of scaled polychaetes (Polychaeta: Polynoidae) from the axial seamount caldera of the Juan de Fuca Ridge in the Northeast Pacific and the East Pacific Ocean off Northern California. *Proceedings of the Biological Society of Washington* **103**, 825-838.
- Pettibone, M.H. 1991a. Polynoids commensal with gorgonian and stylasterid corals, with a new genus, new combinations, and new species (Polychaeta: Polynoidae: Polynoinae). *Proceedings of the Biological Society of Washington* **104**, 688-713.
- Pettibone, M.H. 1991b. Polynoid polychaetes commensal with antipatharian corals. *Proceedings of the Biological Society of Washington* **104**, 714-726.
- Pettibone, M.H. 1993. Scaled polychaetes (Polynoidae) associated with ophiuroids and other invertebrates and review of species referred to *Malmgrenia* McIntosh and replaced by *Malmgeniella* Hartman, with descriptions of new taxa. *Smithsonian Contributions to Zoology* **538**, 1-92.
- Pettibone, M.H. 1996. Revision of the scaleworm genera *Acholoe* Claparède, *Arctonoella* Buzhinskaja, and *Intoshella* Darboux (Polychaeta, Polynoidae) with the erection of the new subfamily Acholoinae. *Proceedings of the Biological Society of Washington* **109**, 629-644.
- Pfannenstiel, H.D., Grothe, C. & Kegel, B. 1982. Studies on *Ophryotrocha geryoncola* (Polychaeta, Dorvilleidae). *Helgoländer Meeresuntersuchungen* **35**, 119-125.

- Pilger, J. 1971. A new species of *Iphitime* (Polychaeta) from *Cancer antennarius* (Crustacea: Decapoda). *Bulletin of the Southern California Academy of Sciences* **70**, 84-87.
- Potts, F.A. 1910. Polychaeta of the Indian ocean. Pt. 2. The Palmyridae, Aphroditidae, Polynoidae, Acoetidae and Sigalionidae. *Transactions of the Linnaeus Society of Zoology, series 2* **16**, 325-353.
- Potts, F.A. 1912. A new type of parasitism in the Polychaeta. *Proceedings of the Cambridge Philosophical Society* **16**, 409-413.
- Potts, F.A. 1915. The fauna associated with the crinoids of a tropical coral reef; with species reference to its colour variations. *Papers from the Tortugas Laboratory, Carnegie Institution* **8**, 71-96.
- Rabaud, E. 1939. *Nereis fucata* Sav. et la notion de commensalisme. *Bulletin de biologie de la France et de Belgique* **73**, 293-302.
- Radashevsky, V.I. 1988. Morphology, ecology, reproduction and larval development of *Polydora uschakovi* (Polychaeta, Spionidae) in the Peter the Great Bay of the Sea of Japan. [In Russian]. *Zoologicheski Zhurnal* **67**, 870-878.
- Radashevsky, V.I. 1989. Ecology, sex determination, reproduction and larval development of commensal Polychaetes *Polydora commensalis* and *Polydora glycymerica* in the Japanese Sea. [In Russian]. In *Simbiosis in marine animals*, V.A. Sveshnicov (ed.), Moscow: A.N. Severtzov Institute, Russian Academy of Sciences, pp. 137-164.
- Radashevsky, V.I. 1993. Revision of the genus *Polydora* and related genera from the North West Pacific (Polychaeta, Spionidae). *Publications of the Seto Marine Biological Laboratory* **36**, 1-60.
- Radashevsky, V.I. 1996. Morphology, ecology and asexual reproduction of a new *Polydorella* species (Polychaeta: Spionidae) from the South China Sea. *Bulletin of Marine Science* **58**, 684-693.
- Rainer, S.F. 1973. *Polydora* and related genera (Polychaeta: Spionidae) from Otago waters. *Journal of the Royal Society of New Zealand* **3**, 345-564.
- Ramberg, J.P. & Schram, T.A. 1982. A systematic review of the Oslofjord species of *Polydora* Bosc and *Pseudopolydora* Czerniavsky, with some new biological and ecological data (Polychaeta: Spionidae). *Sarsia* **68**, 233-247.
- Read, G.B. 1975. Systematics and biology of polydorid species (Polychaeta: Spionidae) from Wellington Harbour. *Journal of the Royal Society of New Zealand* **5**, 395-419.
- Reise, K. & Ax, P. 1979. A meiofaunal "thiobios" limited to the anaerobic sulfide system of marine sand does not exist. *Marine Biology* **54**, 225-237.
- Reish, D.J. 1957. The life history of the polychaetous annelid *Neanthes caudata* (delle Chiaje), including a summary of development in the family Nereidae. *Pacific Science* **11**, 216-228.
- Reiswig, H.M. 1973. Population dynamics of Jamaican Demospongiae. *Bulletin of Marine Science* **23**, 191-226.
- Rhode, K. 1981. The nature of parasitism. In *Australian Ecology Series: Ecology of marine parasites*, H. Heatwole (ed.), St. Lucia: University of Queensland Press, pp. 4-5.
- Ricketts, E.F., Calvin, J., Hedgpeth, J.W. & Phillips, D.W. 1985. *Between Pacific tides*. Stanford: Stanford University Press.
- Ricklefs, R.E. 1990. *Ecology*. New York: W.H. Freeman.
- Riser, N.W. 1982. Observations on some poorly known syllid polychaetes from the Gulf of Maine. *Canadian Journal of Zoology* **60**, 105-111.
- Rosell, D. 1996. Systematics, biology and ecology of Mediterranean excavating sponges. Doctoral Thesis, Universitat de Barcelona, Barcelona.
- Rosell, D. & Uriz, M.J. 1991. *Cliona viridis* (Schmidt, 1862) and *Cliona nigricans* (Schmidt, 1862) (Porifera, Hadromerida): Evidence which shows they are the same species. *Ophelia* **33**, 45-53.
- Rossi, M.M. 1984. A new genus and species of Iphitimid parasitic in an Aphroditid (Polychaeta), with an emendation of the family Iphitimidae. *Bulletin of the Southern California Academy of Sciences* **83**, 163-166.
- Rozbaczylo, N. & Cañete, J.I. 1993. A new species of scale-worm, *Harmothoe commensalis* (Polychaeta: Polynoidae), from mantle cavities of two Chilean clams. *Proceedings of the Biological Society of Washington* **106**, 666-672.
- Ruff, R.E. 1991. A new species of *Bathynoe* (Polychaeta: Polynoidae) from the Northeast Pacific Ocean commensal with two species of deep-water asteroids. *Ophelia* **5**, 219-230.
- Ruff, R.E. 1995. 3. Family Polynoidae Malmgren, 1867. In *Taxonomic atlas of the benthic fauna of the Santa Barbara Basin and western Santa Barbara Channel. Vol. 5 - The Annelida part 2. Polychaeta: Phyllodocida (Syllidae and scale-bearing families) Amphinomida and Eunicida*, J.A. Blake, B. Hilbig & P.H. Scott (eds.), Santa Barbara: Santa Barbara Museum of Natural

- History, pp. 105-166.
- Rullier, F. 1972. Annélides polychètes de Nouvelle-Calédonie recueillies par Y. Plessis et B. Salvat. *Expédition Française sur les Récifs Coralliens de la Nouvelle-Calédonie* **6**, 1-169.
- Rullier, F. 1974. Quelques annelides polychètes de Cuba recueillies dans des éponges. *Travaux du Muséum d'Histoire Naturelle Grigore Antipa* **14**, 9-77.
- Rullier, F. & Amoureux, L. 1979. Campagne de la Calypso au large des côtes Atlantiques de l'Amérique du Sud (1961-1962). I. 33. Annélides Polychètes. *Annales do Instituto de Oceanografia* **55**, 145-206.
- Rzhavsky, A.V. & Britayev, T.A. 1988. Specific features of colonies of *Circeis armoricana* (Spirorbidae, Polychaeta) on hermit crabs on the East Kamchatka coast. [In Russian]. *Zoologicheski Zhurnal* **61**, 17-22.
- Saint-Joseph, A.de 1888. Les Annelides polychètes des côtes de Dinard, pt. 2. *Annals of Scientia Naturae* **5**, 141-338.
- San Martín, G. 1984. Estudio biogeográfico, Faunístico y sistemático de los poliquetos de la familia sílidos (Syllidae, Polychaeta) en Baleares. Doctoral Thesis, Universidad Complutense.
- San Martín, G. & Sardá, R. 1986. Sobre la presencia de un Arabélido (Polychaeta: Arabellidae) parásito de Sílicos (Polychaeta: Syllidae), del género *Labrorostratus* en las costas españolas. *Boletín de la Real Sociedad Española de Historia Natural (Sección Biología)* **82**, 141-146.
- San Martín, G., Ibarzábal, D., Jiménez, M. & López, E. 1997. Redescription of *Haplosyllides floridana* Augener, 1924 (Polychaeta, Syllidae, Syllinae), with notes on morphological variability and comments on the generic status. *Bulletin of Marine Science* **60**, 364-370.
- Sardá, R. 1984. Estudio sobre los Poliquetos de las zonas mediolitoral e infralitoral de la región del Estrecho de Gibraltar. Doctoral Thesis, Universidad de Barcelona.
- Sato-Okoshi, W. & Okoshi, K. 1993. Microarchitecture of scallop and oyster shells infested with boring *Polydora*. *Nippon Suisan Gakkaishi* **59**, 1243-1247.
- Simon, J.L. 1967. Behavioral aspects of *Histriobdella homari*, an annelid commensal of the American lobster. *Biological Bulletin of the marine biological Laboratory, Woods Hole* **133**, 450.
- Simon, J.L. 1968. Incidence and behavior of *Histriobdella homari* (Annelida: Polychaeta), a commensal of the American lobster. *Bioscience* **18**, 35-36.
- Southern, R. 1914. Archannelida and Polychaeta, in Clare Island survey, pt. 47. *Proceedings of the Royal Irish Academy, Dublin* **31**, 1-160.
- Southward, E.C. 1956. On some polychaetes of the Isle of Man. *Annals and Magazine of Natural History* **12**, 257-279.
- Spies, R.B. 1977. Reproduction and larval development of *Flabelliderma commensalis* (Moore). In *Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman*, D.J. Reish & K. Fauchald (eds.), Los Angeles: The Allan Hancock Foundation, University of Southern California, pp. 323-345.
- Spooner, G.M., Wilson, D.P. & Trebble, N. 1957. Phylum Annelida. In *Plymouth Marine Fauna*, (), Plymouth: Marine Biological Association U.K., .
- Steinbeck, J. & Ricketts, E.F. 1941. *Sea of Cortez. A leisurely journal of travel and research. With a scientific appendix comprising materials for a source book on the marine animals of the Panamic faunal province*. New York: Viking Press.
- Stewart, W.C. 1970. A study of the nature of the attractant emitted by the asteroid host of the commensal polychaete *Ophiodromus pugettensis*. Dissertation, University of California.
- Stock, J.H. 1986. Cases of hyperassociation in the Copepoda (Herphyllobiidae and Nereicolidae). *Systematics and Parasitology* **8**, 71-81.
- Storch, V. & Niggemann, R. 1967. Auf Echinodermen lebende Polychaeten. *Kieler Meeresforschungen* **23**, 156-164.
- Storch, V. & Rosito, R.M. 1981. Polychaetes from interspecific associations found off Cebu. *The Philippine Scientist* **18**, 1-9.
- Storm, V. 1881. Bidrag til Kundskab om Thronhjemsfjordens Fauna III. *Kongelige Norske videnskabers selskabs skrifter* **1881**, 73-96.
- Thesunov, A.V., Britayev, T.A., Larionov, V.V., Khodkina, I.V. & Tzetlin, A.B. 1989. Notes on commensals of some crinoids from Maldivian coral reefs [In Russian]. In *Symbiosis among marine animals*, V.A. Sveshnicov (ed.), Moscow: A.N. Severtzov Institute, Russian Academy of Sciences, pp. 166-192.
- Thorson, G. 1949. Om eremit kraeften och dens kommensal *Nereis fucata*. *Svensk faunistisk revy* **11**, 93-98.
- Tkachuk, L.P. 1988. Vermins of the Black Sea mussel plantations. *Ekologika Morya* **30**, 60-64.

- Treadwell, A.L. 1909. *Haplosyllis cephalata* as an ectoparasite. *Bulletin of the American Museum of Natural History* **26**, 359-360.
- Treadwell, A.L. 1921. Leodicidae of the West Indian region. *Publications of the Carnegie Institut of Wasington* **15**, 1-13.
- Treadwell, A.L. 1940. A new genus and two new species of polychaetous annelids from Texas and one new species from the Philippine islands. *American Museum Novitates* **1089**, 1-4.
- Tsurumi, M. & Reiswig, M. 1997. Sexual versus asexual reproduction in an oviparous rope-form sponge, *Aplysina cauliformis* (Porifera, Verongida). *Invertebrate Reproduction and Development* **32**, 1-9.
- Tzetlin, A.B. 1985. *Asetocalamyzas laonicola* gen et sp. n., a new ectoparasitic polychaete from the White Sea [In Russian]. *Zoologicheski Zhurnal* **64**, 269-298.
- Tzetlin, A.B. & Britayev, T.A. 1985. A new species of Spionidae (Polychaeta) with asexual reproduction associated with sponges. *Zoologica Scripta* **14**, 177-181.
- Uchida, H. 1975. Ectocommensal polynoids (Annelida, Polychaeta) associated with the echinoderms. *Bulletin of the Marine Park Reservation Stations* **1**, 19-30.
- Uchida, H. 1978. Serpulid tube worms (Polychaeta, Sedentaria) from Japan with the systematic review of the group. *Bulletin of the Marine Park Reservation Stations* **2**, 1-98.
- Uebelacker, J.M. 1978. A new parasitic Polychaetous Annelid (Arabellidae) from the Bahamas. *Journal of Parasitology* **64**, 151-154.
- Uebelacker, J.M. 1982. *Haplosyllis agelas*, a new polychaetous annelid (Syllidae) from the Bahamas. *Bulletin of Marine Science* **32**, 856-861.
- Uriz, M.J. 1983. Monografia I. Contribución a la fauna de esponjas (Demospongia) de Catalunya. *Anales de la Sección de Ciencias del Colegio Universitario de Gerona* **7**, 1-220.
- Uschakov, P.V. 1950. Polychaetes from the Sea of Okothsk. [In Russian]. *Issledovaniya dal'nevostochnykh Morei SSSR* **2**, 140-236.
- Uschakov, P.V. 1955. Polychaetous annelids of the Far Eastern seas of the USSR [In Russian]. *Akademiya Nauk SSSR* **56**, 1-433.
- Uschakov, P.V. 1962. Polychaetous annelids of the family Phyllodocidae and Aphroditidae from the An tarctic and Subantarctic. [In Russian]. *Isseldovaniya Fauni Moorei* **1**, 129-189.
- Uschakov, P.V. 1982. *Fauna of the USSR. 2(1): Polychaetes. Polychaetes of the Suborder Aphroditiformia of the Arctic Ocean and the Northwestern Part of the Pacific, Families Aphroditidae and Polynoidae.* [In Russian]. Moscow: NAUKA, Academy of Sciences of the USSR, Zoological Institute.
- Uschakov, P.V. & Wu, B.L. 1959. The polychaetous annelids of the families Phyllodocidae and Aphroditidae from the Yellow Sea. [In Russian]. *Archives de l'Institut d'Océanologie Sinica* **1**, 1-40.
- Utinomi, H. 1956. On the so-called 'Umi-Utiwa' a peculiar flabellate gorgonacean, with notes on a syllidean polychaete commensal. *Publications of the Seto Marine Biological Laboratory* **5**, 243-250.
- Uzmann, J.R. 1967. *Histriobdella homari* (Annelida: Polychaeta) in the American lobster *Homarus americanus*. *Journal of Parasitology* **53**, 210-211.
- Verrill, A.E. 1881. New England Annelida. Part I. Historical sketch, with annotated lists of the species hitherto recorded. *Transactions of the Conneticut Academy of Arts and Sciences* **4**, 285-324.
- Vila, P.I. & Bahamonde, N. 1985. Two new species of *Stratiodrilus*, *S. aeglaphilus* and *S. pugnaxi* (Annelida: Histiobdellidae) from Chile. *Proceedings of the Biological Society of Washington* **98**, 347-350.
- Voultsiadou-Koukoura, E., Koukouras, A. & Eleftheriou, A. 1987. Macrofauna associated with the sponge *Verongia aerophoba* in the North Aegean Sea. *Estuarine, Coastal and shelf Science* **24**, 265-278.
- Wagner, R.H., Phillips, D.W., Standing, J.D. & Hand, C. 1979. Commensalism or mutualism: attraction of a sea star towards a symbiotic polychaete. *Journal of Experimental Marine Biology and Ecology* **39**, 205-210.
- Webster, H.E. 1879. The Annelida Chaetopoda of New Jersey. *Annual Reports of the New York State Museum of Natural History* **32**, 101-128.
- Webster, H.E. 1879. The Annelida Chaetopoda of the Virginian coast. *Transactions Albany Institute New York* **9**, 202-272.
- Webster, S.K. 1968. An investigation of the commensals of *Cryptochiton stellaris* (Middendorf, 1846) in the Monterey Peninsula area, California. *The Veliger* **11**, 121-125.
- Wesenberg-Lund, E. 1938. *Ophryotrocha gerionicola* (Bidenkap) (=Eteonopsis geryonicola

- Bidenkap) refound and redescribed. *Göteborgs K niglich vetenskaps- och vitterhetssamh lles handlingar, Series B* **6**, 1-13.
- Wesenberg-Lund, E. 1941. Notes on the Polychaeta I. 1. *Harmothoe bathydomus* Hj. Ditlevsen refound. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i K benhavn* **105**, 31-32.
- Westheide, W. 1982. *Microphthalmus hamosus* sp. n. (Polychaeta, Hesionidae)- an example of evolution leading from the interstitial fauna to a macrofaunal interspecific relationship. *Zoologica Scripta* **11**, 189-193.
- Westinga, E. & Hoetjes, P.C. 1981. The intrasponge fauna of *Speciospongia vesparia* (Porifera, Demospongiae) at Cura ao and Bonaire. *Marine Biology* **62**, 139-150.
- Wiley, A. 1905. Report on the Polychaeta collected by Professor Herdman, at Ceylon, in 1902. *Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar, with supplementary reports upon the Marine Biology of Ceylon, by Other Naturalists. Part IV supplementary report* **30**, 212-324.
- Wiren, A. 1886. *Haematocleptes terebellidis* nouvelle annelide parasite de la famille des euniciens. *Bihang Till K nliga Svenska Vetenskaps-Akademiens Handlingar* **11**, 1-10.
- Wright, J.D. & Woodwick, K.H. 1977. A new species of *Autolytus* (Polychaeta: Syllidae) commensal on a Californian hydrocoral. *Bulletin of the Southern California Academy of Sciences* **76**, 42-48.
- Wu, B.L., Sun, R.P. & Yang, D.J. 1982. On the occurrence of endoparasitic polychaetous annelids in Chinese waters. [In Chinese]. *Oceanologia et Limnologia Sinica* **13**, 201-204.
- Wu, B.L., Sun, R.P. & Yang, D.J. 1985. *Nereidae (Polychaetous Annelids) of the Chinese Coasts*. Berlin: China Ocean Press Beijing.
- Yamamoto, R. & Imajima, M. 1988. A new species of the genus *Spinther* (Polychaeta, Spintheridae) from Japan. *Bulletin of the National Science Museum of Tokyo, Series A* **11**, 129-135.
- Zibrowius, H., Southward, E.C. & Day, J.H. 1975. New observations on a little-known species of *Lumbrineris* (Polychaeta) living on various Cnidarians, with notes on its recent and fossil Scleractinian hosts. *Journal of the Marine biological Association of the United Kingdom* **55**, 83-108.
- Zottoli, R.A. & Carriker, M.R. 1974. Burrow morphology, tube formation and microarchitecture of shell dissolution by the spionid Polychaete *Polydora websteri*. *Marine Biology* **27**, 307-316.

Fig 1.- A. Number of commensal relationships and number of commensal species from each polychaete family including commensal forms. B. Number of species from each taxonomic group of host harbouring commensal polychaetes and number of relationships on which they are involved.

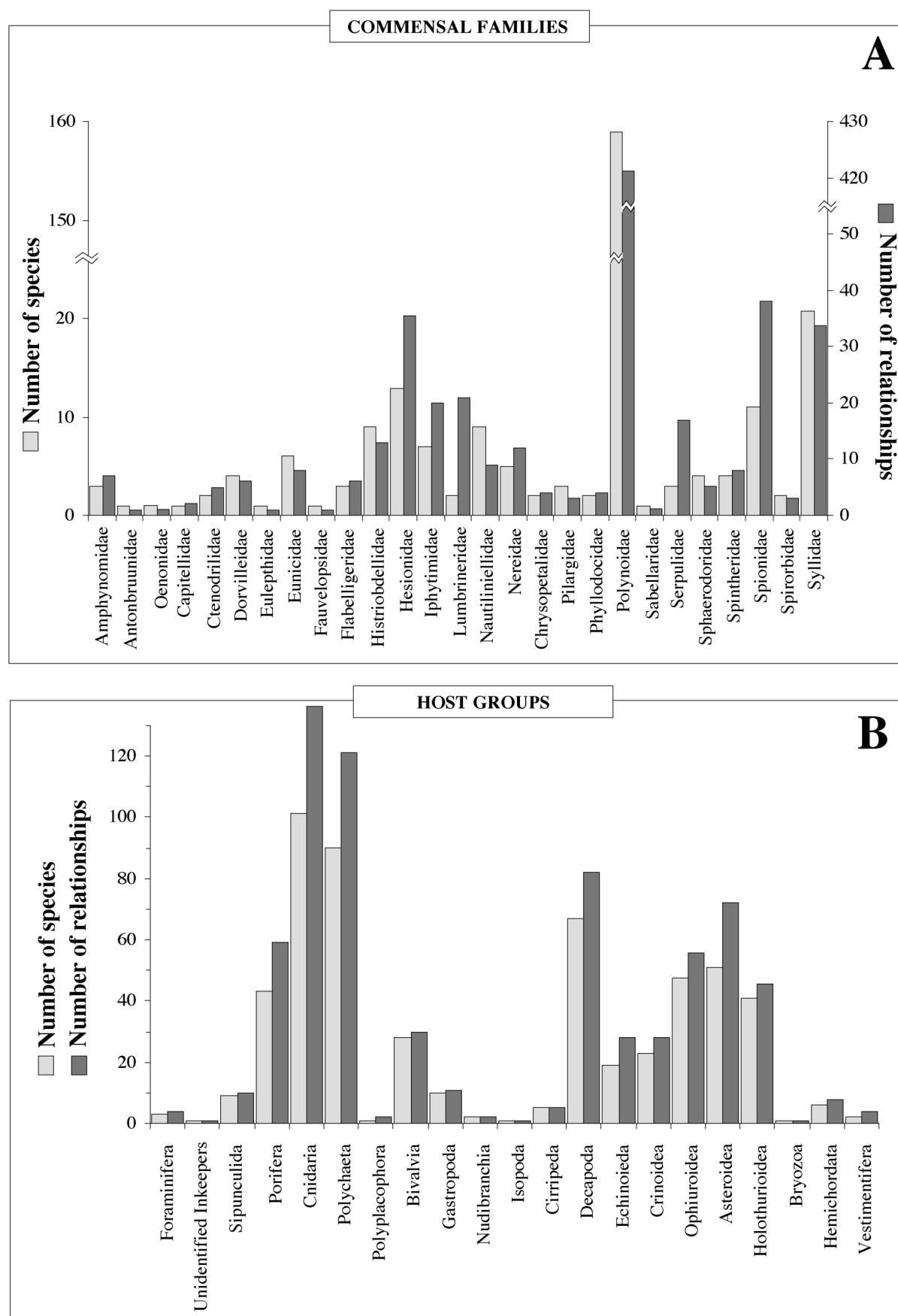


Fig 10.- Examples of hooked setae from commensal Polynoidae. A. *Bathyoe cascadiensis* (redrawn from Ruff 1991). B. *Bathynoe tuberculata* (redrawn from Hanley 1989). C. *Paradyte crinoidicola* (redrawn from Hanley 1984). D. *Australaugeneria pottsi* (redrawn from Pettibone 1969a). E. *Arctonoe pulchra*, F. *Arctonoe vittata*, G. *Arctonoe fragilis* (redrawn from Hanley 1989). H. *Uncapolynoe corrallicola* (redrawn from Hartmann-Schröder 1960). I. *Branchipolynoe symmytilida* (redrawn from Pettibone 1984a). J. *Branchipolynoe pettiboneae*, K. Detail of the parapodium of *Branchipolynoe pettiboneae* (redrawn from Miura & Hashimoto 1991).

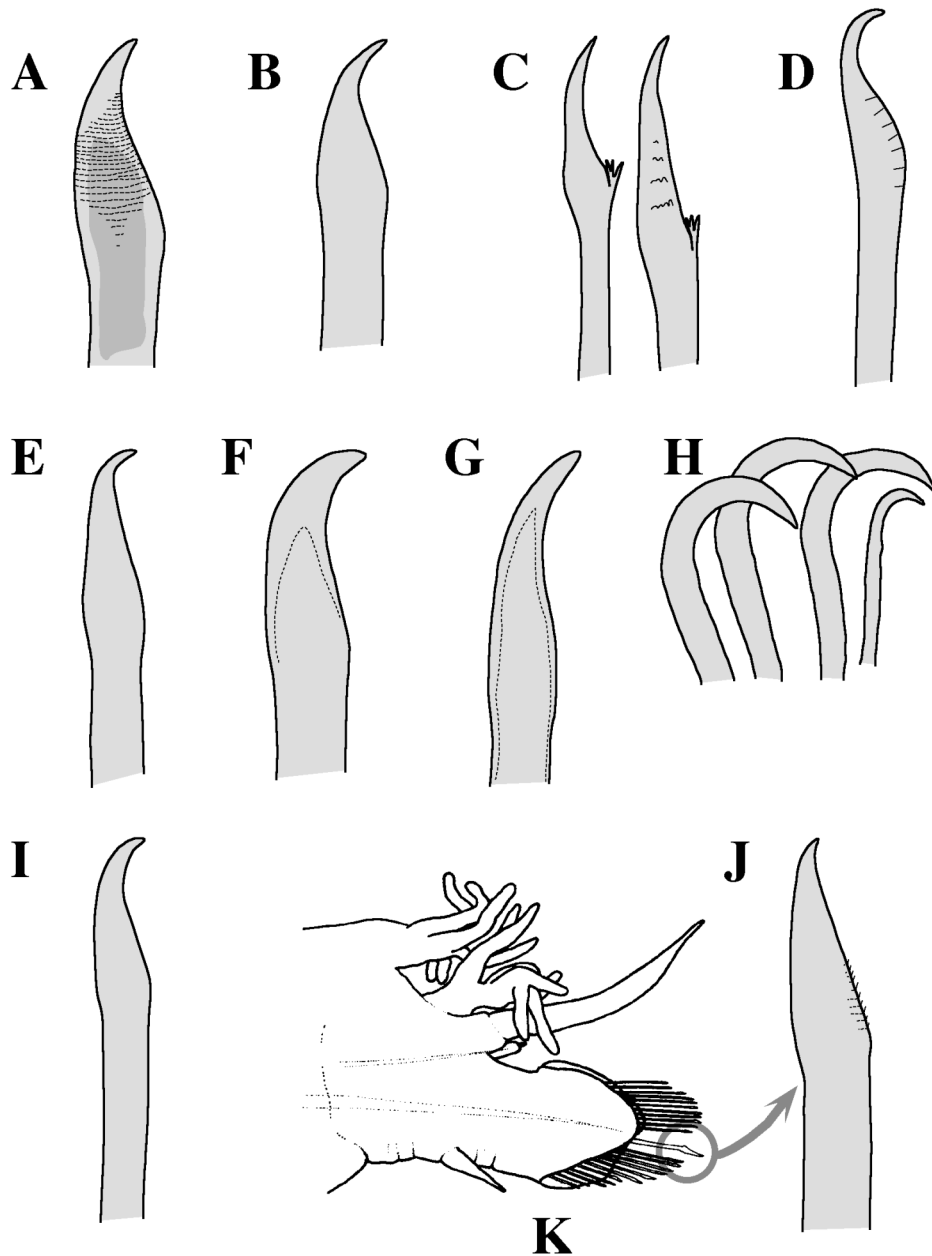


Fig 11.- Examples of hooked setae from the known symbiotic species of *Haplosyllis* and related genus. A. *Haplosyllides floridana* (redrawn from San Martín et al. 1997). B. *Haplosyllis dollfusi* (redrawn from San Martín 1984). C. *Haplosyllis spongicola* (D. Martin, personal observation). D. *Haplosyllis agelas* (redrawn from Uebelacker 1982). E. *Haplosyllis xeniaeicola* (redrawn from Hartmann-Schröder 1993). F. *Haplosyllis anthogorgicola* (redrawn from Imajima & Hartman 1964). G. *Haplosyllis bisetosa* (redrawn from Hartmann-Schröder 1960). H. *Haplosyllis chamaeleon* (redrawn from Laubier 1960). I. *Trypanosyllis asterobia* (redrawn from Imajima 1966).

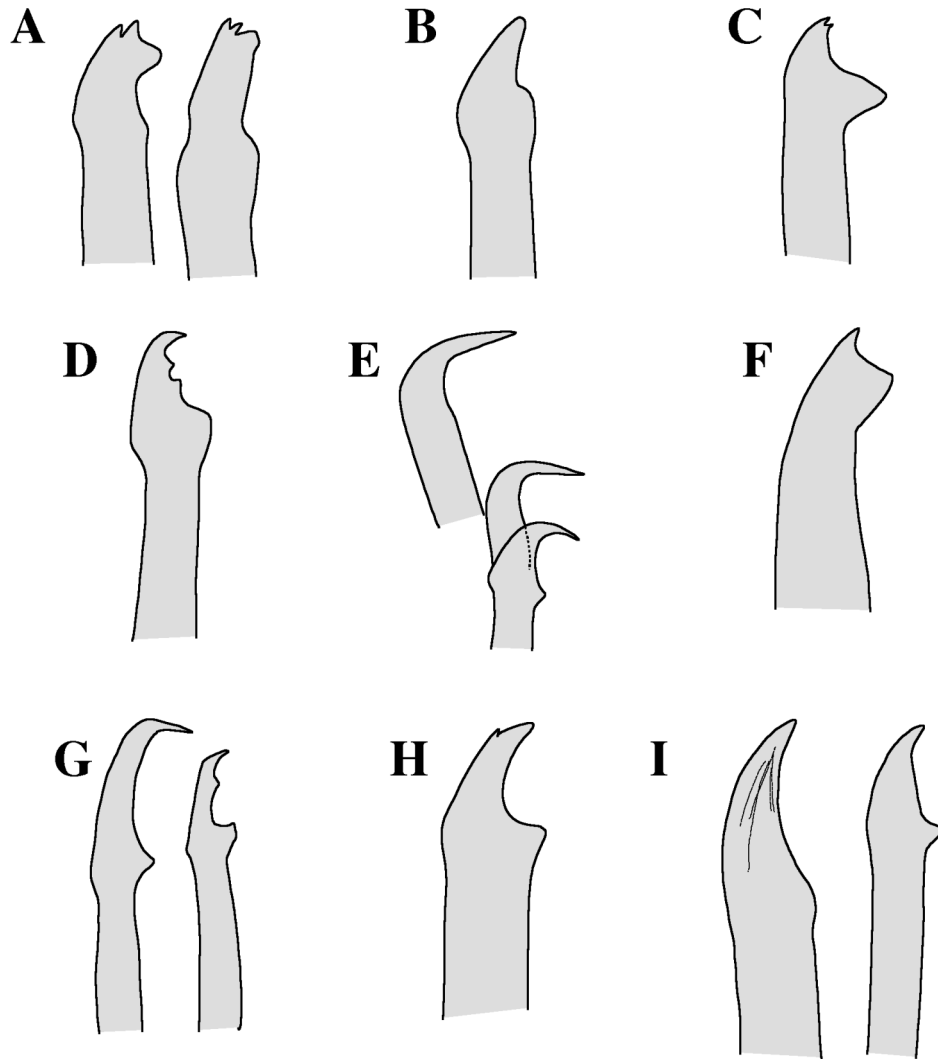


Fig 12.- Jaw apparatus of the known species of *Iphitime*. A. *Iphitime cuenoti* “male” (redrawn from Abelló et al. 1982). B. *Iphitime cuenoti* “female” (redrawn from Abelló et al. 1988). C. *Iphitime dordeleini* (redrawn from Marenzeller 1902). D. *Iphitime holobranchiata* (redrawn from Pilger 1971). E. *Iphitime hartmanae* (redrawn from Kirkegaard 1977). F. *Iphitime paguri* (redrawn from More & Gorzoula 1973). G. *Veneriservia pygoclava* (redrawn from Rossi 1984).

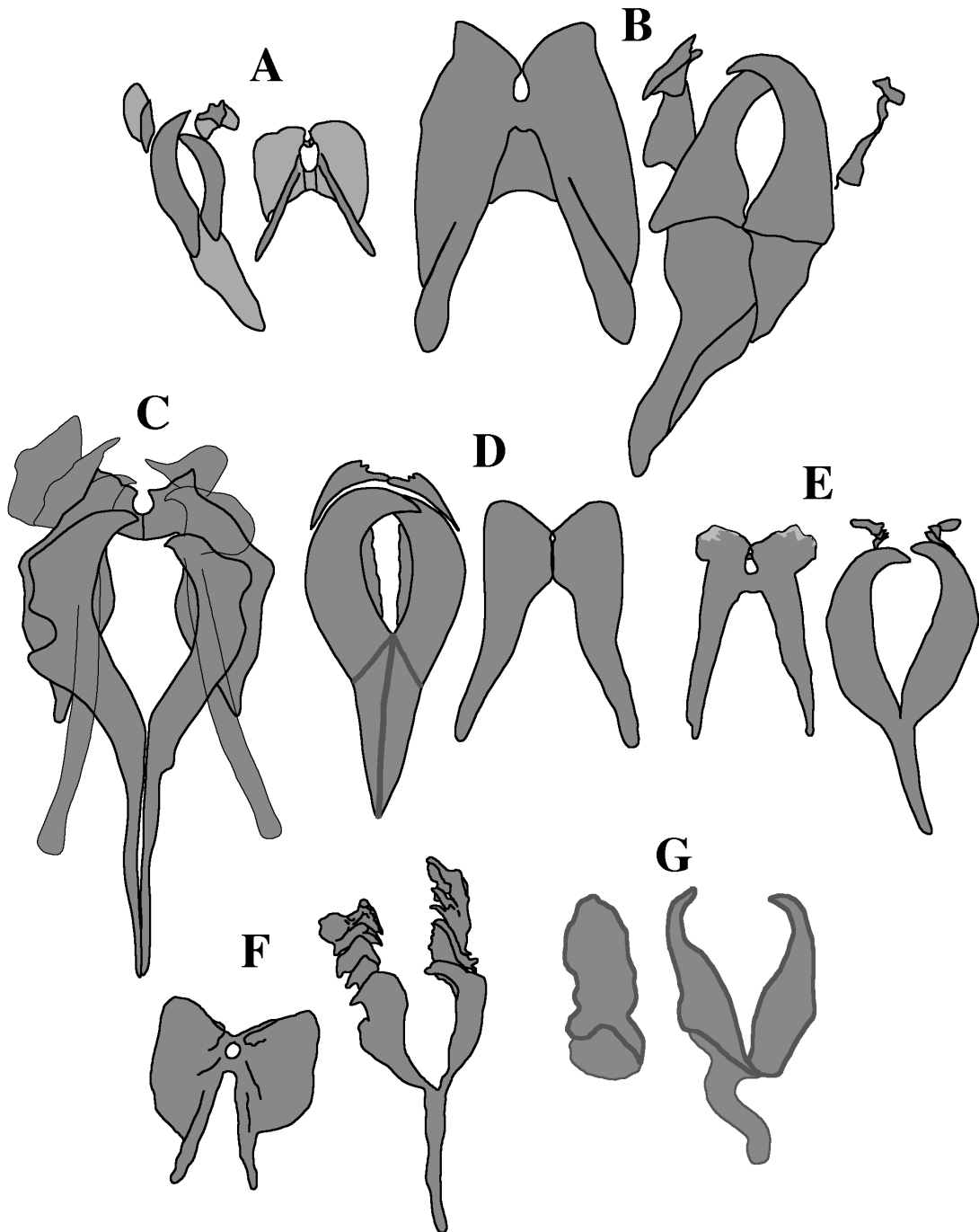


Fig 13.- Examples of morphological modifications in commensal polychaetes. Adaptive modifications: A. Ventral view of *Gastrolepidia clavigera* showing the attachment processes (redrawn from Hanley 1989). B. *Bathynoe cascadiensis* showing the large elytra with numerous prominent nodular macrotubercles (redrawn from Ruff 1991). C. *Asterophilia carlae* showing the swollen head appendages (redrawn from Hanley 1989). D, E. The highly modified males of *Stratiodrilus haswellii* (D, redrawn from Harrison 1928) and *Histriobdella homari* (E, redrawn from George & Hartmann-Schröder 1985). F, G. Dorsal and frontal views of *Ophthalmonoe pettiboneae* head, showing the modified eye position (redrawn from Petersen & Britayev 1997). H, I, J. Progressive elytra smallness in *Lepidasthenia* species: *L. mossambica*, *L. microlepis* and *L. stylolepis* (redrawn from Gibbs 1969).

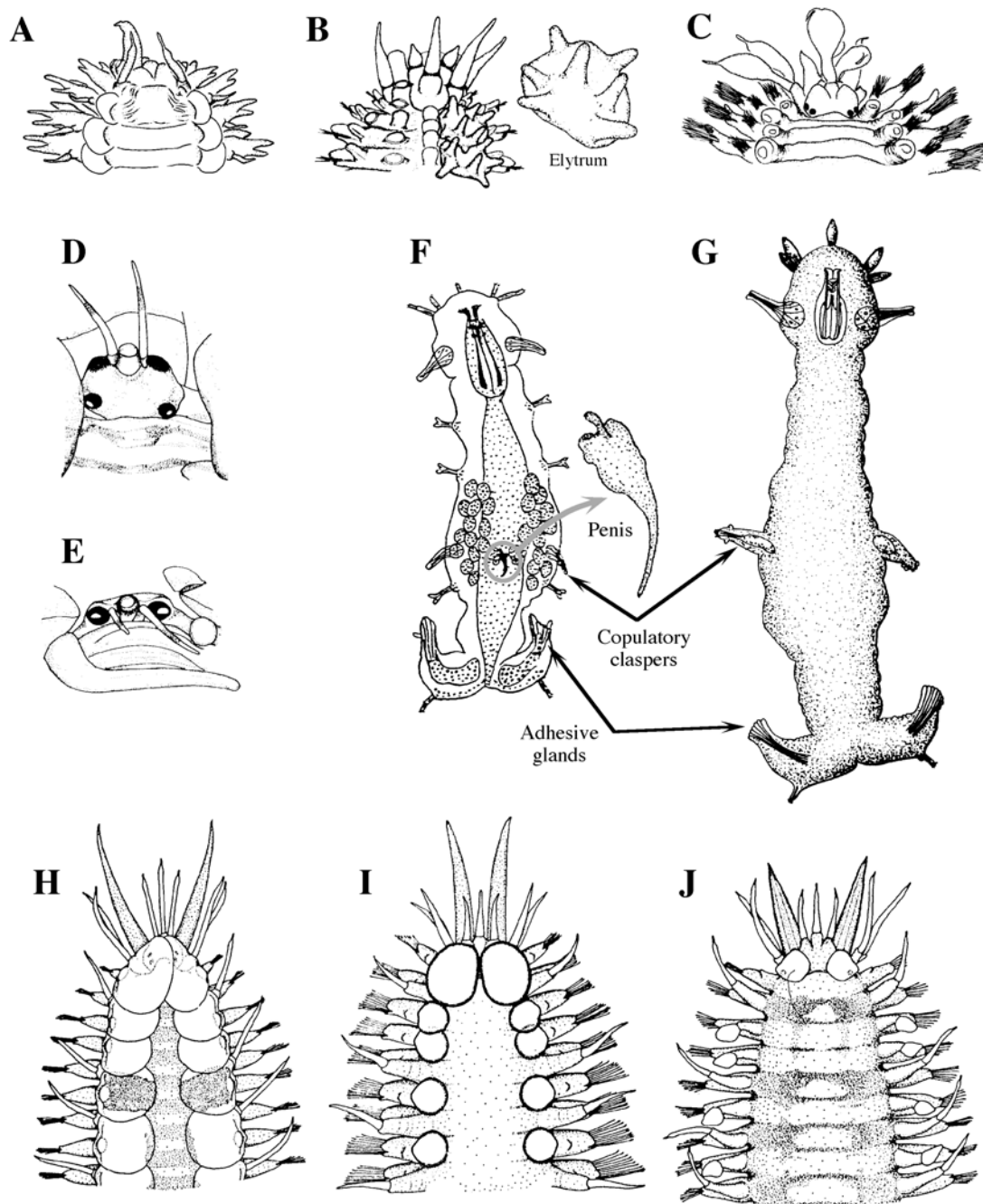


Fig 14.- Life-cycle of *Arctonoe vittata* (redrawn from Britayev 1991).

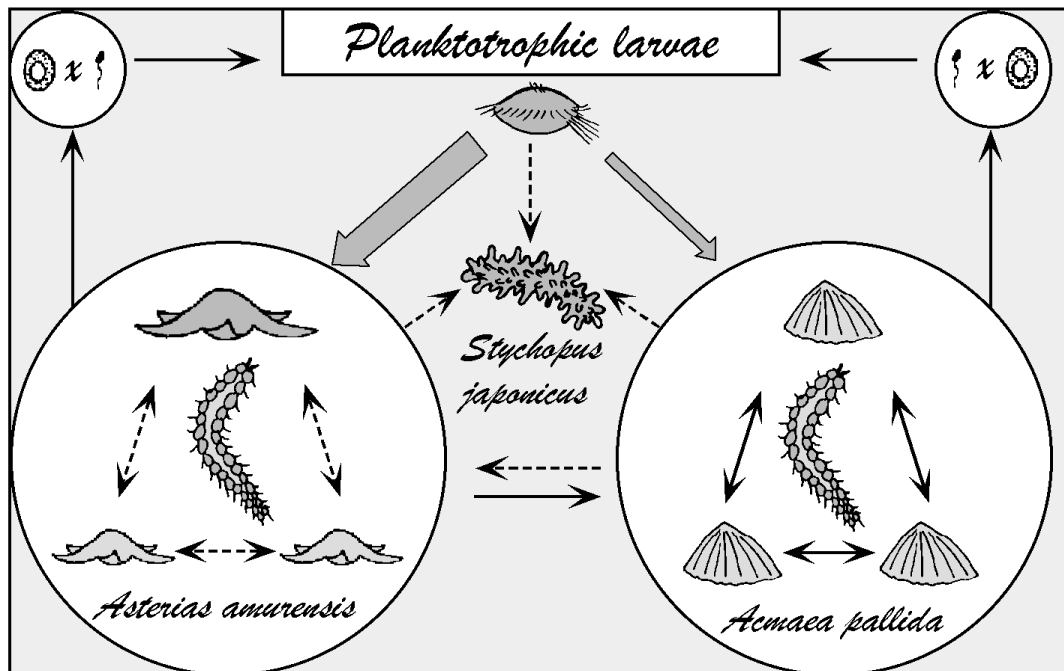


Fig 15.- A. Number of parasitic relationships and number of parasitic species from each polychaete family including parasitic forms. B. Number of species from each taxonomic group of host harbouring parasitic polychaetes and number of relationships on which they are involved.

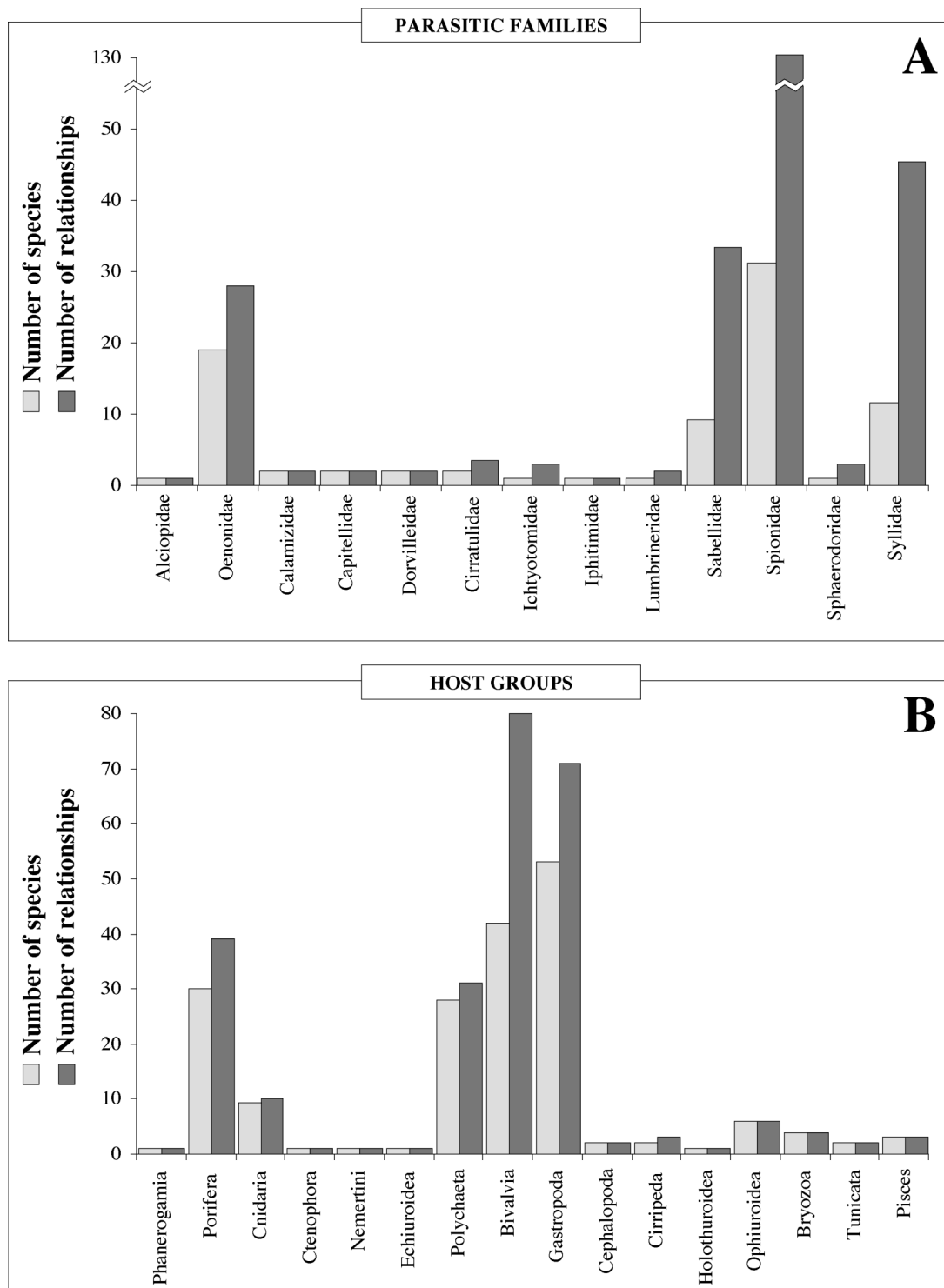


Fig 16.- Examples of endoparasitic polychaetes infesting their hosts. A. *Labrorostratus* sp. on *Grubeosyllis clavata* (redrawn from San Martín & Sardá 1986). B, C. *Labrorostratus parasiticus* on *Sphaerosyllis pirifera* (redrawn from Wu et al. 1982). D. *Labrorostratus luteus* on *Haplosyllis spongicola* (redrawn from Uebelacker 1978). D. *Drilonereis parasiticus* on a terebellid (redrawn from Caullery 1914). E. *Drilonereis* sp. on *Protula tubularia* (redrawn from Pérès 1949). F. *Drilonereis caullery* on *Onuphis conchylega* (redrawn from Pettibone 1957).

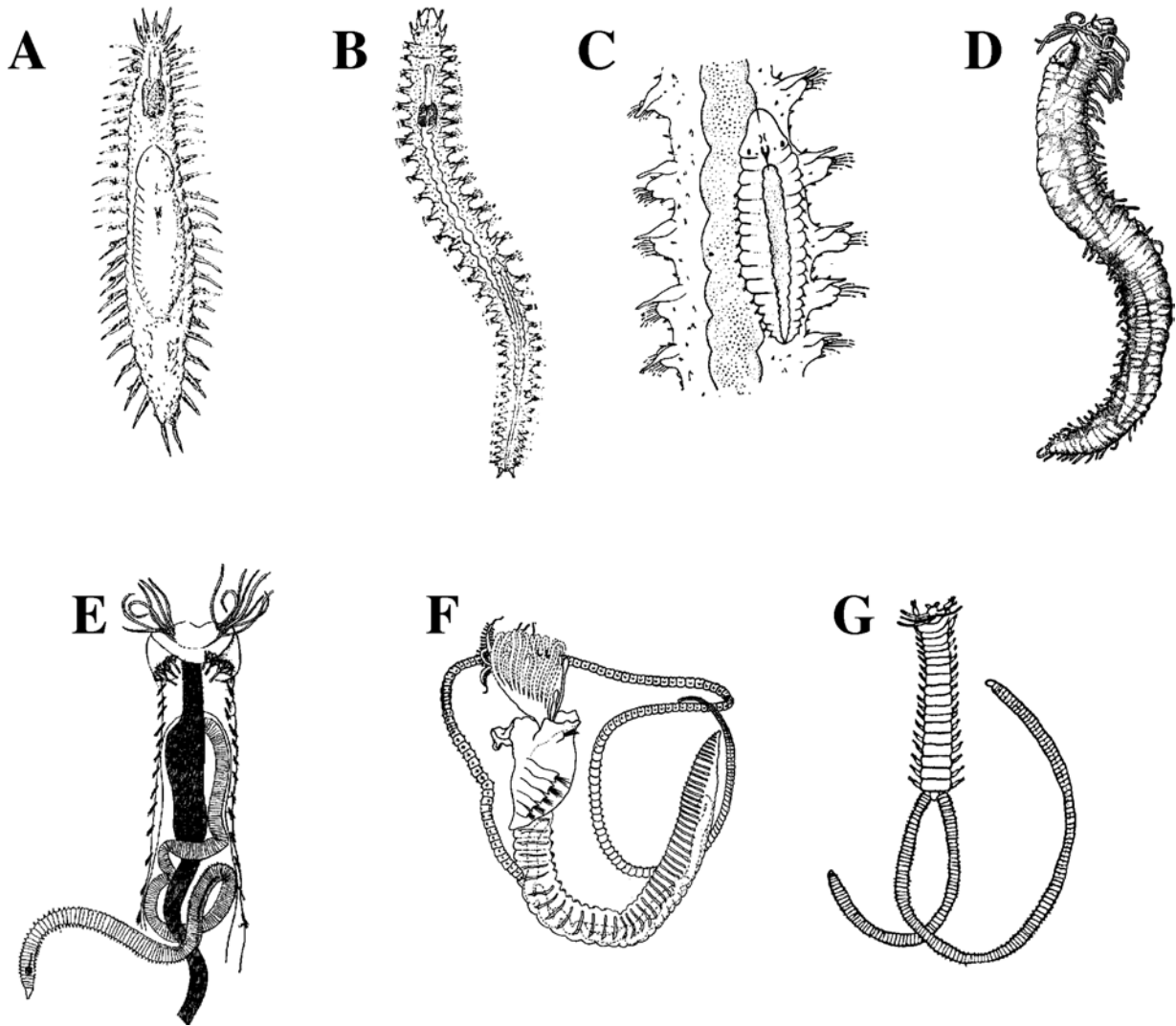


Fig 17.- A. Two specimens of *Haplosyllis spongicola* inside a special chamber formed by the host sponge *Rhizaxinella pyrifer*a (redrawn from Uriz 1983). B. *Haplosyllis spongicola* inside a canal of the *Aplysina cauliformis* aquiferous system, penetrating the canal wall and grazing on the sponge tissues (redrawn from Tsurumi & Reiswig 1997); fa: feeding activity. C. Juvenile *Proceraea* sp. infesting an *Abietinaria turgida* colony, showing a detail of one worm inside a modified hydrothecae (Britayev, San Martin & sheiki, unpublished).

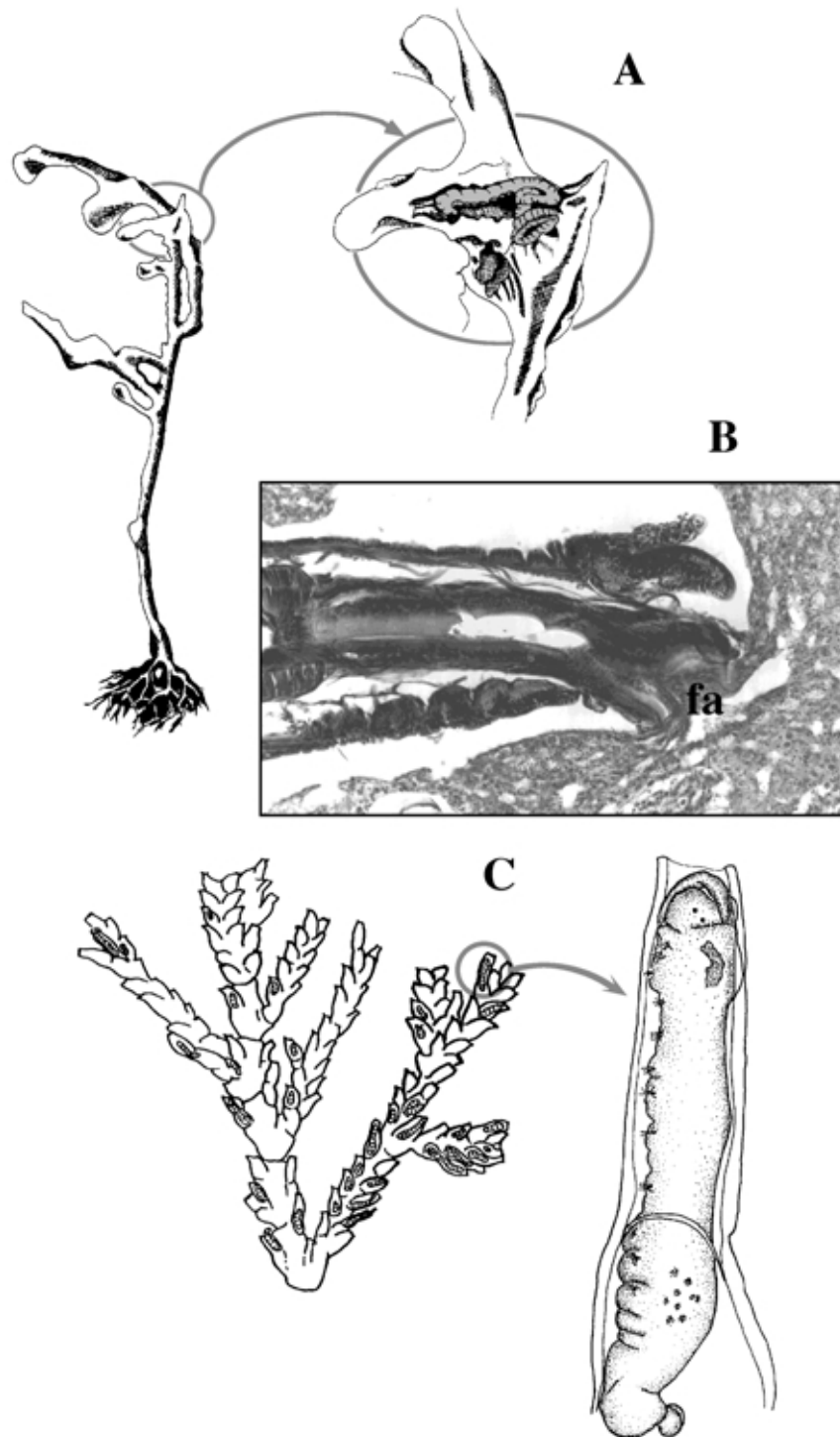


Fig 18.- Scheme of the modifications of the typical setal pattern of Oenonidae as a consequence of the progressive adaptation to the parasitic mode of life (see Table 6 for the respective authorities).

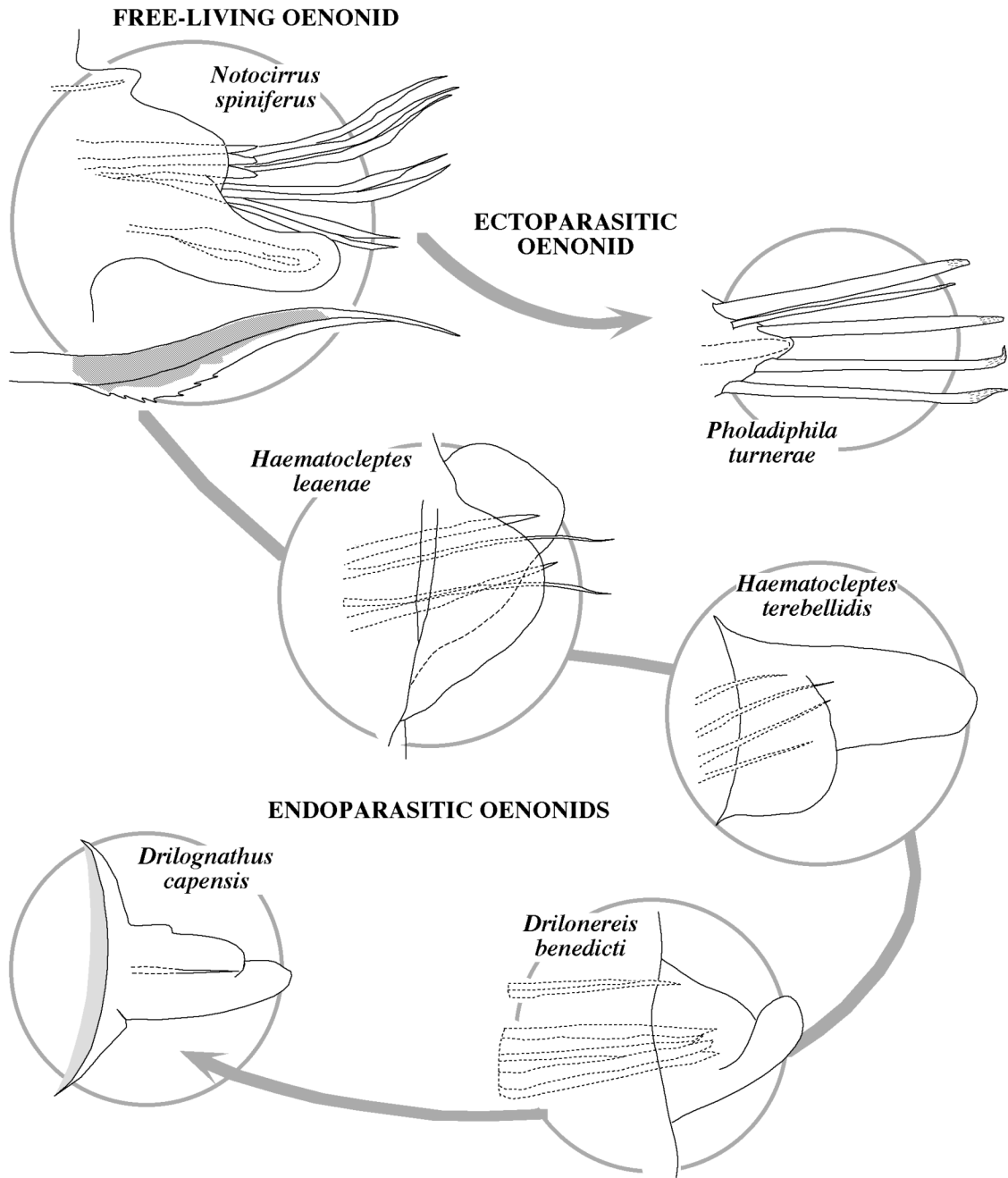


Fig 19.- Jaw apparatus of parasitic Oeononidae, including a representative example of a typical free-living species. A. Free-living, adult *Notocirrus spiniferus* (redrawn from Pettibone 1957). B. *Pholadiphila turnerae* (redrawn from Dean 1992). C. Parasitic juvenile *Notocirrus spiniferus* (redrawn from Pettibone 1957). D. *Drilognathus capensis* (redrawn from Day 1967). E. *Oligognathus bonelliae* (redrawn from Pettibone 1957). F. *Oligognathus parasiticus* (redrawn from Pettibone 1957). G. *Haematoceptes leaenae* (redrawn from Hartman & Fauchald 1971). H. *Haematoceptes terebellides* (redrawn from George & Hartmann-Schröder 1985). I. *Drilonereis caulleri* (redrawn from Pettibone 1957). J. *Drilonereis parasiticus* (redrawn from Pettibone 1957). K. *Drilonereis forcipes* (redrawn from Pettibone 1957). L. *Drilonereis benedicti* (redrawn from Pettibone 1957). M. *Arabella endonata* (redrawn from Emerson 1974). N. *Labrorostratus prolificus* (redrawn from Amaral 1977). O. *Labrorostratus luteus* (redrawn from Uebelacker 1978). P. *Labrorostratus parasiticus* (redrawn from Pettibone 1957)

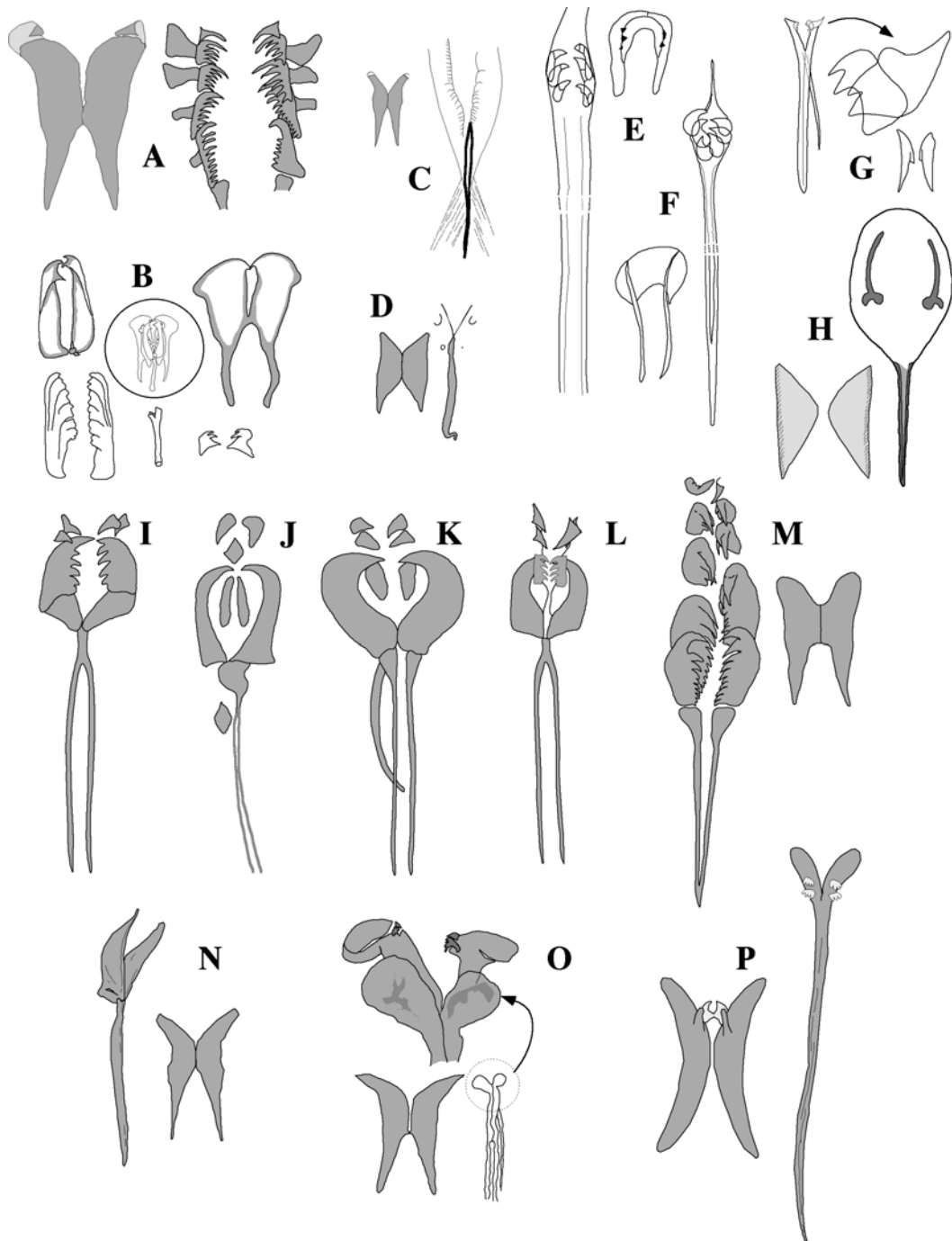


Fig 2.- Examples of commensal polychaetes associated to sponges. A. *Potamilla symbiotica* on *Crytospongia enigmatica* (redrawn from Uschakov 1950). B. *Harmothoe hyalonemae* on *Hyalonema thomsoni* (redrawn from Martin et al. 1992); grey arrows indicate the position of each worm forming a heterosexual pair. C. *Polydorella smurovi* on an unknown red sponge (redrawn from Tzetlin & Britayev 1985).

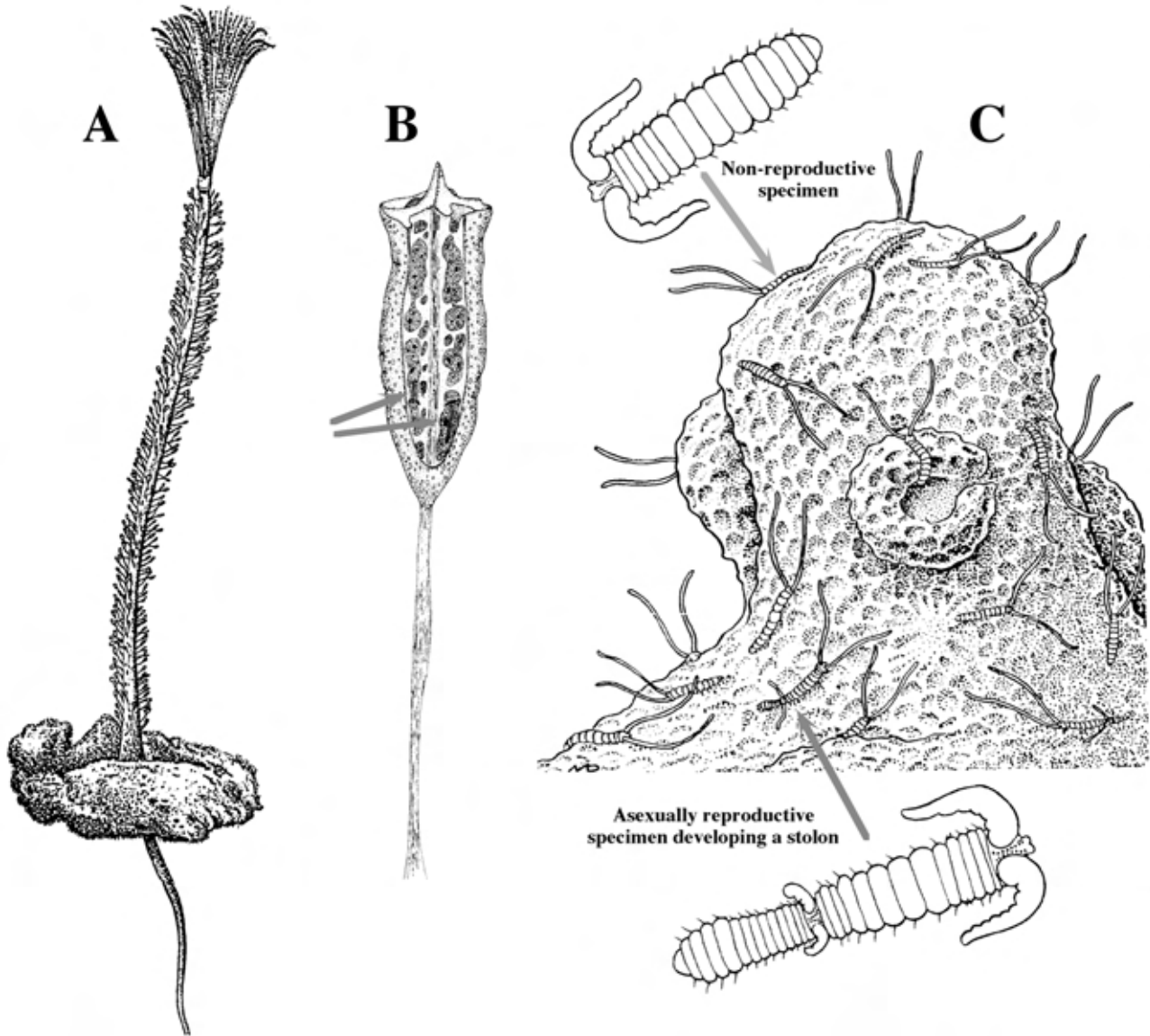


Fig 20.- Examples of ectoparasitic polychaetes infesting their hosts. A. *Asetocalamyzas laonicola* attached to *Laonome cirrata* (redrawn from Tzetlin 1985). B. *Parasitosyllis claparede* attached to an unidentified polychaete (redrawn from Potts 1912). C. *Ichthyotomus sanguinarius* attached to a host eel (redrawn from Eisig 1906 in Fauvel 1923). D. Detail of the anterior end and scissor-like mandibles of *Ichthyotomus sanguinarius* (redrawn from Eisig 1906 in Paris 1955). E. Claw-like hook of *Branchiosyllis oculata* (redrawn from Pawlik 1983). F. Hooked setae of *Procerastea parasimpliseta* (redrawn from Hartmann-Schröder 1992). G. Hooked setae of *Procerastea parasimpliseta* (redrawn from Alós 1989). H. Hooked setae of *Procerastea hydrozoicola* (redrawn from Hartmann-Schröder 1992).

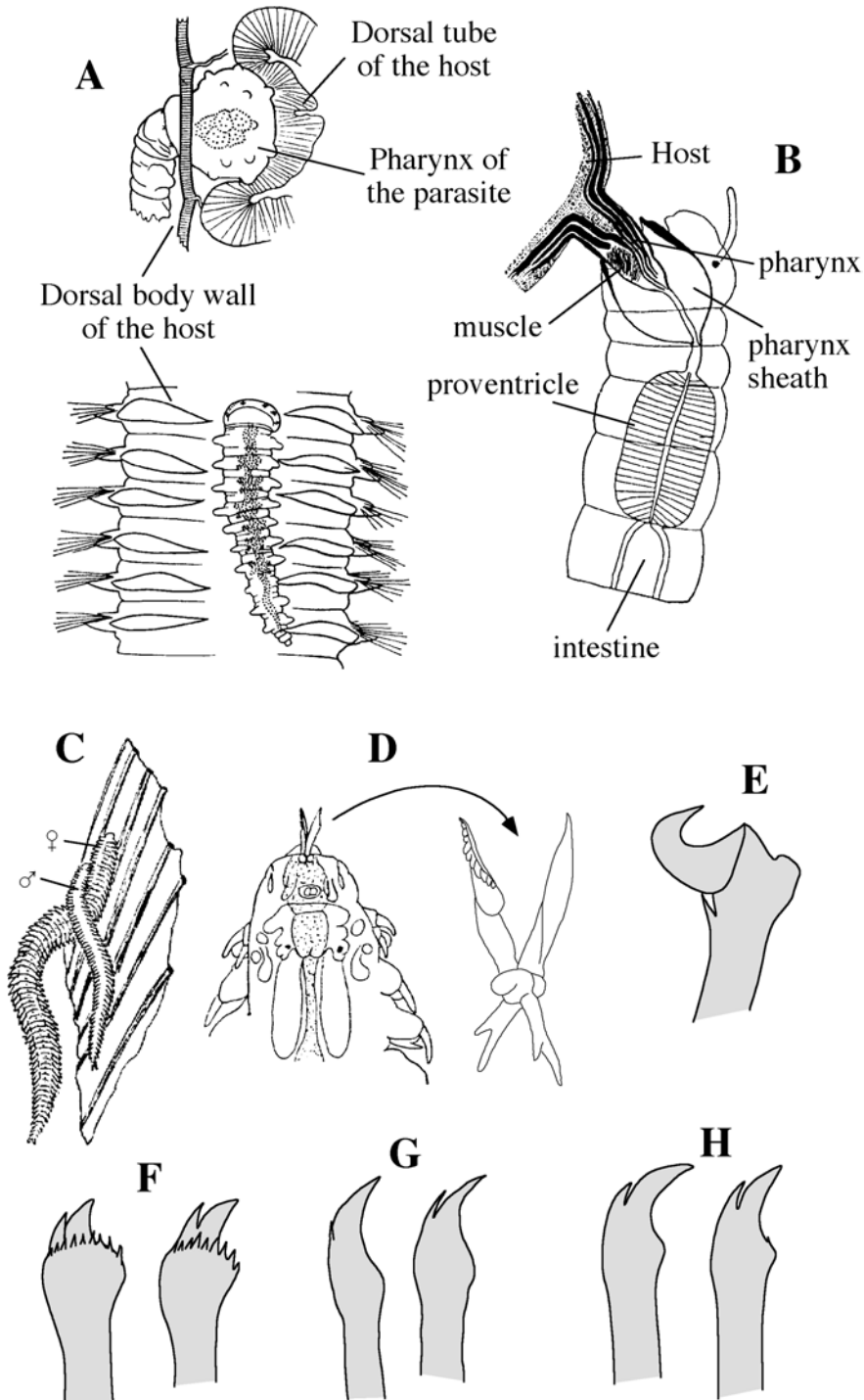


Fig 21.- Bore holes of *Polydora ciliata* (A), *Polydora websteri* on *Mercenaria mercenaria* (B) and on *Plecopecten magellanicus* (C) and *Polydora concharum* on *Plecopecten magellanicus* (D) redrawn from Blake & Evans (1973). E. Settlement and tube formation of *Polydora commensalis* (redrawn from Radashevsky 1989). F. Scheme of a generic mud-blister of polydorid worms (redrawn from Blake & Evans 1973). G. Sequence of formation of a *Polydora ciliata* mud-blister on *Mytilus edulis*: 1. Settlement, 2. Initial bore hole, 3. Mud-blister (redrawn from Tkachuk 1988).

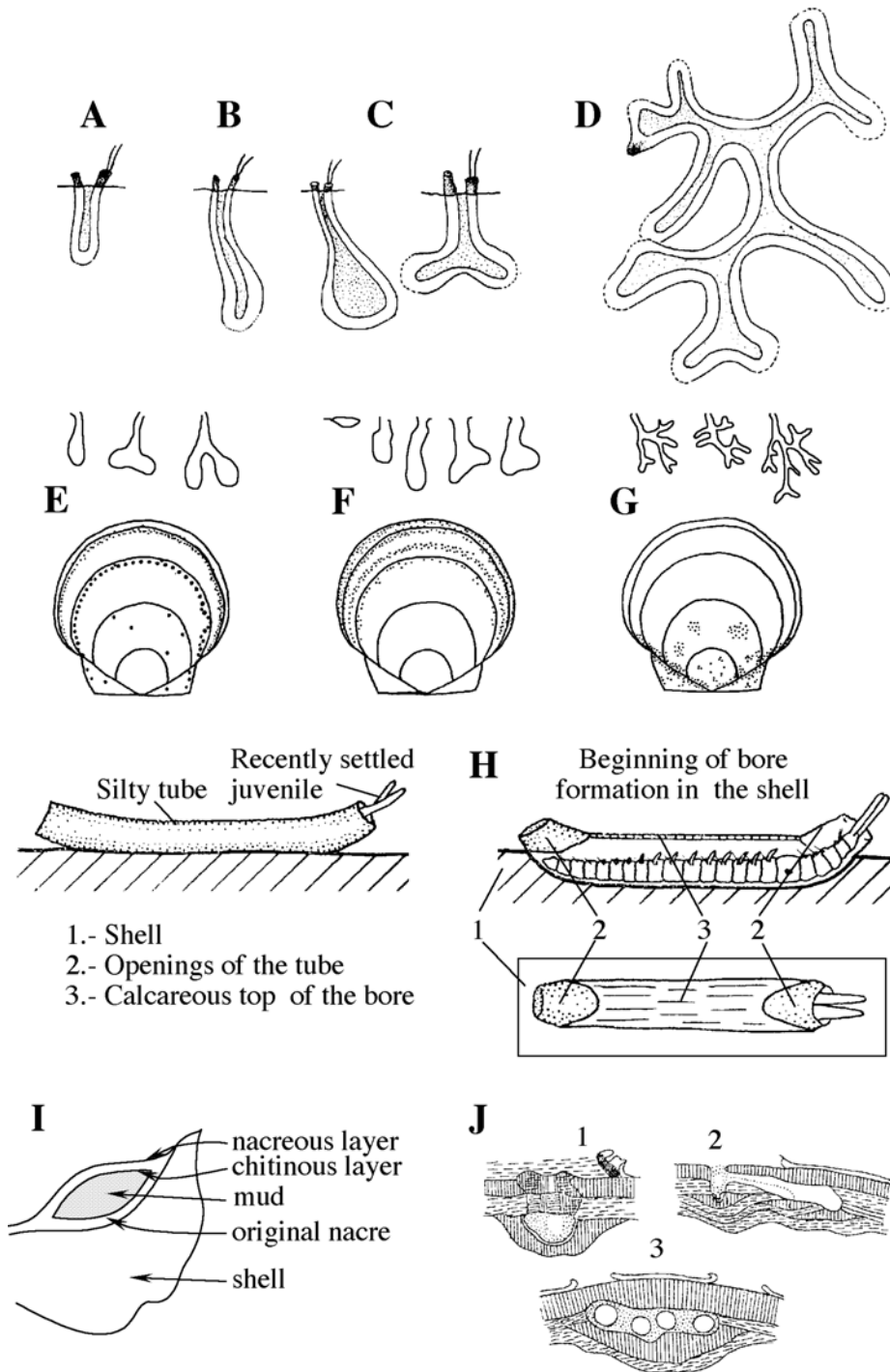


Fig 22.- *Polydora armata* inhabiting bryozoans (redrawn from Laubier 1958). A. *Holoporella sardonica*; B. *Porella concinna*. The arrows indicate the position of tube openings.

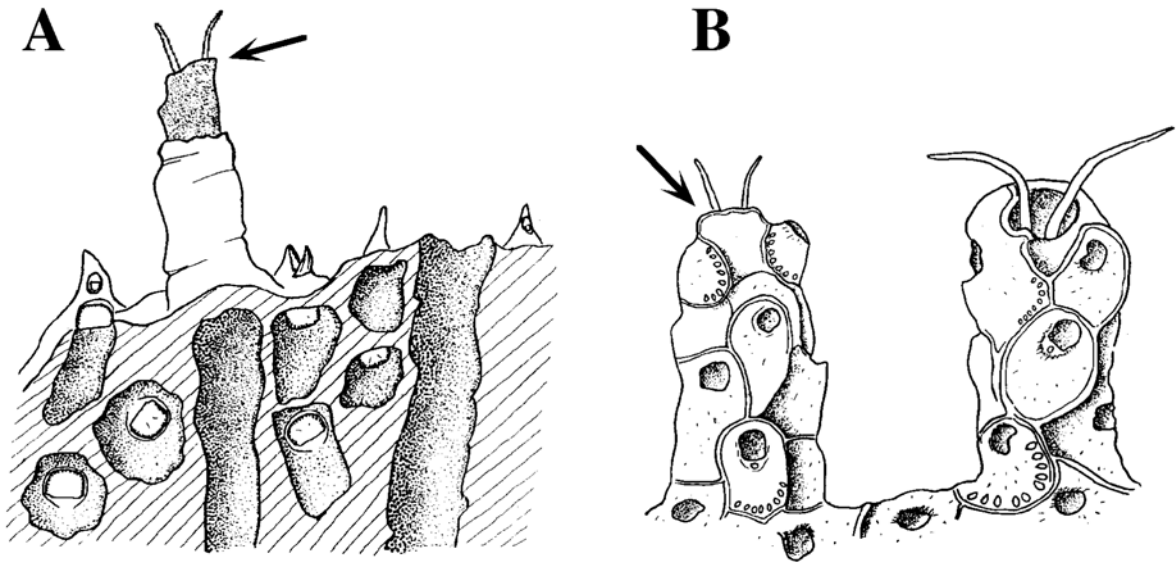


Fig 23.- *Caobangia brandti* bore holes in *Brotia pseudosulcospira* (redrawn from Jones 1974). A. Scheme of the shell with truncated apex. B. Detail of the bore holes on the truncated apex.

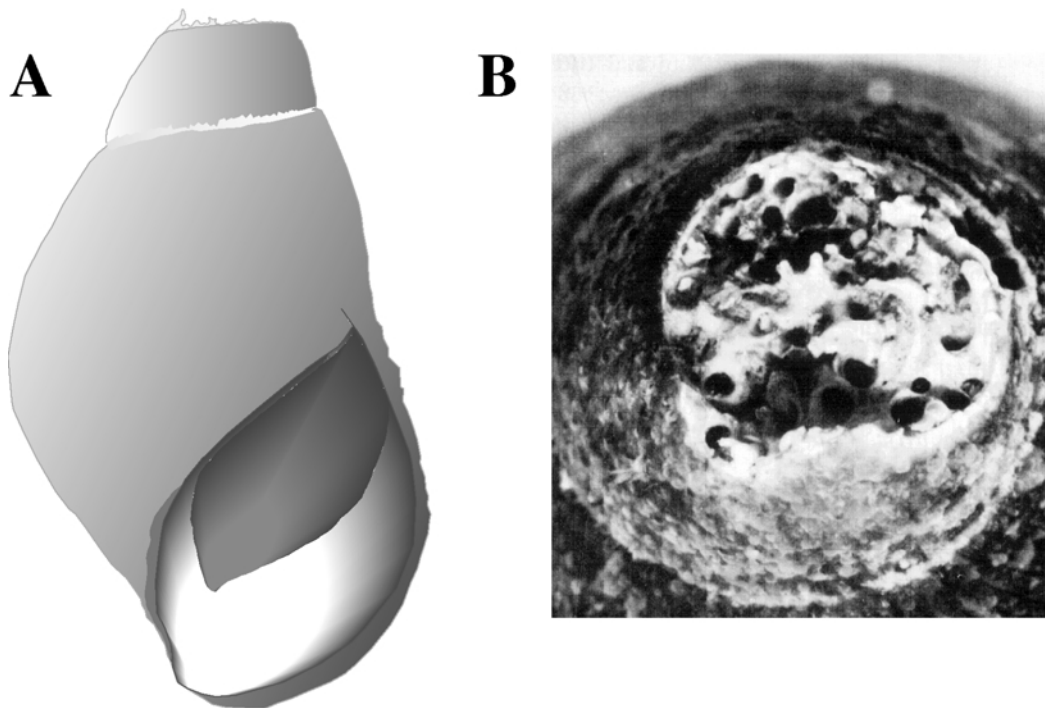


Fig 24.- Sections of an anterior part of the *Polydora rogeri* body inside the calcareous algae excavated by the host sponge *Cliona viridis* (redrawn from Martin 1996). A. Section through a segment from the postbranchial posterior region; B. Section through branchial segment.

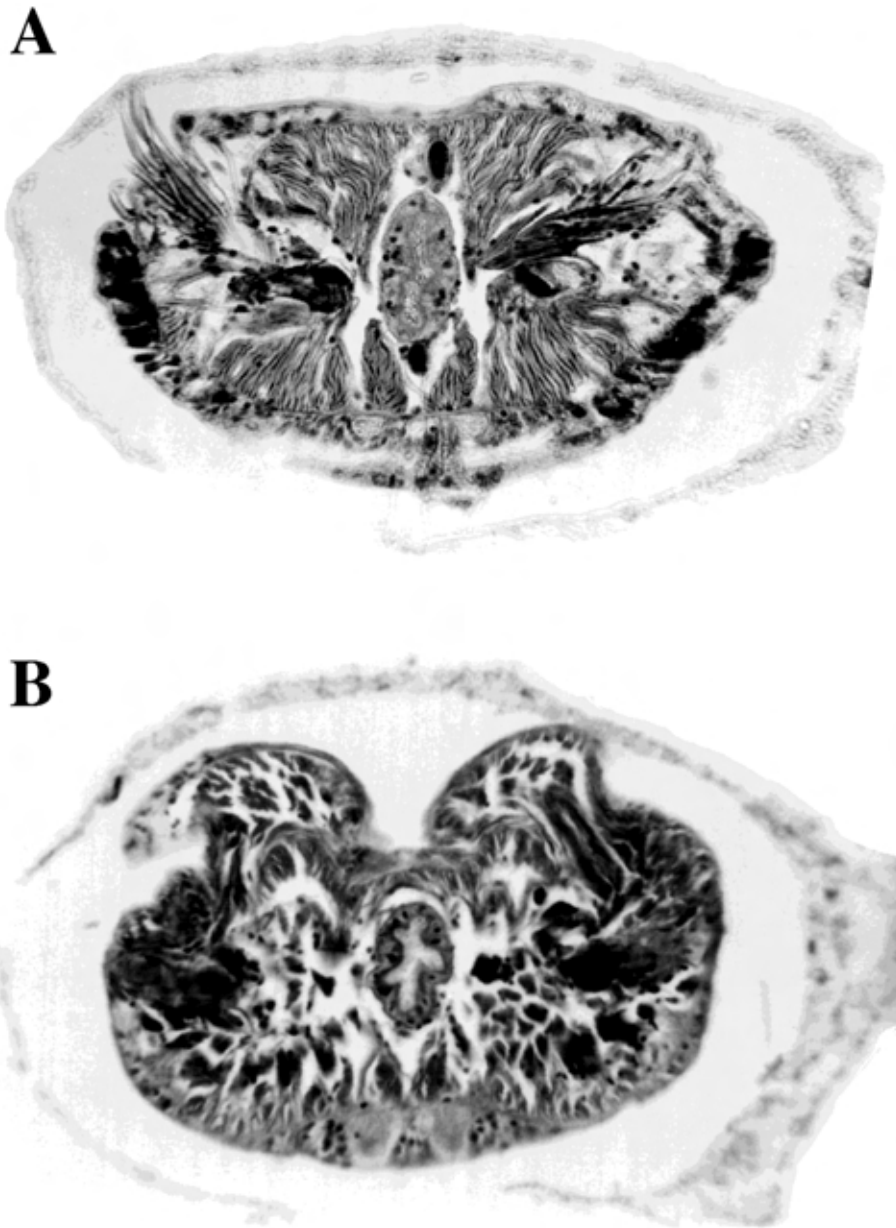


Fig 3.- Examples of commensal polychaetes associated to other worms. A. *Hesperonoe adventor* inside the *Urechis caupo* burrow (redrawn from Dales 1957). B. *Harmothoe brevipalpa* inside the *Phyllochaetopterus* sp. tube (redrawn from Cañete et al. 1993). C. *Harmothoe brevipalpa* inside the *Pectinaria chilensis* tube (redrawn from Cañete et al. 1993). The arrows indicate the position of commensal polychaetes.

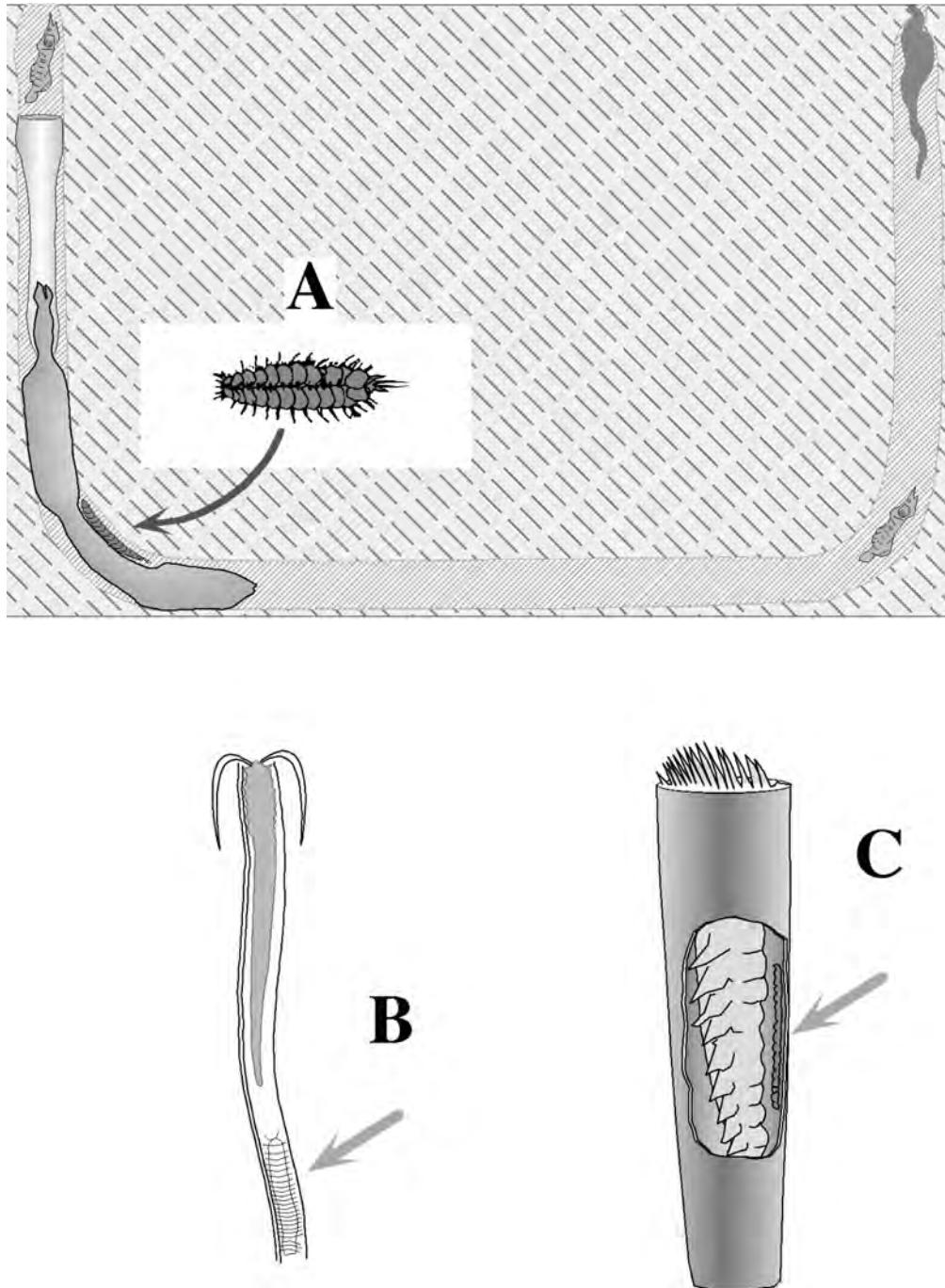


Fig 4.- Examples of commensal polychaetes associated to cnidarians. A. *Vermiliopsis* sp. on *Stephanocenia michelini* (redrawn from Humann 1992). B. *Polynoe uschacovi* inside the tube induced in *Callogorgia* sp. (redrawn from Britayev 1981). C. *Polynoe uschacovi* inside a tube induced in *Alloporea* sp. (redrawn from Britayev 1981). D. Tube induced by *Eunice floridana* on the branches of *Amphielia* sp. (redrawn from Paris 1955). E. *Polynoe thouarellicola* on *Thouarella* sp. (redrawn from Hartmann-Schröder 1989). F. *Lumbrineris flavellicola* on *Cariophyllia decapali* (redrawn from Miura & Shirayama 1992).

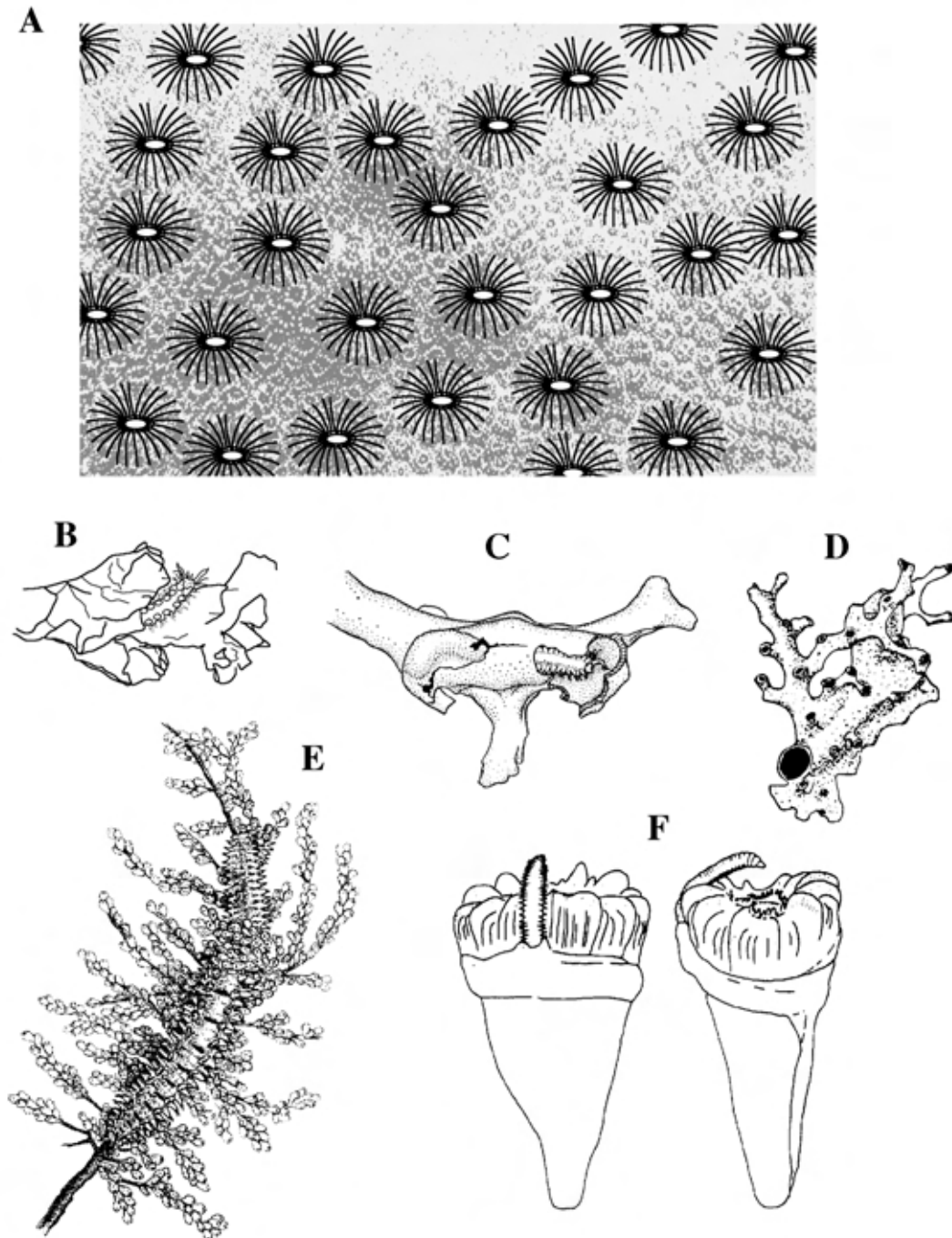


Fig 5.- Examples of commensal polychaetes associated to molluscs and crustaceans. A. *Eunice* sp. on *Cerithium vertagus* (redrawn from Gibbs 1969). B. *Arctonoe vittata* in the *Acmaea pallida* mantle cavity (redrawn from Britayev 1991). C. *Antonbruunia viridis* in the *Lucinia fosteri* mantle cavity (redrawn from Hartman & Boss 1965). D. An adult *Hipponoe gaudichaudi* and the attached young specimen (redrawn from Núñez et al. 1991). E. The position of two *Hipponoe gaudichaudi* inside *Lepas anserifera* (redrawn from Britayev & Memmy 1989). F. *Circeis paguri* inside a *Buccinum* shell inhabited by *Eupagurus bernhardus* (redrawn from Al-Ogily & Knight-Jones 1981). G. *Nereis fucata* and its host *Eupagurus bernhardus* (redrawn from a Christmas card by G. Thorson, drawn by P. Winther, in Dales 1957)

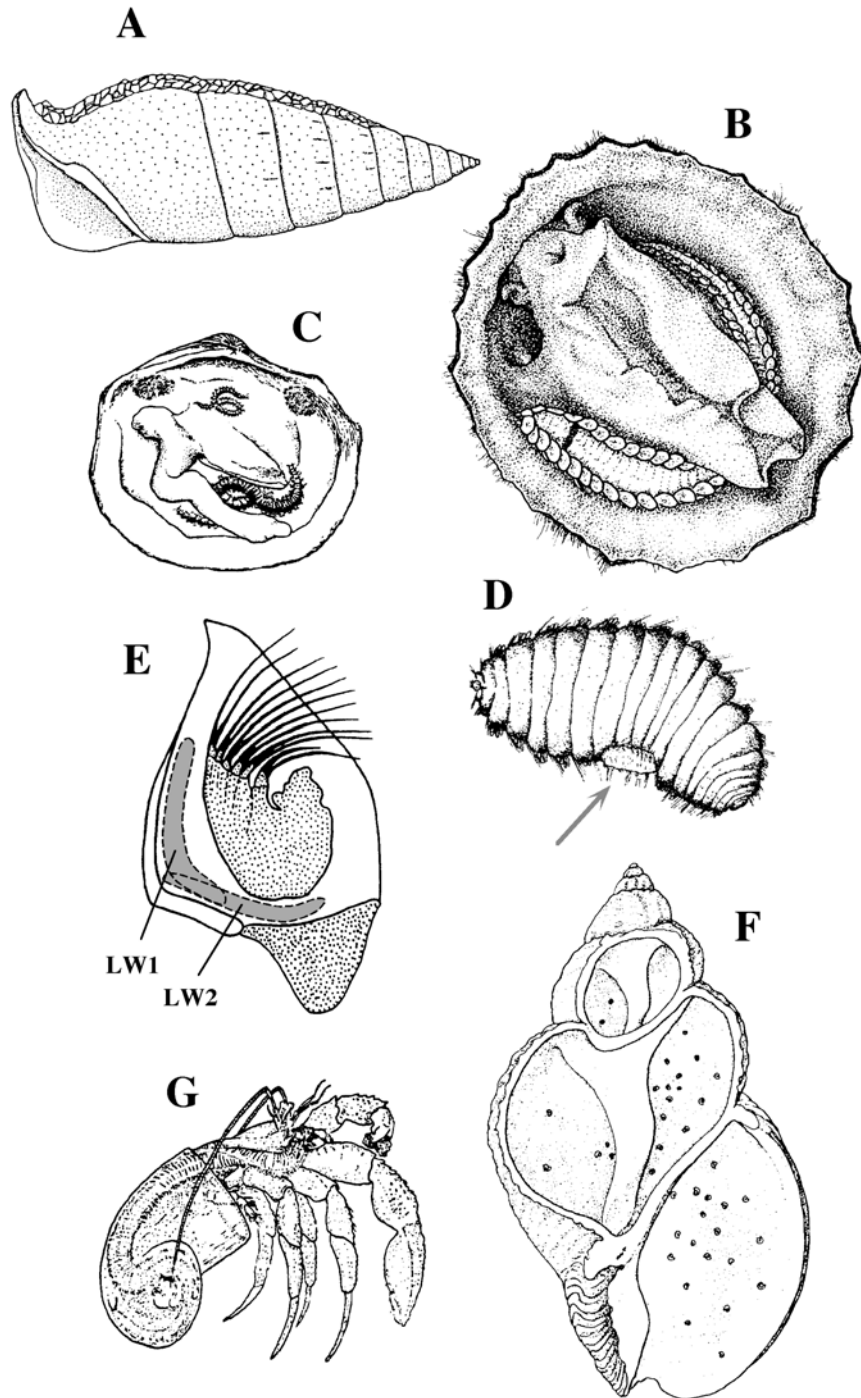


Fig 6.- Examples of commensal polychaetes associated to echinoderms. A. *Acholoe astericola* on *Astropecten irregularis* (redrawn from a Christmas card by G. Thorson, drawn by P. Winther, in Davenport 1953a). B. *Gastrolepidia clavigera* on the *Stichopus chloronotus* surface (Britayev personal observations). C. *Sphaerodorum ophiurophoretos* on a *Amphipholis squamata* arm (redrawn from Martin & Alvà 1988). D. *Branchiosyllis exilis* on a *Ophiocoma echinata* arm (redrawn from Alvà & Jangoux 1989 and Hendler & Meyer 1982). E. *Malmgreniella variegata* on *Ophionereis reticulata* arm and oral disc (redrawn from Alvà & Jangoux 1989 and Millot 1953). F. *Eunoe laetmogonensis* on *Laetmogone violacea* (redrawn from Kirkegaard & Billet 1980).

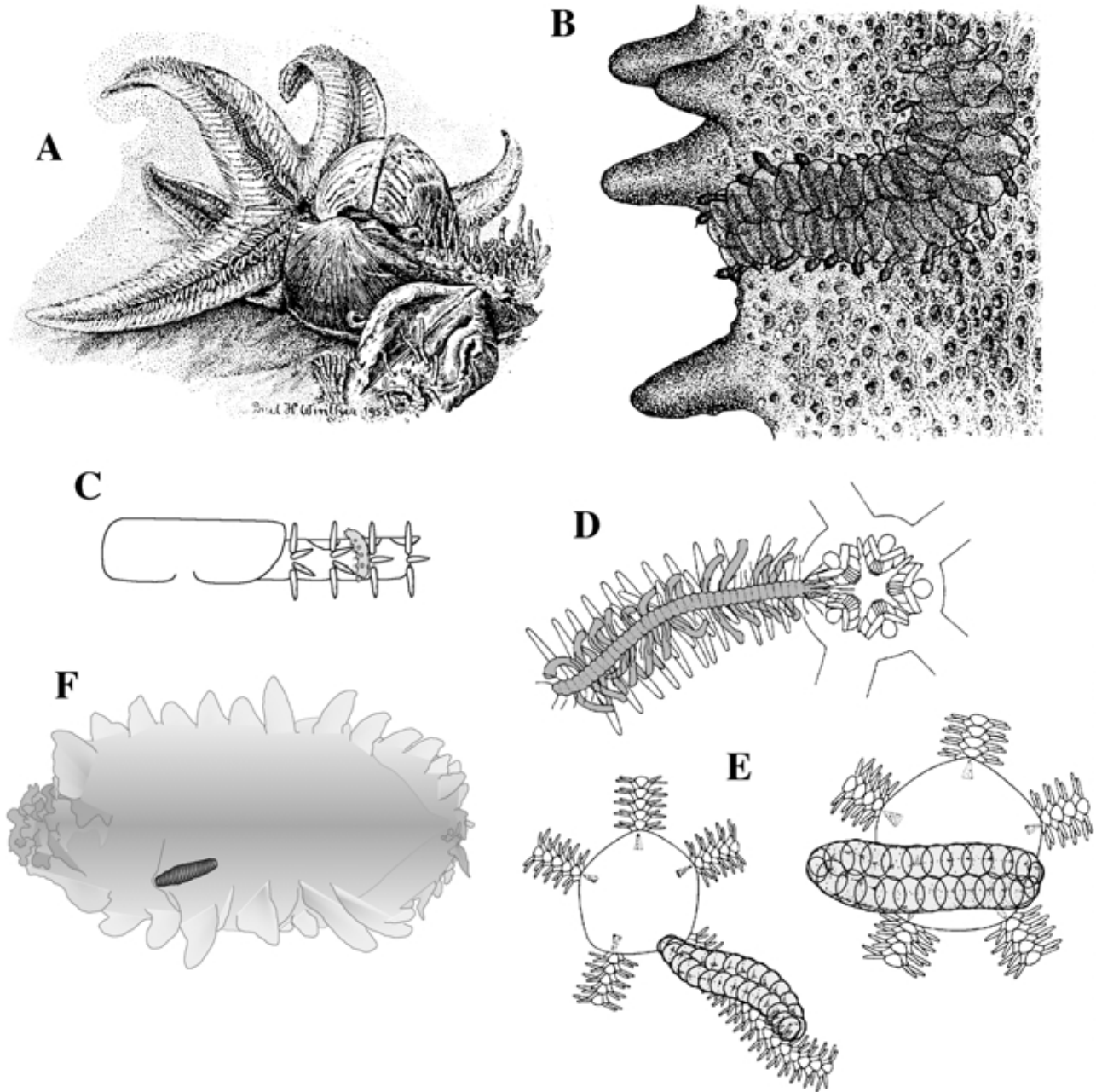


Fig 7.- Examples of variability in infestation prevalence of commensal polychaete populations. A. Changes with depth in Mediterranean *Iphitime cuenoti* harboured by *Liocarcinus depurator* and *Macropipus tuberculatus* (redrawn from Abelló et al. 1988). B. Spatial variability of *Branchiosyllis exilis* on *Ophiocoma echinata* along the Panamanian coast (redrawn from Hendler & Meyer 1982). C. Seasonal pattern of *Branchiosyllis exilis* on *Ophiocoma echinata* at Galeta, Caribbean coast of Panama (redrawn from Hendler & Meyer 1982). D. Seasonal pattern *Ophiodromus pugettiensis* on *Patiria miniata* at Dana Point, California (redrawn from Lande & Reish 1968).

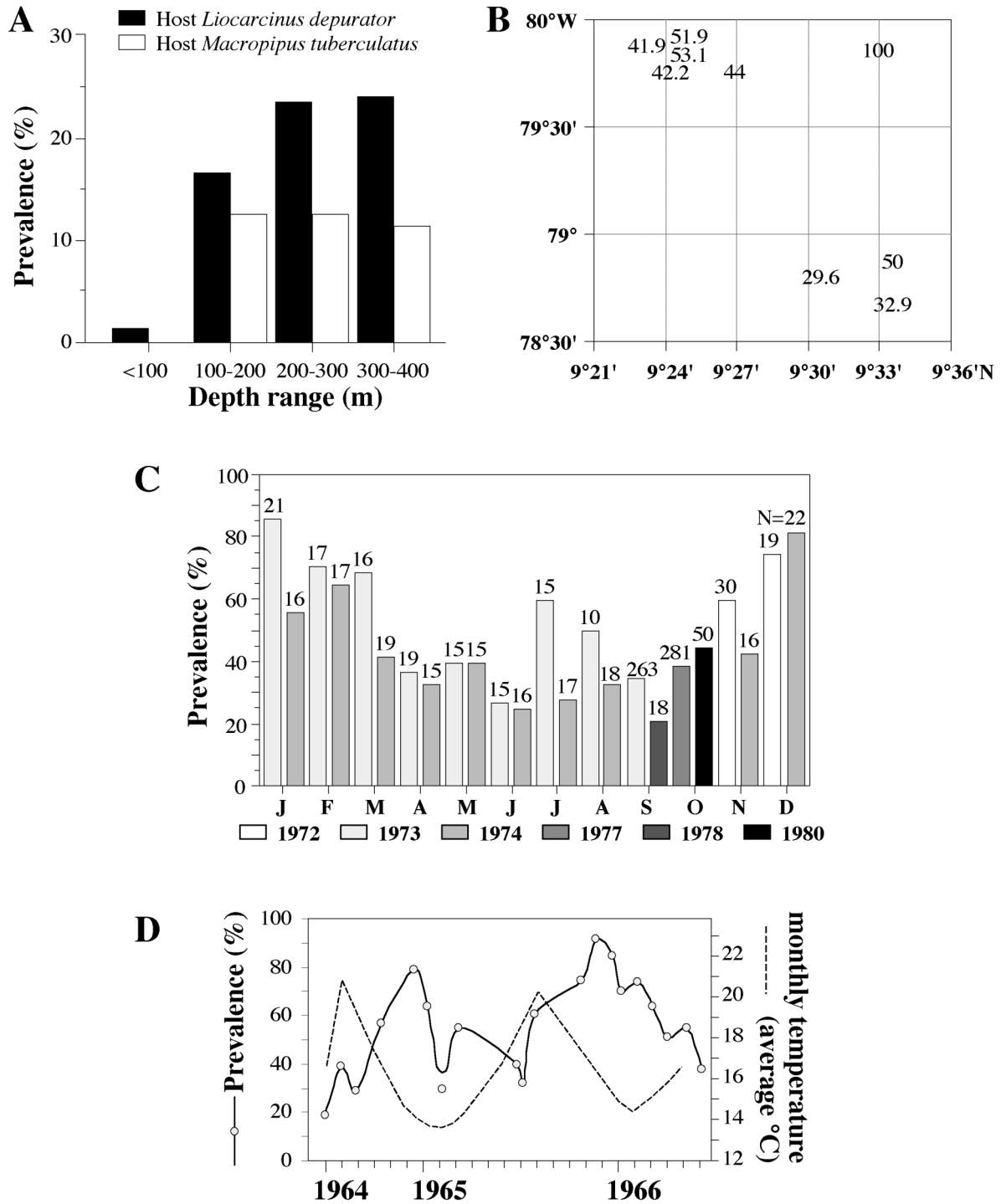


Fig 8.- A. Seasonal variability of infestation intensity in *Ophiodromus pugettensis* infesting *Patiria miniata* at Dana Point, California (redrawn from Lande & Reish 1968). B. Relationship between infestation prevalence and host size in *Branchiosyllis exilis* from the *Ophiocoma echinata* oral disk (redrawn from Hendler & Meyer 1982). C. Relationship between infestation prevalence and host size in *Circeis paguri* attached both to the occupied shell and the body of the host *Eupagurus bernhardus* (redrawn from Al-Ogily & Knight-Jones 1981). D. Relationship between infestation prevalence and host size in *Gastrolepidia clavigera* from the *Stichopus chloronotus* (redrawn from Britayev & Zamishliak 1996). E. *Ophryotrocha mediterranea* on the *Geryon longipes* branchial chambers (redrawn from Martin et al. 1991).

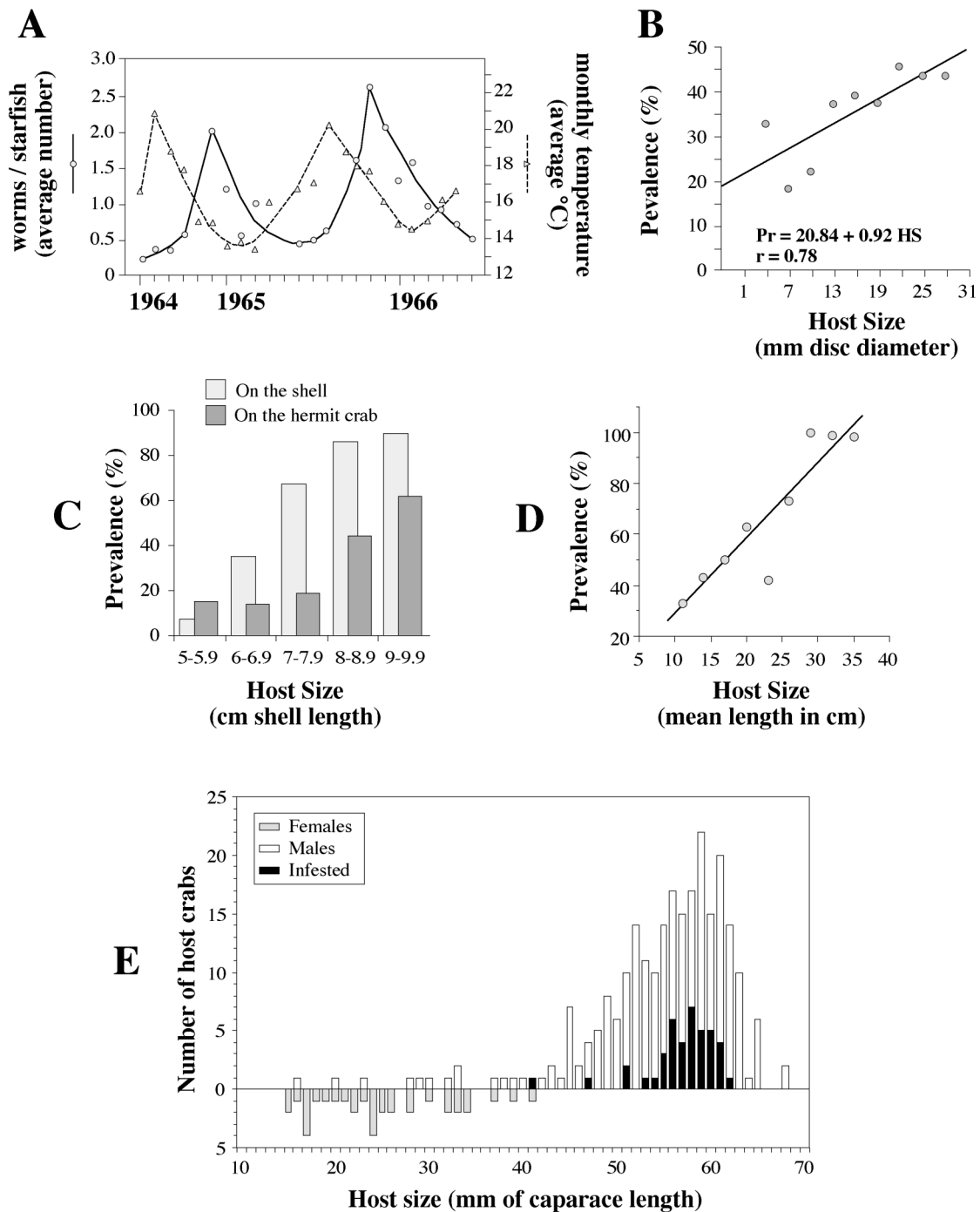
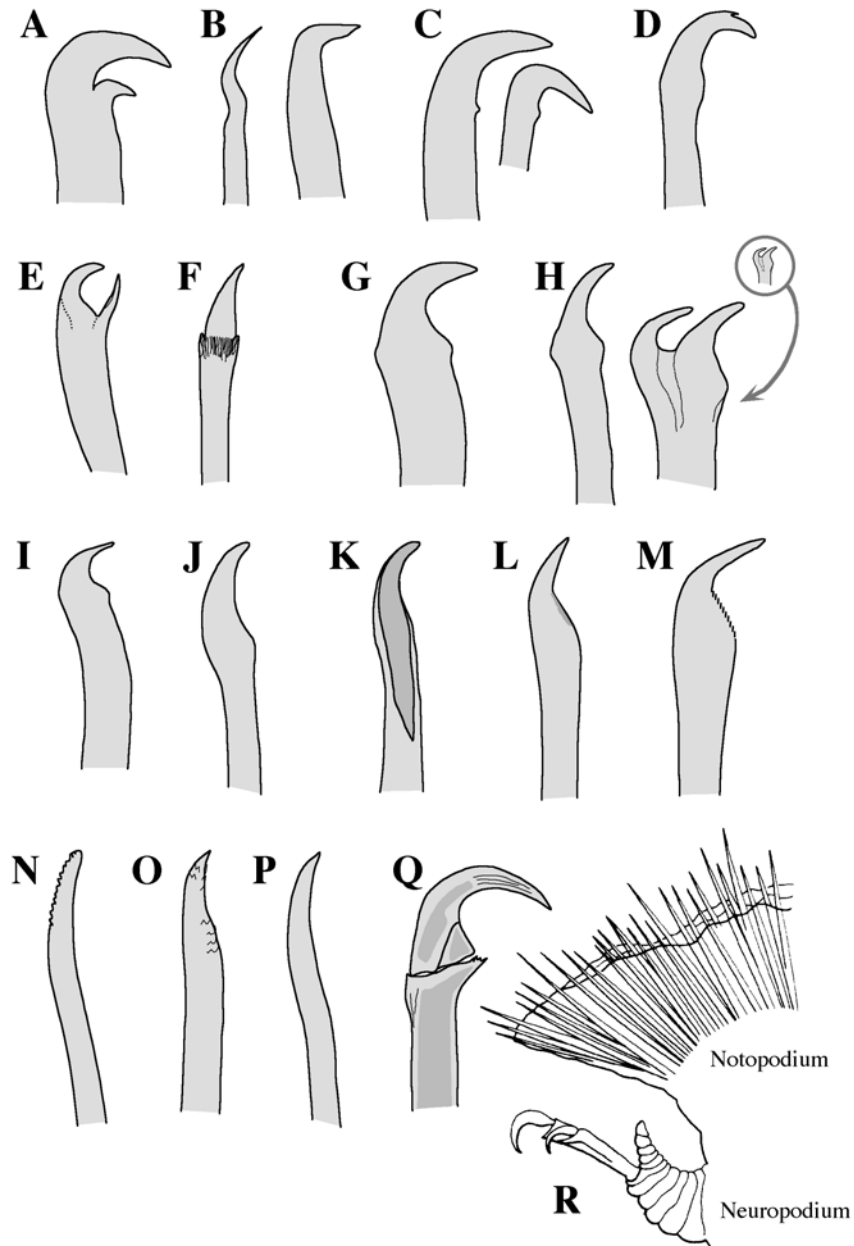


Fig 9.- Examples of hooked setae from commensal polychaetes. Amphinomidae: A. *Hipponoe gaudichaudi* (redrawn from Britayev & Memmy 1989). Syllidae: B. *Bollandia antipathicola* (redrawn from Glasby 1994); C. *Syllis onkilochaeta* (redrawn from Hartmann-Schröder 1991). Sphaerodoridae: D. *Sphaerodorum ophiurophoretos* (redrawn from Martin & Alvà 1989). Antonbruunidae: E. *Antonbruunia viridis* (redrawn from Hartman & Boss 1965). Nautilinidae: F. *Laubierus mucronatus* (redrawn from Blake 1993), G. *Shinkai longipedata* (redrawn from Miura & Ohta 1991), H. *Natsushima bifircata* (redrawn from Miura & Laubier 1990), I. *Shinkai sagamiensis*, J. *Petreca thysira* (redrawn from Blake 1990), K. *Nautiliniella calyptogenicola* (redrawn from Miura & Laubier 1989). Iphitimidae: L. *Iphitime dordeleini* (redrawn from Marenzeller 1902), M. *Iphitime cuenoti* (redrawn from Abelló et al. 1985), N. *Iphitime hartmanae* (redrawn from Kirkegaard 1977), O. *Iphitime paguri* (redrawn from Fage & Legendre 1933), P. *Iphitime holobranchiata* (redrawn from Pilger 1971). Spintheridae: Q. *Spinther citrinus*, R. Detail of the parapodium of *Spinther citrinus* (redrawn from George & Hartmann-Schröder 1985).



Symbiotic Polychaetes: Review of known species

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ABSTRACT

Although there have been numerous isolated studies and reports of symbiotic relationships of polychaetes and other marine animals, the only previous attempt to provide an overview of these phenomena among the polychaetes comes from the 1950s, with no more than 70 species of symbionts being very briefly treated. Based on the available literature and on our own field observations, we compiled a list of the mentions of symbiotic polychaetes known to date. Thus, the present review includes 292 species of commensal polychaetes from 28 families involved in 713 relationships and 81 species of parasitic polychaetes from 13 families involved in 253 relationships. When possible, the main characteristic features of symbiotic polychaetes and their relationships are discussed. Among them, we include systematic account, distribution within host groups, host specificity, intra-host distribution, location on the host, infestation prevalence and intensity, and morphological, behavioural and/or physiological and reproductive adaptations. When appropriate, the possible directions for further research are also indicated.

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INTRODUCTION

Living organisms are always connected in some way to other individuals of the same species and to individuals of other species living in the same area. Many of these established interactions are known as direct relationships (i.e. sex recognition, competition, predation). In these cases, the involved organisms are known as free-living. However, some species have become closely associated, often to mutual benefit (frequently referred to as “symbiosis”). These relationships usually convey a high degree of specificity, to the extent that at least one of the involved partners can no longer be considered a free-living organism.

Among the polychaetous annelids, which for the most part are free-living, crawling, burrowing and tube-dwelling, the setting-up of close associations with other marine invertebrates is a rather common phenomenon. This is not surprising because the polychaetes are probably the most frequent and abundant marine metazoans in benthic environments. They may be numerically less important on hard substrata, and some molluscs and crustaceans may co-dominate on soft bottoms, but of all metazoans only the nematodes are more ubiquitous (Fauchald & Jumars 1979). However, despite the obvious importance and increasing knowledge on the ecological role of polychaetes, the literature on symbiotic polychaetes remains largely anecdotal, likely with the exception of some widely known examples of commensalism practised by some species of the family Polynoidae. Moreover, the information is often scattered among studies dealing with many different subjects (e.g. systematics, descriptive ecology, biology).

The aim of the review is, therefore, to attract the attention of scientists to - and to encourage further studies on - the ecology of this particular and diverse group of symbionts. We make an attempt not only to summarise the available data on symbiotic polychaetes, but also to outline the lacunae in the knowledge of their ecology. However, an exception to these dispositions are the Myzostomida, a highly specialised Order of polychaetes which includes more than 130 species (Pettibone 1982) that live associated with echinoderms (Barel & Kramers 1977, Jangoux 1987). The aberrant characteristics of these worms and their special and intimate associations with echinoderms merit a specific approach that falls outside the scope of the present paper. Thus, the whole order has been omitted, for inclusion in a further generalisation. On the other hand, some associations previously considered as symbiotic, such as those between the orbinids *Orbinia latreilli* and *Phylo foetida* and the holothuroid *Leptosinapta gallieni* (Barel & Kramers 1977), appear to be fortuitous ecological associations (Beauchamp & Zachs 1913). As far as possible, these fortuitous associations were excluded from the present review. Similarly, the presence of epibionts (e.g. on the caparace of crabs, see Okuda 1934, Abelló et al. 1990), endobionts (e.g. inside the aquiferous canals of sponges, see Pearse 1932, Bacescu 1971, Frith 1976, Pansini & Daglio 1980-81, Westinga & Hoetjes 1981, Alós et al. 1982, Votsiadou-Koukoura et al. 1987, Koukouras et al. 1992, 1996, Pascual et al. 1996) or simple associates to other organisms (viz. bryozoans in Morgado & Amaral 1981a, b, c, 1984, 1985, vermetids in Ben Eliahu 1975a, b, 1976, corals in Arvanitidis & Koukouras 1994, wood-borer molluscs in Kirkegaard & Santhakumaran 1967) are not regarded as symbiosis without any demonstration of specificity, because most of the involved organisms will inhabit a wide variety of substrates and the presence or absence of the so-called “host” is irrelevant.

The present review provides a list of known symbiotic polychaetes arranged into several huge tables, including the symbiotic species from each polychaete family, the host group and species name, the type of association and the source of information. There are three main tables: non-boring commensals, non-boring parasites, and symbiotic borers. The main body of the review is divided into three main sections according to these three tables. Each section is sub-divided into several parts, starting with the analyses of the respective list of relationships. Then follow the information on morphological, biological, ecological and behavioural trends characterising the symbiotic polychaetes.

BACKGROUND: PREVIOUS REVIEWS

Although the oldest known review of commensal organisms is probably that by van Beneden (1869), the first - and certainly the only known - reviews entirely dedicated to symbiotic polychaetes are those by Paris (1955), Clark (1956) and Britayev (1989). The former is a collection of some (but not all) of the typical commensal and parasitic relationships involving polychaetes known to date. The second includes a very full list of symbiotic polychaetes (about 73 species from 22 families, involved in about 160 associations), and a description of one new association. The latter, although known only from a Russian version, is certainly the first modern attempt to summarize the main trends of polychaetes as symbionts. There have also been a number of reviews in the past which have addressed particular aspects of symbiotic polychaetes. Dales (1957) reviewed the commensal interactions in marine organisms and mentioned several associations involving polychaetes. The extensive review of symbionts of Echinodermata from the NE Atlantic by Barel & Kramers (1977) included an annotated check list of symbiotic polychaetes, whereas Alvà & Jangoux (1989) updated the known relationships between polychaetes and ophiuroids. Overstreet (1983), in his review on the metazoan symbionts of crustaceans, briefly mentioned some polychaetes. Britayev (1981) described two new polychaete species commensal with coelenterates, and reviewed the bibliography on their associated polychaetes. The symbiotic invertebrates associated with the sea urchin *Echinus sculentus* and with the polychaete *Chaetopterus appendiculatus* were reviewed by Comely & Ansell (1988) and Petersen & Britayev (1997), respectively. The symbiotic relationships within benthic organisms from South California, polychaetes included, were reviewed by Fox & Ruppert (1985). The symbiotic polychaetes from more or less restricted geographical areas have more often been reviewed within the framework of systematic papers (e.g. Gibbs 1969 for the Solomon Islands, Okuda 1936a, 1950, and Uchida 1975 for the Japanese waters), whereas some systematic reviews referred to taxa whose members included well-known symbiotic species, such as the families Caobangidae (Jones 1974), Oeonidae (Pettibone 1957), Histriobdellidae (Moyano et al. 1993), Iphitimidae (Fage & Legendre 1933, Gaston & Benner 1981) and Polynoidae (e.g. Hanley 1989, Pettibone 1993, 1996). The shell-boring spionid species of *Polydora* and related genera were reviewed by Blake (1969, 1971, 1996). Finally, the physiology of commensal polychaetes was discussed by Davenport (1966a, b).

All these review articles, though comprehensive, address individually only particular aspects of the complex symbiotic interactions involving polychaetes. There has been a more or less steady dribble of information on symbiotic polychaetes over the years since Paris (1955) and Clark (1956). Therefore, it is now becoming possible to begin a synthesis of the available information. The present review will attempt to summarise current knowledge on symbiotic polychaetes as well as discuss the main systematic, biological, ecological and behavioural trends of these associations. When appropriate, possible directions for further research will also be indicated.

Before considering the interrelationships between polychaetes and their associated hosts, it is necessary to define the different concepts which are most often used when describing symbiotic associations. However, it would not be appropriate here to discuss extensively the different conceptual approaches, because this aspect has been largely discussed (e.g., Dales 1957, Rhode 1981, Boucher et al. 1982, Margolis et al. 1982, Addicott 1984). The particular terms adopted for the present review and the reasons for this adoption will, however, be considered in more detail.

DEFINITION OF TERMS

Although many attempts to classify the interrelations between organisms have been proposed, distinctions between different types of associations are not always clear. There are many factors that further define the nature of the interactions (e.g. the degree of association among the species, the degree to which the association is necessary for survival, the kinds of benefits, the extent of reciprocal specialisation by one species in response to the other, the temporal pattern, the stage of the life-cycle at which the interaction occurs, the location of the guest on or inside the host). Moreover, there are almost as many definitions as there are authors writing about close associations. In practice, it is difficult to obtain unequivocal demonstrations of all factors affecting a given interaction: the terms should preferably be used as stepping stones in helping to understand the real relationships in any particular association.

A partnership in which the advantage is wholly on one side, usually at the expense of the other partner, will be referred to as “parasitism” (Dales 1957). Where an association is clearly to the advantage (not necessarily from a trophic point of view) of one of the members without seriously inconveniencing or harming the other, the relationship will be referred to as “commensalism” (Dales 1957). Any interaction in which two (or more) species reciprocally benefit from the presence of the other species is referred to as “mutualism” (Addicott 1984). There is also a typical system of symbols to describe these three types of relationships: “+”, “-” and “0” indicate positive, negative and neutral effects for a given associate, respectively. Therefore, the associations can be represent as “++” (mutualism), “+0” (commensalism), and “+-” (parasitism).

The term “symbiosis” has been considered as synonymous of mutualism (e.g. Rhode 1981). However, it may also refer to the extent to which two species live in close association. Thus, in a wider sense, symbiosis is more often used to describe all kinds of organism associations (Henry 1966). In this review, we preferred to retain the generic sense of symbiosis, which will thus include parasitism, commensalism and mutualism. In this case, the partner s involved in “symbiotic” associations will be referred to as “the symbiont” (or “the guest”) and “the host”. The host harbours the symbiont, which is usually smaller than the host and always derives benefits from the association. In addition, the symbionts tend to have a more active role in the formation of associations than the hosts. In the case of commensalisms and parasitisms, however, the symbiont may be more specifically referred to as “the commensal” and “the parasite”, respectively.

Because of the difficulties of applying the experimental method to such a complex network of interactions, we often know little about their nature. Strict borderlines can not be easily drawn between the various types of associations. For instance, a parasite may become a predator by killing the host, or it may become beneficial to the host species, i.e. the relationship may become mutualistic. A commensal may affect the host and sometimes damage it, and thus become a parasite. In practice, it is difficult to infer unequivocal demonstrations of benefit (be it reciprocal or not) from the analysis of an association or from the existing literature. Moreover, the interpretations of the relationships become peculiarly susceptible to anthropomorphic bias: the parasites simply seem “bad”, the mutualists and commensals seem “good”. There are, however, many examples of associations which where initially considered as parasitisms that, with increasing knowledge, have been redefined s commensalistic or even mutualistic. Some examples will be mentioned in coming chapters. For the purposes of this review, we will thus consider two broad groups of associations, parasitisms and commensalisms. The cases of mutualism involving polychaetes are very few, so we have included them within the commensalisms, with indications of the bi-directional trends if known. Some species will be labelled as parasites or commensals according to the original criteria of their descriptors, without it being possible to give much more information so that the character of the interactions can be determined. However, when possible, special care will be taken to pinpoint the known relevant trends of the associations, so allowing the readers to judge. Moreover, a special chapter will be dedicated to the polychaetes that bore into living organisms (i.e., those that produce burrows mainly, but not exclusively, in organisms with calcareous structures), which are often difficult to catalogue into the two types of associations.

Other labels that will be frequently used to define the nature of an association are: “ecto-” and “endo-” (for guests living outside or inside the host, respectively), “obligatory” and “facultative”

(for guests that can not survive without the host or that can also be free-living, respectively), “permanent” and “temporary” (for guests living as symbionts during their whole life or only during one phase of their life-cycle, respectively), and “monoxenous” and “polyxenous” (for symbionts inhabiting one or a few hosts and inhabiting many different hosts, respectively). Moreover, by considering the close associations as infestations, some specific terminology applied (Margolis et al. 1982). The relationship between the number of infested hosts and the total number of hosts will be referred to as “prevalence”, whereas “intensity” will be the number of symbionts present in each infested host, “mean intensity” will be the mean number of individuals of a particular symbiotic species per infested host in a sample, and “abundance” or “relative density” will be the mean number of symbiont individuals per host examined (i.e. equal to prevalence multiplied by mean intensity).

COMMENSAL POLYCHAETES

Commensalisms are the most abundant relationships among symbiotic polychaetes. This statement may reflect a real dominance of “+/0” associations. However, the low level of knowledge and scattered available information on the biology of the species involved may artificially exaggerate their relevance. Most known symbiotic polychaetes have been considered as “commensals” as their associations with other organisms lack clear “parasitic” features. However, their status may be further modified with the appraisal of new information on host-symbiont relationships. For example, the relationships involving the scaleworms *Arctonoe vittata* (with its gastropod host *Diodora aspera*) and *Gastrolepidia clavigera* (with its holothuroid hosts), rather than commensalisms, are closer to mutualism and parasitism, respectively (Dimock & Dimock 1969, T.A. Britayev personal observations). However, we decided to include within the commensals those species often considered as parasites but lacking specific behaviour descriptions. For example, the highly modified species of the family Spintheridae are often described as feeding on their host sponges (Pettibone 1963, 1982). However, whether this feeding activity damages the host or benefits it by cleaning its surface has not yet been demonstrated. A high morphological specialisation is not in itself a demonstration of parasitism, as pointed out with the re-evaluation of the histriobdellids as commensals of their host crustaceans (Jennings & Gelder 1976, Cannon & Jennings 1987).

TAXONOMICAL DISTRIBUTION OF COMMENSAL POLYCHAETES

292 species of commensal polychaetes belonging to 28 families are reported to be involved in 713 different commensal relationships in the present review (Tables 1 and 2; Fig 1). The total number of polychaete families may range between 84 (Fauchald 1977) and 87 (Pettibone 1982), with more than 16,000 known species (Blake 1994). Commensals are thus present in just over 31% of the known polychaete families and comprise about 1.8% of the known species. For the most part, commensal polychaetes are obligatory symbionts (67%) and belong to families formerly grouped in the artificial Errantia group. However, some others are included in the so-called Sedentary families, namely the Capitellidae, Fauveliopsidae, Flabelligeridae, Sabellariidae, Serpulidae and Spionidae, with symbiotic species being more abundant in this last family (see Tables 1 and 8).

According to Clark (1956), almost two-thirds of the polychaetes that were reported as commensals were members of the scaleworm family Polynoidae. With the increasing number of commensal polychaete species described since then, this proportion has been slightly reduced. However, more than half of all currently known commensal species (55%) belong to this family (Fig 1A). In fact, the polynoids are a very large family, including diverse and numerous species inhabiting different marine habitats. The majority are sluggish and crawling and are found under stones, in crevices and in available tubes or burrows. Most of them are carnivorous, feeding on a great variety of animals. Thus, although the lack of information on most known associations prevented us speculating on the curious dominance of polynoids within commensal polychaetes,

the symbiotic habits of this family seem to be more or less easily inferred from their “normal” (i.e. free-living) modes of life (Fauchald & Jumars 1979). According to our present evaluation, the family consists of about 700 species, the commensals representing 22.7% of the total. Commensal and free-living scaleworms do not show a marked taxonomical differentiation, the former often belonging to genera that include free-living species as well. The huge genus *Harmothoe*, for example, consists of more than 120 species within which about 15 are commensal, whereas the “typically” free-living genus *Eunoe* includes 3 commensal species (Table 1). On the other hand, some genera (viz. *Arctonoe*, *Asterophyllia*, *Australaugeneria*) and one subfamily, the Arctonoinae (Hanley 1989), could be considered as wholly, or at least mostly, commensal.

The weight of commensal species within the non-polynoid polychaete families is significantly less than within polynoids. The relative number of commensals does not exceed 10% and the number of commensal species is always less than 10, with the exception of syllids, hesionids, spionids and serpulids (Fig 1A).

Three small polychaete families are entirely symbiotic. The Iphitimidae (*sensu* Fauchald 1970) includes a single genus, *Iphitime*, with 1 parasitic (see Table 6) and 7 commensal species, all the latter inhabiting the branchial cavities of decapod crustaceans (crabs and hermit crabs). Also belonging to the order Eunicida, the family Histriobdellidae consists of two genera and 9 species, all of them living epizoically in branchial chambers or carapaces of crustaceans. The single species of *Histriobdella* lives associated with marine lobsters in northern Europe and along the north-eastern American coast. The remaining species belong to *Stratiodrilus* and are known as commensals of freshwater crayfish (from Australia, Tasmania, Madagascar, and South and Central America) and marine isopods (from South Africa). The third commensal family, the Nautiliniellidae, has been recently described by Miura & Laubier (1989) and consists of 9 species, all them associated with bivalves (Table 1). The nautiliniellids inhabit deep-water hydrothermal vents and seep-site communities and are closely related to the monotypic “commensal” family Antonbruuniidae. *Antonbruuniaviridis*, the single species, is also associated with a bivalve. Both families are morphologically very close, suggesting that a further review would probably lead to their union under the older family name, Antonbruuniidae.

MARINE HOST TAXA HARBOURING COMMENSAL POLYCHAETES

Commensal polychaetes are associated with as many as 569 species included within the main taxa of marine Metazoans (excluding flatworms, nemerteans and nematodes) and even with Protozoans (i.e. foraminifers) (Fig 1B). However, they clearly prefer organisms providing them with good shelter, such as tube-dwelling or burrowing animals (viz. tubicolous polychaetes, sipunculids, balanoglossids) or relatively large animals possessing “advantageous” protective physiological or morphological characteristics. Among them, organisms having holes, grooves, chambers or channels (e.g. sponges, starfishes), as well as those showing good chemical or physical defences (e.g. sponges, cnidarians, sea urchins) are included. The highest number of host species harbouring polychaetes belong to the echinoderms, and the highest number of commensal polychaetes are also associated with this group. In fact, about 36% of all host species belong to one of the five echinoderm classes and the same percentage of all commensal polychaetes are associated with species of this group (Fig 1B). The following most dominant groups are the cnidarians (20% of the host species and associated commensal polychaetes) and the polychaetes themselves (16% of the host species and 17% of associated commensal polychaetes), whereas only 7.2% and 13% of the host species are included among such abundant and widely distributed marine animals as molluscs and crustaceans, respectively.

SPECIFICITY AMONG COMMENSAL POLYCHAETES

All degrees of host-commensal specificity may be found among commensal polychaetes. Although several polychaete species may be associated with many hosts from very different groups, most of

them are symbiotic with only one or a few closely related hosts ([Table 1](#)). In fact, 59% are strictly “monoxenous associates” (i.e., occurring on 1 host), this figure becoming 87% if those commensals occurring on 2 or 3 different hosts are included. The high degree of specificity of the relationships involving polychaetes may explain these proportions. However, as repeatedly mentioned, the often vague and accidental information on most commensal polychaetes may contribute to exaggeration of the monoxenous pattern. Therefore, only a few species that have been studied in detail could be mentioned as examples of real monoxenous associates. Among them, *Histriobdella homari* inhabiting branchial chambers of two species of Atlantic lobsters (*Homarus vulgaris* and *H. americanus*), *Adyte assimilis* associated with two related species of echinoids (*Echinus sculentus* and *E. acutus*), and *Haplosyllis chamaeleon* associated with the gorgonian *Paramunicea clavata*.

On the other hand, polyxenous polychaetes are usually associated with hosts that frequently belong to the same taxa (i.e. class, order or even family). For example, *Iphitime cuenoti* inhabits the branchial chambers of 11 species of Mediterranean and Northern Atlantic crabs, *Paradyte crinoidicola* is associated with 20 species of unstalked crynoids, and *Gastrolepidia clavigera* lives symbiotically with 13 species of tropical holothuroids from two families (Stichopodidae and Holothuridae). Usually, this kind of specificity may be related to strict morphological adaptations of symbionts. Accordingly, *I. cuenoti* has a more or less simplified jaw apparatus (see [Figs 12A, 12B](#)), *P. crinoidicola* is equipped with hooked modified ventral setae (see [Fig 10C](#)), and *G. clavigera* has ventral sucker-like lobes (see [Fig 13A](#)). A strict preference of commensals for a given host taxon may also be extendable to the family level, such as the nautiliniellids associated with bivalves, the iphitimids with crabs or the serpulids with haerematipic corals ([Table 1](#)). More commonly, however, commensals from a given polychaete family are associated with a taxonomically wide range of host groups (e.g. the families Hesionidae, Polynoidae and Syllidae, [Table 1](#)).

Polyxenous associations involving host species from very different taxonomic groups are less common among polychaetes, occurring mainly within hesionids and polynoids. The hesionid *Ophiodromus flexuosus* inhabits the ambulacral grooves of 5 starfish species, as well as the tubes of 2 polychaetes, 1 balanoglossid and 1 burrowing holothuroid. *Hololepidella nigropunctata* is associated with 10 ophiuroids, 4 asteroids, 1 echinoid, 1 sponge and 1 cnidarian. *Arctonoe pulchra* is associated with 4 asteroids, 2 holothuroids, 1 gastropod, 1 polyplacophoran and 1 polychaete. However, the most surprising polyxenous species is *Arctonoe vittata* from the North Pacific ocean. Its host list includes about 30 species from very different taxa: cnidarians, gastropod and polyplacophoran molluscs, polychaetes, asteroids, holothuroids and echinoids! ([Table 1](#)). It is interesting to note that the areas of distribution of hosts harbouring *A. vittata* overlap only partially and, also, that its host preferences differ from one geographical area to another (Davenport 1950, Britayev et al. 1977). For example, its preferred host in Vostok Bay and the south-west coast of Sakhalin Island (Sea of Japan) is the gastropod *Acmaea pallida*, whereas in Avacha Bay (Pacific coast of Kamchatka peninsula) the host is the starfish *Asterias rathbunae* (T.A. Britayev personal observations).

These polyxenous associates with a wide range of host species require special attention and may be of great taxonomical interest, as the possibility of sibling or pseudosibling species-complex being hidden under the same species name remains always open. Probably one of the most striking cases was exemplified in Pettibone (1993), a recent paper reviewing the formerly “widespread”, “polyxenous” scaleworm *Harmothoe lunulata* (delle Chiaje 1841). This species was associated with a huge number of hosts, including asteroids, ophiuroids, holothuroids, cnidarians, polychaetes, sipunculids and balanoglossids. As a result of Pettibone’s (1993) careful taxonomic study, the different commensal specimens of this species were transferred to 15 species belonging to 3 different genera: *Malmgreniella*, *Lepidonopsis* and *Wiltoniella* (plus one additional genus, *Paragattyana*, and several more non-commensal species). The final result was that the number of hosts harbouring each new commensal species was restricted to one or a few closely-related species, from geographically closer areas.

INTRA-HOST DISTRIBUTION PATTERNS OF COMMENSAL POLYCHAETES

Since the first specific studies by Palmer (1968) and Dimock (1974) on symbiotic polychaete distribution patterns, a lot of new information has been reported. Nowadays, it seems clear that most adult symbiotic polychaetes with known distributions occur alone on their hosts ([Table 2](#)). In other words, their symbiotic populations show regular distributions. This type of distribution not only characterises most commensal polynoids, nereids, pilargids and amphinomids, but also some hesionids, syllids and sphaerodorids. Occasionally, several individuals have been reported on the same host, these worms always being one adult and several juveniles. More often, however, the juvenile individuals of a given species with solitary adults display a random or even an aggregated distribution pattern (Dimock 1974, Britayev & Smurov 1985). The transition from random toward regular patterns of distribution necessarily implies the existence of mechanisms regulating the distribution of adult symbionts on their hosts. As direct observations and specific experiments have shown, several polynoids (e.g. *Arctonoe pulchra*, *A. vittata*, *Halosydna brevisetosa*, *Hololepidella nigropunctata*) and nereids (e.g. *Nereis fucata*) may show strong territorial behaviour, fighting against other conspecific specimens (Devaney 1967, Goerke 1971, Dimock 1974, Britayev 1991). However, we suggest that territorial behaviour may be generalised to most symbiotic polychaetes with regular distributions. Two possibilities arise from the negative intraspecific interactions generated by territorial behaviour: the death of one of the competitors or its relocation to another host, with the final result of the successive fights leading to the formation of regular patterns of distribution. Therefore, both territorial behaviour and intraspecific aggressiveness emerged as major factors controlling the appearance and maintenance of regular distributions within symbiotic polychaetes. However, there are some other possible factors which should not be excluded. For example, the possession of its own host-territory may allow a solitary commensal to exploit by itself the limited resources supplied by its host (i.e. safe place or food sources).

As most polychaetes are heterosexual, the isolation of single specimens will apparently prevent successful reproduction. Therefore, regular distributions must be associated with mechanisms raising the chance of commensal males and females being in close proximity during the reproductive period. Among them, we may mention: (1) high densities of available hosts allowing successful reproduction of commensals (which do not force the symbiont to develop any specific adaptation), (2) a synchronised gamete release by the commensals (which will make them independent of the host distribution), and/or (3) the formation of temporary host aggregations (i.e. linked to its own reproduction or feeding activity) synchronised with the reproductive period of the commensals (which probably implies the recognition of chemical cues linked to host reproduction which will trigger reproduction in commensals).

The occurrence of isolated heterosexual pairs on the same host individual may be considered as a particular solution of reproductive problems within regularly distributed symbionts. This type of distribution, more typical among symbiotic crustaceans (e.g. Huber 1987), has been reported for only 5 polychaete commensals. These are the syllid *Ambliosyllis cincinnata* (from sponges of the genus *Halichlona*, *Halichondria* and *Isodyctia*), the pilargid *Antonbruunia viridis* (inhabiting the mantle cavity of the bivalve *Lucinia fosteri*) and the scaleworms *Bathynoe cascadiensis* (associated with the brisingid starfish *Astrocles actinodetus* and *Astrolirus panamensis*), *Harmothoe hyalonemae* (living in atrial cavities of deep-water hexactinellid sponges of the genus *Hyalonema*) and *Gastrolepidia clavigera* (associated with tropical holothuroids) (Hartman & Boss 1965, Riser 1982, Ruff 1991, Martin et al. 1992, Britayev & Zamyshliak 1996). Although there is no information on the reproductive cycle of these species, this pattern of distribution seems clearly more favourable to reproductive success. Moreover, there is no indication that the species living in heterosexual pairs are not as aggressive as the species living alone, which strongly supports the existence of sex-specific recognition for the symbiotic species living in pairs. Among polychaetes, sex-specific recognition has been previously reported for aggressive species such as *Neanthes fucata* (Reish 1957).

Several species of commensal polychaetes aggregate on their hosts ([Table 3](#)), along with most parasitic boring polychaetes ([Table 10](#)). This seems to be valid for the symbiotic iphitimids, some histriobdellids, dorvilleids, syllids, serpulids, spirorbids, caobangids and spionids. Since the

formation of aggregations among symbiotic polychaetes has not been the subject of specific studies, we can hypothesise that this pattern may result either from a peculiar gregarious habit in the settling larvae (i.e. chemically mediated settlement cues), or from the existence of mechanisms allowing the symbionts to increase their number on the host after an initial infestation by only one or two founders. This second strategy may be accomplished either by short larval development without pelagic phase, viviparity or asexual reproduction.

The aggregated distribution of the serpulid *Spirobranchus giganteus* living on corals (Hunte et al. 1990a), as well as of the spirorbid *Circeis armoricana* and the spionid *Polydora commensalis* on the inner surface of host hermit crab's shells (Rzhavsky & Britayev 1988, Radashevsky 1989) may result from gregarious behaviour. In fact, aggregated distributions are common among tubicolous polychaetes and has been attributed to the attraction of settling larvae towards the tubes of conspecific adults (Eckelbarger 1978, Jensen & Morse 1984, Pawlik 1988, Marsden et al. 1990). A particular case of aggregated distribution in tubicolous polychaetes occurs in an undescribed species of *Vermiliopsis* from the Caribbean Madreporid coral *Stephanocenia michelini*. The worm tubes of this serpulid are surrounded by the coral tissues and, according to Humann (1992), the crowns are regularly distributed on the coral surface (Fig 4A). We suggest that this special distribution may result from negative adult/larval interactions. In fact, the circulation generated by the crowns may very well prevent the settlement of larvae on the host surface areas controlled by resident worms. Therefore, settling larvae would only be able to start building their tubes at a given distance from all previously existing neighbours, this distance being almost always the same.

The dense populations of the small polydorid species of the genus *Polydorella* inhabiting the surface of cork-sponges (Fig 2C) apparently resulted from their asexual reproductive cycles, allowing them to reach quickly very high densities of up to 130 individuals per cm² after the colonisation of a suitable host sponge by a single new larva (Tzetlin & Britayev 1985, Radashevsky 1996). However, at least one *Polydorella* species (*P. smurovi*) may also reproduce sexually, since cocoons with eggs and embryos at different developmental stages have been found inside the adult tubes. In spite of the absence of direct observations, we can hypothesise that pelagic larvae resulting from sexual reproduction may be responsible for long-distance dispersion. Therefore, the combination of both reproductive strategies may allow them to succeed in finding and quickly colonising the rare suitable host sponges. A detection of chemical cues from the host sponges by pelagic chemosensitive larvae may be involved in host location, as was suggested for the parasitic syllid *Branchiosyllis oculata* (Pawlik 1983).

In *Histriobdella homari*, the males impregnated the females hypodermically by means of specialised copulatory organs, allowing the spermatozoa to avoid the necessity of swimming to reach the mature eggs, which are directly fertilised in the body cavity of females (Jamieson et al. 1985). Then, the female attaches the eggs both to the ventral surface and egg masses of the host, the young worms being then released as minute adults without planktonic phase (Haswell 1913). Thus, the juveniles directly colonise the host infested by their own parents. This leads to a clustered distribution of the commensals and to high infestation intensities reaching more than 600 worms per host lobster (Simon 1967). The transference from one host to another is probably accomplished by direct migration of adults.

LOCATION OF COMMENSAL POLYCHAETES ON THEIR HOSTS

Most commensals are characterised by a defined location on the host surface or, less frequently, inside the hosts (Figs 2, 3, 4, 5, 6). Since hosts may be considered as commensal refuges, the symbionts are normally located in the most protected sites. For example, commensals of decapods are usually located inside the host's branchial chambers (e.g. most *Iphitime* species, *Ophryotrocha geryoncola*, *O. mediterranea*, *Histriobdella homari*), inside the shells inhabited by hermit crabs (e.g. *Iphitime paguri*, *Nereis fucata*, *Circeis paguri*) or under the tails of egg-bearing female crabs (e.g. *Iphitime hartmanae*). The commensals of tubicolous polychaetes, burrowing holothurians or ghost shrimps (e.g. species of *Harmothoe*, *Lepidastenia* or *Malmgreniella*) occur inside host tubes

or burrows. The numerous associates of starfishes, sea-urchins and brittle starfishes (among them, many scaleworms, hesionids and some syllids) prefer the more protected oral surface of their hosts. The commensals of bivalves or limpets often live inside the mantle cavity (e.g. *Parasyllidia humesi*, *Antonbruunia viridis*, *Harmothoe commensalis*, *Arctonoe vittata*), whereas a similar position has been reported for cirriped associates (e.g. *Hipponoe gaudichaudi*). Although rare, some commensals may live inside the host's body, e.g. the amphinomid *Bentoscolex cubanus* living in the intestine of the deep-water sea urchin *Archeopneustes hystrix* (Emson et al. 1993).

Some commensals have slow movements and, when disturbed, tend to keep themselves firmly attached to their hosts. For example, the syllid *Haplosyllis chamaeleon* living on the branches of the gorgonian *Paramunicea clavata* (Laubier 1960). The worm usually extends its body along the longitudinal axes of the host branches, preferably near zones with a high number of living polyps (mainly the apical parts). When disturbed, the polychaetes introduce their strong hooks into the coenochym and cannot be taken off without damage to the host. However, most commensal polychaetes are agile animals able to change their position according to different stimuli. For example, *Gastrolepidia clavigera* are usually located near anterior or posterior ends of their holothurian host's body, quickly hiding in the oral or cloacal openings when threatened (Britayev & Zamyshliak 1996). Most commensal locations are reported from animals extracted from their natural habitats, meaning that observed locations may not be those preferred by the symbionts. Only a few data on the location of commensals in natural conditions are available. The commensal syllid *Branchiosyllis exilis* occurs on the arms or disc of its ophiuroid host *Ophiocoma echinata* (Hendler & Meyer 1982). The polychaete was observed moving along the ventral arm plates, between the alternating rows of arm spines and tube feet. They have also been found partially or entirely hidden in the oral cavity of the ophiuroid. However, immediately after host collection, *B. exilis* occurred more frequently on the arms of the ophiuroid than on the disk. Conversely, *in situ* observations of the scaleworm *Arctonoe vittata* associated with starfish *Astherias rathbunae* indicated that the worm occurred more frequently on the oral surface of starfish, in the ambulacral grooves or even partially inside the oral cavity (Britayev et al. 1989). Nevertheless, it had been reported as more frequently inhabiting the oral disk (65%) than the arms of the starfish.

It should be pointed out that the locations of *Haplosyllis chamaeleon*, *Branchiosyllis exilis* and *Arctonoe vittata* on their respective hosts are not simply connected with the finding of shelter or physical protection. *H. chamaeleon* was observed with its anterior end inside the gastral cavity of the gorgonian polyps. The slow movements and sensibility of the polyps may favour this behaviour, allowing the worm to feed either on the preys inside the polyp's stomach or on the polyps themselves. Although some pigmented parts inside the worm's gut supported the last possibility, no damage was observed in the polyps (Laubier 1960). Thus, it is not likely that *H. chamaeleon* behaves as a commensal or cleaner than as a parasite. *B. exilis* generally lies on the proximal portion of the ventral surface of its host's arms, directly in the path of food boluses carried by the tube feet towards the ophiuroid mouth. As suggested by Hendler & Meyer (1982), such a location allows the commensals to gather food from the alimentary tract of its hosts. Similarly, the preferred location of *A. vittata* on the host's oral disk seems likely to be connected with food supply. Direct observations on *A. vittata* feeding behaviour in natural conditions demonstrated that the worms gather pieces of their hosts' preys by biting them off both from the everted starfish stomach or directly through the mouth opening (Britayev et al. 1989).

The location on the host may change during the life-history of symbionts. The adult specimens of *Hipponoe gaudichaudi* occur inside the branchial chambers of its goose-barnacle host, whereas the juveniles may be located between the mantle and the calcareous plates of the host or attached to the adult symbionts *H. gaudichaudi* (Figs 5D, 5E) (Britayev & Memmy 1989, Núñez et al. 1991). The characteristic position occupied by *Iphitime cuenoti* is at the extreme anterior dorsal end of the branchial cavity, where the individual worms lie with the ventral surface of body closely applied to the branchiostegal fold separating the viscera from branchiae (Comely & Ansell 1989). When more than one worm occurs in a single host crab, the largest individual generally occupies this position, while other individuals may be found in a similar position in the opposite branchial chamber, at another point on the walls of each chamber, or among the gills. Moreover, in the

largest worms, the body is generally coiled. The smallest worms are only found in the interlamellar gill spaces and, when growing, the majority moves out and became established in the roof of the branchial chamber (Comely & Ansell 1989).

We suggest that a low availability of optimum larval settlement sites on the host surface could be one of the reasons why the commensals alter their locations during their life-cycle. Other probable reasons are: (1) differential preferences of juveniles and adults, (2) inaccessibility to optimum sites for juveniles, as a consequence of the competition with conspecific adults or other symbiotic species. The influence of intraspecific interactions between commensals on their location was demonstrated for the scaleworm *Arctonoe vittata* (Britayev et al. 1989). Its preference for the ventrum of its host's starfish oral disk was apparently inhibited when two worms infested the same host. In fact, the two symbionts were never found together on the oral disk. Whenever one of them occupied the oral disk, the other was on one arm (69% of starfish), the preferred area (i.e. oral disk) being always occupied by the larger worm. Moreover, the location of the two symbionts separately on the arms was also frequent (31% of starfish).

The location of commensal polychaetes must necessarily be influenced by the presence of other symbionts on the same host. However, although it is well-known that some commensal polychaetes may share their hosts with symbionts from different taxonomic groups (see Dales 1957 for *Hesperonoe adventor* and the complex network of guests associated with the innkeeper *Urechis caupo*) (Fig 3A), this discussion has not yet been developed. Changes in the location of commensal species may also vary in accord with the morphology or behaviour of their different host species. The scaleworm *Malmgreniella macginitiei*, for example, has been reported in the burrows of its host shrimp *Callinassa californina*, inside the parchment-like tubes of its host polychaete *Axiiothella rubrocincta*, or on the arms of its host brittle starfish *Amphiodia urtica* (Pettibone 1993). Another species of the same genus, *M. andreapolis*, was found inside the burrows of host holothurians, as well as curved around the disk and mouth of host brittle starfish s.

A special comment should be reserved for those commensal polychaetes that are not "satisfied" by the shelter or the protective abilities of their hosts. These symbionts may either construct their own refuges on the host's surface or stimulate their hosts to build protective structures around them. Among them, the eunicid *Eunice floridana* and the scaleworms *Harmothoe melanicornis*, *Malmgreniella dicirra*, *Polynoe uschacovi* and several species of *Gorgonyapolynoe* live inside tunnels or gall-like cavities formed by coenenchymal walls of gorgonian or hydrocoral hosts (Figs 4B, 4C, 4D) whose formation seems to have been brought about by the presence of the commensals (Britayev 1981, Pettibone 1991a, b), the lumbrinerid *Lumbrineris flabellicola* associated with scleractinian corals lives in membranous transparent tubes attached to the side of the host (Zibrovius et al. 1975, Miura & Shirayama 1992) (Fig 4F) and *Eunice* sp. constructs a fragile tube attached to the length of the upper surface of its gastropod host *Cerithium vertagus* (Gibbs 1969) (Fig 5A).

CHARACTERISTICS OF THE INFESTATIONS BY COMMENSAL POLYCHAETES

The prevalences of infestations by commensal polychaetes are highly variable, ranging from very low values (e.g. 0.03% for *Iphitime sartoral* associated with *Portunus spinicarpus*) up to host populations being infested as a whole (e.g. *Liocarcinus corrugatus* infested by *Iphitime cuenoti*, and some host populations infested by *Acholoe astericola* or *Bentoscolex cubanus*) (Table 4). The prevalence has been seldom considered as characteristic at the species level. In *Sphaerodoridium commensalis*, for example, a low prevalence of 3.5% seems to be the normal condition for all known populations of the species (Lutzen 1961), whereas in *Acholoe astericola* the characteristic prevalence is as high as 75-100% (Barel & Kramers 1977). However, each population of a given commensal species is usually characterised by different prevalences. Although bathymetric, spatial and temporal (i.e. seasonal and annual) variability in infestation prevalence and intensity may be expected in commensal populations, the corresponding patterns have seldom been documented.

Changes in infestation prevalence with depth have been reported for the Mediterranean populations of *Iphitime cuenoti* inhabiting *Liocarcinus depurator* (Belloni & Mori 1985, Abelló et

al. 1988). Although host abundance increases above 100 m depth, the commensal appears to avoid this depth range, the prevalence of the infestation increasing with depth (Fig 7A). This seems to be closely related with the temperature, colder and more stable in deep waters (> 100 m deep). In fact, the prevalence of the commensal population infesting another Mediterranean host crab, *Macropipus tuberculatus*, was independent of depth, but this host never occurs deeper than 100 m. It is a common fact that species occurring both in the Mediterranean and the Atlantic tend to inhabit cooler waters in the latter (e.g. Laubier 1973). Accordingly, no relationship between depth and prevalence was observed for *Ophryotrocha mediterranea* infesting *Geryon longipes* (Martin et al. 1991). In this case, although the host crab occurs both in the Mediterranean and in the Atlantic, *O. mediterranea* appears to be endemic to the former, whereas in the latter, the ecological niche was occupied by *O. geryoncola*.

Hendler & Meyer (1982) reported spatial variability in infestation prevalence from the different populations of the brittle starfish *Ophiocoma echinata* harbouring the tropical syllid *Branchiosyllis exilis* along the Panamanian coast (Fig 7B), where the maximum prevalence occurs in late Autumn and in Winter. Moreover, near Galeta, on the Caribbean coast of Panama, the prevalence of *B. exilis* varied over time between 20 and 90% (Fig 7C). It was highest from November to March (i.e. the dry season) and lowest in the local rainy season. The hesionid *Ophiodromus pugettensis* infesting the starfish *Patiria miniata* at Dana Point (California) reached its highest (79-92%) and lowest (19-32%) prevalence in November-December and Summer (prior to the decrease of water temperature), respectively (Lande & Reish 1968) (Fig 7D). The prevalence of the sphaerodoridae *Sphaerodorum ophiurophoretus* infesting the brittle starfish *Amphipholis squamata* at Wimereux (English Channel coast of France) was maximal during early Spring (11.9%), decreased in May (6.6%) and totally disappeared in Summer (Alvà & Jangoux 1989). The prevalence of *Iphitime cuenoti* in the Scottish waters showed different seasonal pattern depending on the host (Comely & Ansell 1989). In *Liocarcinus puber* and *L. depurator*, the prevalence ranged between 70 and 100%, with no indication of seasonality. In *L. depurator*, however, there was an apparent prevalence fall during April, independently of the catch size. *Carcinus maenas* showed a low level of infestation which apparently varied seasonally, the maximum prevalence occurring in October (i.e. 14%). It was suggested that the decreasing prevalences of *B. exilis* linked to the rainy season resulted either from seasonal changes in salinity (and other environmental parameters) or from seasonal fluctuations in the mortality of the polychaetes because of the recurrent, low-tide emergence of the reef flat (Hendler & Meyer 1982). The marked seasonal pattern of *O. pugettensis* seemed to be connected with commensal reproductive dynamics (Lande & Reish 1968). The absence of clear seasonal pattern in *I. cuenoti* from some of their host crabs was attributed to the persistence of small worms throughout the year, whereas the well-defined seasonal peak in the host *Carcinus maenas* was clearly correlated with the peak season for the commensal spawning in October (Comely & Ansell 1989). Conversely, in *S. ophiurophoretos*, there was no further analysis of what caused the seasonal pattern.

With the exception of the impressive fidelity of the year-to-year counts of a regular seasonal trend demonstrated for the infestation prevalence in *Branchiosyllis exilis* (Fig 7C), the only known data on year-to-year variability are on *Arctonoe vittata* infesting the starfish *Asterias amurensis* (Britayev & Smurov 1985). These authors reported a progressive increase in infestation prevalence from 0% in 1975-76 to 8.4% in 1978 and to 79.1% in 1980.

An additional source of variability in the respective prevalences of commensal populations emerges from the association with different hosts, even if this occurs in the same locality. In these cases, the different prevalences are linked to the greater or lesser suitability of different host suitability. As pointed out by Dimock (1974), the infestation prevalence of the scaleworm *Arctonoe pulchra* on the coasts of Santa Barbara (California) was higher in the preferred host, the sea cucumber *Stichopus parvimensis*, than in the limpet *Megatúra crenulata*. Similarly, the infestation prevalences of *Arctonoe vittata* in Vostok Bay progressively increased from the starfish *Aphelasterias japonica* (2-5%) and *Asterias amurensis* (79.1%) to the limpet *Acmaea pallida* (94%), the latter being the preferred host for the scaleworm (Britayev & Smurov 1985). The prevalence of the infestation by *Iphitime cuenoti* in Scottish waters was also higher in the preferred hosts,

Liocarcinus corrugatus and *L. puber*, than in the non-preferred hosts (such as *L. depurator*, *Carcinus maenas* and *Hyas araneus*) (Comely & Ansell 1989).

Data on intensities of infestations by commensal polychaetes have been more widely reported than prevalences, ranging from 1 to 648 symbionts per host (Tables 2 and 3). However, the 1:1 associations are clearly dominant owing to the usually low symbiont densities or to the regular distribution pattern linked to intraspecific aggressive behaviour (see above). Moreover, the list of species characterised by an intensity of 1 individual per host (Table 2) should probably be larger than it is, as most species included in Table 3 are indeed characterised by a normal intensity of only one large adult worm per host with the occasional presence of one to several more juveniles. Among these species, we may mention those of the genera *Acholoe*, *Adyte*, *Branchiosyllis* and, probably, some others whose growth status was not indicated in the original descriptions.

Infestation intensities may be considered as more species-specific than prevalences. Nevertheless, they may also differ seasonally within the same population, as also occurs with the relative densities (or abundances). However, this variability has been seldom reported. The abundance of the commensal *Ophiodromus pugettensis* was maximum in winter (2.0 - 2.6 worms per host) and minimum in the middle of summer (0.26-0.44 worms per host) (Lande & Reish 1968) (Fig 8A). In *Arctonoe pulchra*, intensity and abundance reached maximum values in August for *Stichopus parvimensis* associates (7 and 3.97 worms per host, respectively) and in September for *Megatūra crenulata* associates (4 and 1.06 worms per host, respectively) (Dimock 1974). Although it was not clearly demonstrated, these maximum values were due to an increasing number of juvenile commensals. Thus, the seasonal pattern in *A. pulchra* seems to be related to the reproductive cycle of the species. In *Iphitime cuenoti*, seasonal peaks of infestation intensities apparently occurred in the host crabs *Carcinus maenas* (maximum of 5 worms) and *Liocarcinus puber* (maximum of 9 adults and 98 juveniles) in October and May, respectively (Comely & Ansell 1989). Both peaks were clearly related to the reproductive cycle of the symbiont. However, it was difficult to attribute the character of seasonal pattern to the trends shown during a given year, at least in *L. puber*. Comely & Ansell (1989) pointed out that, although they considered unlikely that any considerable numbers of juveniles were overlooked during their routine examinations of the gills, the peaks of intensity found during one year (1986) were not observed during the next (1987). In fact, this seems to indicate that the seasonal patterns are linked to the reproduction of the symbiont, which may vary from one year to another, as it occurs in virtually all marine organisms (either symbionts or free-living).

As occurred with prevalences, we may expect additional changes in intensity of infestation among commensal populations from a given locality that are associated with different hosts. An example of this variability was reported for the scaleworm *Arctonoe pulchra*, whose populations associated with the sea-cucumber *Stichopus parvimensis* and the gastropod *Megatūra crenulata* showed infestation intensities of 1 to 7 and 1 to 4 commensals per host, respectively (Dimock 1974). In this case, the differences in intensity are likely to be connected with the amount of living space available to the commensal polychaetes, which is clearly higher in the first host species than in the second. For *Iphitime cuenoti*, the incidence of intensities higher than 1 commensal per host was higher in the preferred host crabs (Comely & Ansell 1989).

RELATIONSHIPS BETWEEN HOST AND COMMENSAL POLYCHAETE CHARACTERISTICS

When reported, the relationship between size structure of commensal and host populations is, if anything, unclear (Martin et al. 1991, 1992, Emson et al. 1993, Rozbaczylo & Cañete 1993, Britayev & Zamyshliak 1996). This suggests that the life-histories of commensal polychaetes are usually independent of their hosts', the host tending to live longer than the symbiont. In many cases, this dynamic implies that the same host population may successively harbour different polychaete populations. More detailed studies focusing on population dynamics of symbiotic polychaetes and their hosts may well reveal the existence of positive correlation between the respective size structures, as occurs among other symbiotic animals (e.g. the pontoniin shrimp *Anchistus custos* associated with the host bivalve *Pinna bicolor* in Britayev & Fahrutdinov 1994).

The size of host may affect the prevalence of infestation, with the largest individuals more often showing the highest prevalence (Figs 8B, 8C, 8D). Examples of this trend are found in the associations between *Circeis paguri* and *Eupagurus bernhardus* (Al-Ogily & Knight-Jones 1981), *Branchiosyllis exilis* and *Ophiocoma echinata* (Hendler & Meyer 1982), *Arctonoe vittata* and *Asterias rathbunae* (Britayev et al. 1989), and *Gastrolepidia clavigera* and *Stichopus chloronotus* (Britayev & Zamyshliak 1996). Certainly, a similar pattern may be expected for many other associations. Many reasons may explain why large hosts are more favourable to symbionts. They are usually older and so have been exposed to planktonic larvae settlement or adult migration for a longer period than small hosts. Moreover, large hosts provide more room for symbionts. Accordingly, many examples of the existence of low host-size limits have been reported. Among them, starfish *A. rathbunae* with disc radii lower than 35 mm were not inhabited by *A. vittata*, whereas those with radii up to 90 mm harboured only 1 symbiont and the largest starfish were infested with 1-4 symbionts (Britayev et al. 1989). Also, the scaleworm *Harmothoe commensalis* was not present in shells of the clam *Gari solida* lower than 60 mm in length (Rozbaczylo & Cañete 1993). In the case of *Circeis paguri*, both small shells and hermit crabs are rarely colonised (Fig 8C). In fact, the few small shells that are colonised are not very suitable habitats for the symbionts within them, which are rarely or never reach breeding size, presumably because the space available is too small to provide enough food or to satisfy their respiratory needs (Al-Ogily & Knight-Jones 1981).

The associations involving sexually dimorphic hosts merit special mention. One of the clearest examples was of the association between the dorvilleid *Ophryotrocha mediterranea* and the deep-water crab *Geryon longipes* (Martin et al. 1991). The polychaete was not detected in any of the small female crabs examined, while the prevalence among the large male crabs reached up to 19%. Indeed, the carapace length of the smallest infested host male (41 mm) was similar to the maximum length of the female's carapace (Fig 8E). Thus, it was suggested that the symbionts need a minimum of vital space, which the branchial chambers of juvenile and female crabs do not satisfy. This concurs with the fact that the closely related dorvilleid *O. geryoncola* was detected in females of *Geryon* species that reached larger sizes than males (Gaston & Benner 1981, Pfannenstiel et al. 1982). The opposite situation was reported for *Capitella capitata* living as commensal with the pea-crab *Pinnixia littoralis* (who lives itself as a commensal of the mactrid bivalve *Schizothaesus capax*). The commensals are always associated with the female crabs and never with the males, although both sexes may share the same host bivalve (Clark 1956). The worms lived more often inside thin mucous tubes attached to the crab's carapace, but could also be found burrowing inside a mass of detritus accumulated on the basis formed by the tubes. The most obvious solution was that males were too small to provide a suitable area on which the large *Capitella* could settle and, also, to support the large bolus of detritus. This was unlikely, however, because young female crabs, smaller than full-sized males, did carry the worms. The alternative and more likely explanation, proposed by Clark (1956), was that the males were too active. They were able to leave their own host bivalve, which was never observed of any females crab. By moving, the males prevented the accumulation of detritus on which the worms were presumed to feed and this caused the absence of commensal worms on the male's carapace.

When several hosts may be infested by the same commensal species, we may also expect that the relative size of the different host species would affect the respective symbiotic populations. In *Iphitime cuenoti*, for example, the largest commensals are usually reported on those hosts which are also larger (e.g. *Liocarcinus corrugatus* and *L. puber*). Thus, the total size of the commensal may be a function of the size of its crab host. However, this is valid for the small host species of the genus *Macropodia* and *Inachus* but not for the large *Cancer pagurus*, suggesting that other factors may limit the success of the worm (e.g. moulting frequency or stage). The commensal iphitimids seems able to support moulting stress, as worms have been found inhabiting recently moulted soft crabs (Abelló et al. 1988, Comely & Ansell 1989). However, a high moulting frequency may significantly disturb the success of the infestation. Hartnoll (1962) and Comely & Ansell (1989) also suggested that the substrata inhabited by the different hosts or by different individuals of the same host may affect the success of the infestation.

Theoretically, we may expect that the host's population structure will influence the structure of the symbiont population. Nevertheless, the available data to illustrate this statement are very scarce. The relationships between host size and prevalence mentioned above, lead to the speculation that higher values of the infestation indexes will be positively correlated to the presence of large and more numerous hosts. A positive relationship between host population density and infestation characteristics was reported for the starfish *Asterias rathbunae* and its commensal *Arctonoe vittata* (Britayev et al. 1989). In Avatcha Bay, Pacific coast of Kamchatka, the highest infestation prevalence, mean intensity and abundance occurred in the area most densely populated by the host. The high number of intraspecific traumas reflected the frequency of intraspecific interactions resulting from the high density of commensals in the mentioned area (i.e. higher than in the neighbouring ones). This may probably be related to a high mobility of the commensals among hosts, affecting also the structure of the commensal populations.

In most cases, however, the mechanisms to explain how the population density of hosts influences the commensal population remain unclear. We may hypothesise that the accumulation of chemical cues released from dense host populations may attract a high number of settling larvae of the commensal polychaetes more effectively than less dense host populations. Thus, we may expect higher recruitment and more young worms associated with dense host populations. Nevertheless, the influence of other external factors, such as predation pressure, can not be discarded. In fact, predatory activity will probably decrease the fitness of commensals associated with less abundant host populations more significantly than those harboured by dense host populations.

ADAPTATIONS OF POLYCHAETES TO THE COMMENSAL MODE OF LIFE

Cryptic colouring in commensal polychaetes

The colour patterns of commensal polychaetes frequently differ from those of its free-living relatives, even if the latter belong to strictly the same species. For example, the only apparent morphological difference between free-living and commensal specimens of *Lepidonotus glaucus* is the degree of pigmentation (Hanley & Burke 1990). The specimens associated with the *Eunice* hosts were more darkly pigmented, often appearing almost black, when compared with free-living specimens. We may tentatively suggest that the dark colouring of the commensal *L. glaucus* is closely related to the dark colour of its host. In fact, one of the most peculiar features of commensal polychaetes (mainly ectocommensal) is their cryptic colouring masking them on the host's surface.

The fact that many commensal animals inhabiting crinoids and holothuroids (including polychaetes) resembled their hosts was pointed out by Potts (1915). Later, the similarity of symbiont worms' colouring to their hosts' was stressed by nearly all authors studying commensal associations. Thus, when describing the association of the scaleworm *Malmgreniella variegata* [as *Harmothoe lunulata*] with the ophiuroid *Ophionereis reticulata*, Millot (1953) noted that "worms matched the ophiuran very closely, being white, with a well defined repetitive black pattern borne on elytra". This matching was also reported and well illustrated by Pettibone (1993). Another remarkable similarity in colouring is that of the hesionid *Gyptis ophiocoma* with its ophiuroid host *Ophiocoma scolopendrina* (Storch & Niggemann 1967). Moreover, the effectiveness of the polychaete's camouflage is often heightened by their location on an appropriate site on the host surface. The segments of the syllid *Branchiosyllis exilis* each had a thin white border so that they displayed light striations on close examination. This pattern of pigmentation was reinforced by the location of polychaetes on the black and white banded arms of the ophiuroid host *Ophiocoma echinata*, between colonnades of black and white striped spines (Fig 6D), which made it difficult to distinguish the commensals (Hendler & Meyer 1982).

The colour pattern of commensals inhabiting several host species is usually appropriately similar to the corresponding host colouring. For example, the individuals of the scaleworm *Gastrolepidia clavigera* associated with the uniformly black sea cucumber *Stichopus chloronotus* are usually black, whereas those associated with the yellow to brown *Thelenota ananas* are light

brown, and those with the greenish-grey *Stichopus variegatus* are greenish-grey with brown spots (Britayev & Zamyshliak 1996). However, some exceptions to this general rule may be observed. Dark brown worms typical to *S. chloronotus* have been found on *S. variegatus*, probably because the scaleworm changed from one host to another (Britayev & Zamyshliak 1996). Gibbs (1969) noted similar changes between hosts by this scaleworm species.

In light of the above, we may certainly assume that *Gastrolepidia clavigera* is not able to change its colour in a short time interval, such as octopus or flatfish do. A dual question then arises: does the observed colour pattern result from the host influencing the developing symbiotic polychaetes? or does a commensal population consist of several “sub-populations”, genetically pre-adapted to each appropriate host species? With the exception of the experimental demonstration of the trophic origin of the colour pattern in the parasitic syllid *Branchiosyllis oculata* (Pawlik 1983), there are no specific studies on this particular aspect of the arrangement of symbiotic associations. However, the accidental observation of commensal specimens with unusual “hybrid” colouring inclined us towards the first question. Indeed, hybrid colouring may result from the regeneration of posterior sections of the body. In *Arctonoe vittata*, the colour of the posterior part was yellowish-white in accordance with the body colour of its current host, the limpet *Acmaea pallida*, whereas the anterior (i.e. old or original) half of the body was pink-brown, closely resembling the colouring of the worms associated to the starfish *Asterias amurensis* (T.A. Britayev personal observations). As relocation from one host to another has been demonstrated (see above), the logical sequence of events may be as follows. A symbiont inhabiting the initial starfish host is disturbed (either as a result of intraspecific aggressive behaviour or predator attack), losing the posterior part of the body (i.e. autotomised or bitten). Then it is obliged to relocate to a new host, the limpet in this case, with the subsequent regeneration of the posterior half being in accord with the colour of the new host. It should be pointed out that how these changes in colouring are accomplished has not yet been assessed. In fact, we may hypothesise that the changes may be produced by a substance (or substances) obtained by the polynoids from their hosts (i.e. by partly feeding on them or by incorporating some kind of secretion) but, also, that the substance stimulating the different colourings are obtained both by the hosts and the commensals by feeding on the same kind of food. These two hypotheses clearly had different consequences in the allocation of the involved relationships within parasitisms or commensalisms.

A comparable case of colour mimicry occurs in the relationship between the syllid *Haplosyllis chamaeleon* and its single known host, the gorgonian *Paramunicea clavata* (Laubier 1960). The colouring of the worms varied from pale yellowish to dark red, matching exactly the colours of its host. Although these colours actually occur on the same host colony, there are no evident relationships between the colour of the host branch and that of the attached polychaetes. Moreover, hybrid specimens showing all possible colour combinations may occur. Uniform colour patterns may indicate symbionts growing to their adult size on the same gorgonian branch, then moving to different parts of the colony without any preference for the colour of the branches. Hybrid forms may be the result of these displaced specimens being bitten or autotomised and then regenerating on a differently coloured branch.

Although all these examples support the idea of the influence of the host on the colouring of its commensal polychaetes, the question of how the mimicry is accomplished still remains open. Is there an intrinsic metabolic reaction of the symbiont to the different stimuli provided by the different hosts? or are the symbionts taking pigments directly from the hosts, i.e. feeding on it? If the second answer is correct, then the associations involved should be re-evaluated as being closer to parasitisms. However, without specific descriptions of the behaviour of symbiotic polychaetes and its effects on their hosts, we decided to include them within the commensalisms.

Morphological adaptations of commensal polychaetes

Forty years ago Clark (1956) noted that “Although some worms ... to be found in more or less intimate association with other animals, very little structural adaptations appear to have taken place to suit them for this mode of life”. However, after carefully re-analysing the significantly high

number of commensal species described since this classic paper, it becomes clear that most, or even all, commensals have more or less defined morphological features allowing us to distinguish them from their free-living relatives.

The symbiotic features of commensal polychaetes can be divided into two categories: those significantly adapted to the commensal mode of life, and those repeatedly connected with the commensal mode of life, but lacking any obvious adaptive significance. The first group includes structural adaptations such as: i) modifications permitting the attachment of the symbionts to their hosts, ii) modifications allowing the symbionts to reproduce without leaving their hosts and so prevent gamete losses, iii) modifications affecting the buccal equipment of symbionts, and iv) modifications enabling the symbionts to mimic their hosts. The best known modifications included in the second group are those of elytra and parapodia in scaleworms, but the eyes may also show interesting modifications. Moreover, it has also been pointed out that commensal polynoids are often larger than their free-living relatives. This modification, however, has been interpreted as a consequence of - instead of an adaptation to - the commensal mode of life. This fact was supposed to be due to a decreasing necessity of exercise in the commensals, and to a food supply being greater and more easily accessible to commensals than to free-living worms (Essenberg 1918).

The observation and correct interpretation of all morphologically evident commensal features (whether they have clearly adaptive significance or not) is important: in particular, whether these features enable symbiotic and free-living polychaetes to be distinguished, despite the specimens being found separately from their hosts. It should be pointed out that this situation is quite common when studying worm collections, which are based on trawl or dredge samples that often reach the polychaetologists already sorted.

Adaptive morphological modifications

Attachment structures are frequently related to the setal arrangement. Hooked setae apparently modified to facilitate the attachment have been reported for a wide number of species from many different families (viz. Iphitimidae, Polynoidae, Amphinomidae, Sphaerodoridae, Nautiliniellidae, Spintheridae, Syllidae) (Figs 9, 10, 11, 12). Some of them show remarkable coincidence in shape and, although not demonstrated, probably in functionality, too. In the case of polynoids, some species seem able to continually replace the hooked setae becoming blunt from wear by new pointed ones growing out from the basis of the parapodia (e.g. *Arctonoe fragilis*). This characteristic is not common to all polynoids but is an exception observed in a few species which are in a habit of attaching themselves to other organisms (Essenberg 1918).

Attachment structures other than those based on setae have been reported only twice: for the holothurian-associated scaleworm *Gastrolepidia clavigera* (Fig 13A) and for the highly modified species of the crustacean-associated family Histriobdellidae. The highly peculiar attaching structures of *G. clavigera* consist of semicircular, serially arranged, shield-like ventral lobes of the segments. These lobes considerably increased the area of contact between the commensal and the smooth, mucus-covered holothurian body. Moreover, when combined with a characteristic arching of the worm's body, they probably function like suckers (Gibbs 1971). Such an attaching organ, unique among polychaetes, is reminiscent of the small clam *Entovalva semperi* Oshima, which attaches itself to the burrowing sea cucumber *Protankyra bidentata* by means of a highly modified foot that functions like a suction cup (Dales 1957).

The attachment structure of the histriobdellids clearly differs from that of the scaleworm. The body of these commensal worms is so highly modified that they were initially considered as larval serpulids (van Beneden 1853), then as adult leeches (van Beneden 1958) and as Archiannelids (Hermans 1969). Although some differences may occur at the species level, the attachment structures are located on the distal end of two widened lateral expansions present on the posterior end of the body (Figs 13D, 13E) and consist on several adhesive glands. Modified reproductive structures are also present in this family. Indeed, the males are provided with a copulatory complex (Fig 13D) composed of a penis with one (*Stratiodrilus* spp.) or two (*Histriobdella*) projecting structures, a highly developed musculature, peniform external structure and several lateral or

median expansions or lips. Moreover, the males have also one or two lateral retractile or claspers. This complex organ enables the males to inject the sperm directly into the body cavity of females (Lang 1949, Jamieson et al. 1985), assuring the effectiveness of fertilisation in the limited space provided by the host.

Modifications of jaw apparatus have not been so often reported for commensals as for parasitic polychaetes (see the corresponding chapter). The mandibles of the histriobdellids closely resemble those of the eunicids (Mesnill & Caullery 1922), among which they are currently included (Fauchald 1977), and do not have any apparent adaptive modification. Although it was pointed out that they were not solid but hollow, the relationship of this characteristic with the symbiotic mode of life of these worms has not been defined. In addition, it is often very difficult to describe their exact composition as they vary from individual to individual (Lang 1949). *Stratiodrilus* species have denticulated bucal lips surrounding the mouth opening (Moyano et al. 1993). As these worms feed by grazing on the microflora that grow on the different surfaces of the host's body (Cannon & Jennings 1987), this mouth structure is likely to be related to its feeding mode. In fact, most of the jaws defined as highly specialised do not differ greatly in complexity and function from those of related free living-polychaetes (e.g. commensal *Ophryotrocha* spp. versus other dorvilleids). Moreover, the jaw apparatus may vary in size and appearance according to the size of the worms and the time of usage, such as in *O. geryoncola* (Pfannestiel et al. 1982). The mandibles of the iphitimids also resemble those of the free-living relatives (i.e. eunicids such as *Halla* spp.). However, evidences of tissue damage in their host crabs has never been reported, although all the species have mandibles well equipped for biting and chewing (Fig 12). In this case, commensal iphitimids are not notably simpler, their jaws being only modified in that the basal pair of maxillae (the only well-developed pair) are fused together to form a pair of pincers (Hartnoll 1962). Conversely, the single parasitic iphitimid, *Veneriservia pygoclava*, shows a highly simplified jaw apparatus (see Fig 12G). Additional variability was initially related to the fact that some species are sexually dimorphic (e.g. *Iphitime cuenoti*), with the males being significantly smaller than females (Hartnoll 1962, Abelló et al. 1988). More recently, however, it was demonstrated that individuals of *I. cuenoti* may have either small or large jaws (Figs 12A, 12B), independently of sex, and that those with small jaws were probably young sexually undifferentiated individuals (Comely & Ansell 1989).

Morphological adaptations also allow the commensal polychaetes to mimic the surface structure of their hosts. *Bathynoe cascadiensis*, a scaleworm associated with starfish, has unusually large elytra with numerous prominent nodular macrotubercles (Fig 13B). These tubercles are likely to be a specific adaptation for living with hosts from the order Forcipulata, a group characterised by having numerous knobs and spines and being heavily armed with large pedicellaria. By mimicking the spines and tube feet of starfish, it has been suggested that the camouflaged worms may protect themselves from being attacked and rejected by their own hosts (Ruff 1991). A spectacular example of mimicry has been demonstrated by the individuals of the scaleworm *Gastrolepidia clavigera* that are associated with the sea cucumber *Holothuria atra*. The holothurians are black, sometimes with tints of violet, and usually have white coral sand grains adhered to their surface so that they appear to be covered by a silvery-white "coat". The commensal worms are deep violet, almost black, with the elytra dark brown to black with bright white tubercles (Potts 1910, Gibbs 1969). Moreover, the distal part of antennae, palps, and tentacular and dorsal cirri are swollen and white. These white tubercles and appendages on the dorsal side of the worms exactly mimic the holothurian papillae with attached white sand grains (Britayev & Zamyshliak 1996). In the case of *Asterophilina carlae*, this uncoloured scaleworm is very conspicuous on the surface of its blue host starfish *Linkia laevigata*. However, the large swellings of the appendages and raised mounds of the posterior edge of each elytron of the polynoid (Fig 13C), as well as the elliptical outline of its body, perfectly mimic the host in that, often, the starfish has only a portion of each ambulacral groove open and this groove, through which the tube feet protrude, is elliptical in outline (Hanley 1989).

Non-obviously adaptive morphological modifications

Many commensal polychaetes have structural modifications of their external features which differentiate them from their free-living relatives, but lack an obvious adaptive significance. Often, the finding of some of these characteristics in newly described species allowed its commensal habit to be inferred without reliable observations of the specimens living with any host species (e.g. *Minusculiscama hughesi* and its maldanid hosts in Pettibone 1983). The most typical series of “commensal” trends are certainly found within the polynoids.

The elytra of many commensal scaleworms are small (leaving much of the dorsal surface uncovered), thin and smooth, and lack the ornamentations frequently found on free-living species. A good example of these small elytra occurs in the species of the genus *Lepidasthenia*: in *L. mossambica*, the elytra are very thin, whereas they are smaller in *L. microlepis* and so diminished in overall size as to be mere vestiges at the end of long elytophores in *L. stylolepis* (Figs 13H to 13J). Additionally, some polynoids (viz. species of the genus *Arctonoe*, *Bathynoe*, *Branchipolynoe*, *Disconatis*, *Gastrolepidia*, *Hololepidella*, *Lepidasthenia*, *Minusculiscama*) have very small notopodia (subbiramous parapodia) with a limited number of purely developed notosetae or even without setae (e.g. *Branchipolynoe pettiboneae* in Fig 10K). Although some of these modifications may occur in commensal polychaetes associated with bivalves (e.g. *Branchipolynoe symmytilida* in Pettibone 1984a), they appear more frequently as a result of sharing tubes or galleries with a host. Perhaps the protection afforded by the tube and the clean water circulated through the tube by the host diminish the need for elytra to form a defensive covering, the requirement for large elytra and the presence of notosetae to help keep the dorsal respiratory surface of the body clean. In fact, certain species (e.g. *Disconatis contubernalis*, *Lepidasthenia microlepis*) have the first pair of elytra much larger than the subsequent pairs. This may be closely related to the protective role of elytra, particularly if commensal habits include sticking its head out of the tube (Hanley & Burke 1988). A limitation of movement requirements may also be related to the decreasing importance of notosetae in the commensal tube-inhabitant scaleworms.

The scaleworm *Ophthalmonoe pettiboneae*, which lives inside the tubes of the large chaetopterid *Chaetopterus appendiculatus*, also show a very interesting modification. This commensal species has two pairs of eyes, with the anterior one being enlarged, directed anteriorly and with conspicuous lenses (Figs 13F, 13G). Both this orientation and structure of eyes are rather rare among polynoids, but are typical for tube-dwelling acoetids. Therefore, although this eye shape seems clearly to be an adaptation of the scaleworm to inhabiting tubes (Petersen & Britayev 1997), the relationship with its commensal mode of life is not clear.

Adaptive behaviour in commensal polychaetes

Although the behaviour of any commensal polychaete should undoubtedly be adapted to the symbiotic mode of life, very often this adaptive behaviour seems easy to deduce from the normal habits of the free-living polychaetes. Some typically symbiotic types of behaviour we expect in commensal polychaetes are: the co-ordination of movements with those of their host when feeding and moving, the finding of a new host (i.e. during recruitment or if they are moved out from their current host, either as a result of intra-specific competition or death of the host), the finding of a reliable way of attaching themselves to their hosts, and the selection of the most protected area in the host body. The last two types are closely connected with morphological adaptive modifications which have already been discussed in other sections. The first two require a more specific discussion. As mentioned in the introduction, commensal relationships are often known as “0+” associations. However, detailed behavioural studies strongly support the view that certain commensal associations are, in fact, “++” or mutualistic relationships, when the benefits are bilateral. This mutualistic behaviour also merits a specific discussion.

It should be pointed out that behavioural information often results from direct field or experimental observations of living associates. Consequently, it tends to be very rare.

Nevertheless, some interesting examples have been reported and will be discussed in the following sections.

Co-ordination of host/symbiont movements

Remarkable host/symbiont co-ordination in movements and feeding behaviour occurs between the reddish scaleworm *Hesperonoe adventor* and its host echiuroid *Urechis caupo*. The host constructs a large burrow in mud flats and feeds with the aid of a mucous bag, drawing water through the bag by peristaltic movements of the body. The commensal usually lives alongside the host ([Fig 3A](#)) and so is obliged to move back and forth along the wall of burrow to avoid the peristaltic swellings of the host. The commensal feeds on parts of the mucous bag formed by the host, but can reach the bag only when the host itself is eating it (Dales 1957).

The behaviour of *Hesperonoe adventor* closely resembles that of an undetermined species of polynoid (probably belonging to the genus *Malmgreniella sensu* Pettibone 1993) found associated with a tube-dwelling synaptid holothurian on the Catalan coast of the Mediterranean (D. Martin personal observations). The scaleworm was observed inside the host burrow, lying below the holothurian with its dorsum touching the ventral side of the host. The symbiont moved in order to avoid the host's peristaltic swellings, exactly as *H. adventor* does. In this case, however, there is not a clear trophic relationship between the deposit-feeding host and the probably carnivorous symbiont.

Nature and specificity of host recognition behaviour

The most widely studied aspect of host-commensal relationships among polychaetes is probably host recognition behaviour (viz. Davenport 1950, Davenport & Hickok 1951, Davenport 1953a, b, 1955, Bartel & Davenport 1956, Hickok & Davenport 1957, Davenport 1966a, b, Gerber & Stout 1968, Webster 1968, Dimock & Davenport 1971). In the well-known series of experiments using different models of choice-apparatus, most of these authors clearly demonstrated that all the symbiotic polychaetes studied were able to recognise their hosts and to respond to their presence or to some signals (i.e. the so-called host-factor) released from the host into the water (i.e. in absence of the hosts themselves). The known symbiotic polychaetes showing host recognition behaviour in experimental conditions include 14 species and 25 relationships ([Table 5](#)). Some commensal polychaetes (viz. some *Arctonoe* spp., *Ophiodromus puggetensis*, *Hesperonoe adventor* and *Hololepidella nigropunctata*) seemed able to detect their hosts from a distance. Other commensal worms did not show distant host recognition. *Acholoe astericola*, for example, seems only able to recognise its host starfish when adjacent to, or even touching, host's. As soon as its head contacts the host, the worm becomes active almost at once, fastening itself to the host either by climbing quickly to the aboral surface or into the ambulacral groove, or by wrapping itself entirely around the tip of the host arm (Davenport 1953a). *Haplosyllis chamaeleon* shows a similar specific response to its gorgonian host (Laubier 1960). When separated from the gorgonian, the polychaetes remain particularly immobile and coiled around themselves. Only after contacting a host branch, do they start to crawl and reach their habitual position on the branches.

The mechanism of host recognition appears highly specific in some commensal polychaetes, at least in experimental conditions. Commensal polychaetes seem able to recognise their host, to distinguish it from taxonomically related species, and to distinguish the original host species from alternative ones. *Arctonoe fragilis* was attracted by water from a tank occupied by its host starfish *Evasterias troschelii*, but not by water from a tank of another starfish of the genus *Pisaster*, with which the worm is not associated. Similarly, *Arctonoe pulchra*, was attracted by water coming from the sea cucumber *Stichopus* (i.e. the host), but not by water from *Cucumaria* (non-associated, but common in the same habitat) (Davenport 1950, Davenport & Hickok 1951).

The specificity of the response is highly variable depending on the different commensal polychaetes. *Acholoe astericola*, for example, may respond positively both to its host and to many other taxonomically related animals (see below). Conversely, *Arctonoe pulchra* showed undifferentiated liking for animals belonging to different taxonomic groups. Indeed, this

commensal repeatedly show preference for the arm of the choice-apparatus with water flowing from: starfish (*Dermasterias imbricata*), sea cucumbers (*Stichopus californicus*, *S. parvimensis*) and molluscs (*Megathura crenulata*), all of which were in fact their natural hosts. The specimens of *Arctonoe vittata* harboured by *Asterias amurensis* positively respond to chemical signals both from the original host and from its alternative host mollusc *Acmaea pallida*. However, the positive responses of worms associated with *A. pallida* were restricted to the host mollusc (Britayev 1991). The behaviour of *A. vittata* has clear implications for the population dynamics and life-cycle of the species (see Fig 14). In fact, recruitment may occur on both hosts. However, the symbionts (i.e. juveniles or adults) driven off the host starfish as a result of intraspecific competition will be able to relocate not only on other starfish but also on the host mollusc, whereas those worms initially associated with the mollusc have only one relocation possibility, i.e. another host mollusc.

Certain chemical cues released by or from the host to the surrounding water seem to hold the key of host recognition behaviour in polychaetes (Davenport & Hickok 1951). When the asteroid *Evasterias troschelii* was suspended in a bolting-silk bag in an aquarium and then carefully removed, the commensal *Arctonoe fragilis* was able to detect the signal released by the host. When the host starfish was suspended in an aquarium overnight in a dialysis bag, the commensal did not respond to the water outside. However, by splitting the bag with a razor the attractive cue was released and the commensal immediately responded. But it is not at all clear what this cue substance (or substances) is. It seems to be very labile, as the positive response of *A. fragilis* to the water in absence of the host was only maintained for between 15 and 30 minutes. Also, a temperature higher than 64 °C either alters or completely destroys the attractant, eliminating any response (Davenport 1953a).

The fact that, in some cases, commensal responded positively to several taxonomically close hosts suggests a possible biochemical similarity between them, with their cues having the same or very similar chemical composition. The specimens of *Acholoe astericola* originally associated with the starfish *Astropecten irregularis* at Plymouth positively respond not only to their original host but, to some extent, to other asteroids of the order Phanerozonia from the same area (e.g. *Astropecten*, *Luidia*, *Porania*, *Solaster*) and to certain spinulose starfish (*Asterina*, *Palmipes*, *Henricia*), but they did not ordinarily respond to forcipulate starfish (*Asterias*, *Marthasterias*, *Stichastrella*).

The scaleworm *Polynoe scolopendrina* showed a more specific response than *Acholoe astericola* when tested against a wide spectrum of terebellid polychaetes. Although certain reduced responses to two species of *Amphitrite* (not its normal hosts) were detected, the polynoid consistently responded only to its original host (i.e. *Eupolymnia nebulosa*). This commensal has two alternative hosts, the terebellid *Lanice conchilega* (described from deep water on the French coast) and the eunicid *Lysidice ninetta* (occurring also in the Plymouth area). Interestingly, however, the commensal polynoid responded strongly to *L. ninetta* and did not respond to *L. conchilega*. Accordingly, it was suggested that, although belonging to the same polychaete family, the attractants released by the hosts *E. nebulosa* and *L. conchilega* and recognised by the respective commensal populations, did not share the same chemical composition (Davenport 1953b).

Biochemical studies on the “host factor” based on disc electrophoresis with polyacrylamide gel revealed that seven protein fractions (five of them mucoproteins) were very likely responsible for the attraction of symbionts. These interesting studies were carried out on a copepod, *Sabelliphilus sarsi*, living in symbiosis with a sabellid polychaete, *Spirographis spallanzani* (Carton 1966a, b, 1967, 1968a, b). Apart from the studies mentioned above, there are no further studies on the nature of the “host-factor” and on the specificity of host recognition in polychaetes. This is certainly one of the most promising lines of research into symbiosis in polychaetes, particularly as many studies suggest the importance of host recognition behaviour. According to Carthy (1958), the difference between taste (contact chemoreception) and smell (distant chemoreception) in aquatic organisms is a question of threshold, smell receptors having a low, and taste receptors a high, threshold. In support of this, Gerber & Stout (1968) demonstrated that *Arctonoe vittata* (from the host *Diodora aspera*) apparently had two different chemoreceptors, one for distant reception (the antennae) the other for contact reception (the palps). However, these authors also demonstrated that the behaviour of the commensals indicated that the distant chemoreceptors did not function in

contact chemoreception, which strongly supported the existence of two different host factors involved in this particular relationship. Gerber & Stout (1968) also pointed out that “further work needs to be done to demonstrate the presence of two possible host factors and their chemical nature and to identify morphologically and physiologically the receptors involved”. Although recommended in 1968, this work has still not been done.

Several classical studies on host recognition behaviour have repeatedly been considered conflicting and obscure. The most representative is probably the study on *Harmothoe lunulata* and its hosts from Plymouth (Davenport 1953b). The scaleworms associated with the terebellid *Amphitrite johnstoni* unexpectedly demonstrated slight positive responses to the alternative hosts *Arenicola marina*, *Lanice conchilega* and *Golfingia elongata*, but not to species taxonomically related to the original host such as *Amphitrite edwardsi*. In fact, the recent taxonomic review on *H. lunulata* and related species (Pettibone 1993) enables light to be cast on Davenport’s conflicting observation. According to Pettibone (1993), the specimens of “*H. lunulata*” should probably be considered as belonging to different species. The population associated with *A. johnstoni* was transferred to *Malmgreniella andreapolis*, whereas those associated with the ophiuroid *Acrocnida brachiata* and the holothuroid *Leptosynapta galliennii* reallocated to *M. arenicola*. Moreover, the three hosts which triggered unexpected positive responses in Davenport’s “*H. lunulata*” associated with *A. johnstoni* (i.e. *A. marina*, *L. conchilega* and *G. elongata*) were reported as natural hosts of *M. arenicola* by Pettibone (1993). These observations seem to clarify the unexpected commensal responses, but pose new questions about the “nature of the host-factor” problem.

It has been demonstrated that the high frequency of commensals migrating from host to host (including other species than the original host) may result from intraspecific competition (Lande & Reish 1968, Palmer 1968, Dimock 1974, Britayev 1991). Therefore, the classic authors, working before these dates, could not fully assess the relevance of the host recognition behaviour they found. In 1966, Davenport wrote that “...during adulthood of the commensals, the chaemotaxis serves merely to keep the commensal on the surface of the hosts...under natural conditions an annelid... would seldom be forced to seek a new host when its own is damaged or dying. Such an event is probably too rare to be considered a factor in the evolution of the powerful chaemotactic response ...”. However, the fact that the spatial pattern formation in symbiotic polychaete populations strongly depends on intraspecific competition and resulting symbiont relocation revealed the significance of host recognition behaviour in life-cycles of symbionts.

Host-entering behaviour

The section above may suggest that chaemoreception is the dominant mechanism contributing to the maintenance of marine symbiotic partnerships. However, other kinds of stimuli produced by the hosts may trigger characteristic adaptive responses from commensal polychaetes. As pointed out by Gilpin-Brown (1969), the nereidid *Nereis fucata* seemed unable to discriminate between different species of hermit crabs. Thus, the peculiar association of *N. fucata* with hermit crabs seems to display non-chemically regulated behaviour. Surprisingly, this association has been studied by many authors (Rabaud 1939, Thorson 1949, Brightwell 1951, Gilpin-Brown 1969, Goerke 1971, Jensen & Bender 1973, Cram & Evans 1980) and, unusually, it has even been filmed (Goerke 1977a, b).

The most distinctive attribute of *Nereis fucata* is, probably, its intricate mode of entering the gastropod shell inhabited by the host. Settlement of this species occurs directly on the sea bottom, without any kind of host specificity. Both young recruits and adults that had moved out from their shells owing to the death or moulting of their hosts, are found inside tubes in the bottom sediments. When a hermit crab is placed in the vicinity of such pseudo “free-living” commensals in an experimental aquarium, the worms immediately begin to come out of their tubes. As the worms stretch out of their tubes, the anterior portion of their bodies rise up from the bottom and begin to wave about in a wide, sweeping movement. When the hermit crab enters the search area delimited by these sweeping movements and touches the worm head, the worm starts moving straight to the shell and quickly enters it. A similar reaction was experimentally triggered by bouncing an empty and carefully washed shell on the bottom or even by tapping the edge of the culture vessel with a

finger nail. All these experiments demonstrated that the characteristic searching behaviour of *N. fucata* was triggered by the perception of substrate vibrations. Presumably, this behaviour will also be present in natural commensal populations, starting as soon as substrate vibrations are perceived by the worms. This behaviour appears 4 months after settlement and is maintained during the whole life of the commensal. This fact was the main argument used to consider the association of this species and hermit crabs truly commensal (Gilpin-Brown 1969).

On contacting a host hermit crab, the individuals of *Nereis fucata* take up a position behind the shell, then crawl over it, usually along its sutures, before eventually reaching the aperture. The worm enters *via* the upper lip of the aperture and rapidly crawls inside the shell to adopt its habitual position (see [Fig 5G](#)). *N. fucata* is able to crawl on the smooth shell surface by secreting mucous from special glands located in its parapodia. These glands have not been reported in free-living nereidids, so constitute a differential character of this symbiotic species. Therefore, *N. fucata*'s characteristic adaptive behaviour is accompanied by a singular physiological adaptation.

Mutualistic behaviour

The fact that some commensal associations may probably be transferred to mutualistic interactions may be indicated both by specific behavioural response of hosts to the presence of symbionts and also by the absence of hostile host reaction. A typical example of host response was described in the association between the hesionid *Ophiodromus puggetensis spinapandens* and its echinoid host, the sand dollar *Clypeaster humilis* (Storch & Niggemann 1967). The commensal is usually found crawling among the spines on the oral side of the host. When the head appendages of the symbiont contact the host's spines, these start moving apart, which allows the commensal to go further on the host surface. During its movements, the worm directs its parapodia vertically downwards. Conversely, when different free-living species of polychaetes (viz. nereidids, syllids, chrysopetalids) were experimentally forced to touch the surface of the sea urchin and placed among the host's spines, the spines were motionless. This behaviour prevented any kind of worm movement and was reinforced by the pedicellaria attempting to snatch the intruders. Such very specific host behaviour closely resembled that of giant sea-anemones in their well-known association with clown fishes and crabs inhabiting their crowns. In these cases, the symbionts are tolerated by the host, whereas their free-living relatives are damaged or killed by the nematocysts, as soon as any contact with anemone tentacles occurs. Symbiont recognition may also occur in the associations between predator hosts and polychaetes, such as those involving hermit crabs and *Nereis fucata*. Adult *N. fucata* stretch from the inner surface of the shell and crawl out to take food from the pagurid's maxillipeds. Either owing to the worm's avoidance of the hermit crab's buccal equipment or to some chemical signal from the symbiont that is effectively recognised by the host, the fact is that the commensals are never attacked by the host. However, other polychaete species may perfectly well be preys of the hermit crab.

Symbiont recognition by hosts would be meaningless if the hosts derived no benefits from the association with their symbionts. Benefits for the host may include defence against predators or cleaning, which imply steps from a unidirectional towards a mutualistic relationship. The most evident benefit from the host's association with an aggressive inquiline, like a polynoid (Dimock 1974), is certainly assistance in fending off predators by biting them. This behaviour has been suggested in certain associations involving polynoids (e.g. *Harmothoe hyalonemae* in Martin et al. 1992), but was earlier demonstrated in the association between *Arctonoe vittata* and its host limpet *Diodora aspera* (Dimock & Dimock 1969). In this case, the symbiont aggressiveness towards the predatory starfish *Pisaster ochraceous* was not displayed by worms on their own, which strongly suggests that stimuli linked to the host (i.e. chemical or mechanical cues) may trigger the commensal's aggressive behaviour.

Hosts may also benefit from symbionts' cleaning activity, though this may bear no relation to symbiont aggressive behaviour. Benefits based on cleaning activity have been suggested for the associations between spionids and molluscs (*Polydora glycymerica* and *Glycymeris yessoensis* in Radashevsky 1993) or sponges (*Cliona viridis* and *Polydora rogeri* in Martin 1996). In these cases, the ability of the polydorids to manipulate relatively large particles may favour the filtering

activity of the hosts by cleaning the water around the bivalve's siphons or the sponge's inhalant papillae (see the section on boring symbiotic polychaetes). However, the so-called aggressive polynoids may also act as cleaning symbionts either by removing epi- or endobionts or by feeding on mucus or settled detritus. In bathyal muddy benthic environments, the Mediterranean hexactinellid sponges of the genus *Hyalonemae* were certainly suitable refuges likely to attract the existing vagile fauna. However, those sponges inhabited by the polynoid *Harmothoe hyalonemae* were never occupied by endobionts other than the commensal worms (Martin et al. 1992). In the association between the polynoid *Arctonoe vittata* and the starfish *Dermasterias imbricata*, the commensal may benefit the host by feeding on sea star mucus and settled detritus (Wagner et al. 1979). In fact, *D. imbricata* lacks pedicellariae, structures which are thought to function in part by keeping the aboral surface of other starfish free of epibionts and detritus. As pointed out by Wagner et al. (1979), most starfish hosts reported for *A. vittata* also lack pedicellariae. All these observations strongly suggest that *A. vittata* may be involved in a mutualistic, rather than a unidirectional, association with its host starfish. Moreover, the series of experiments carried out by Wagner et al. (1979) are the only demonstration of a host, *D. imbricata*, being attracted toward its commensal polynoid, *A. vittata*. Although this attraction was clear in the laboratory, its precise role in nature was not clear. Rather than acquire symbionts from a pool of free-living worms (*A. vittata* is considered an obligatory commensal), the host response more likely served to re-establish an existing association after the symbiont had become temporarily separated from its host. In fact, this suggestion coincides with the importance attributed to host-relocation behaviour in the life-cycle of symbiont *Arctonoe* species (Dimock 1974, Britayev 1991).

LIFE-CYCLES OF COMMENSAL POLYCHAETES

Little is known on the life-cycles of commensal polychaetes. The available data, however, allow us to surmise that, in fact, the life-cycle structure of most commensal species does not significantly differ from those of their free-living relatives. The well-known generic scheme of polychaetes' life-cycle, divided into planktonic larval and benthic adult phases may perfectly be applied to commensal polychaetes, with a single main difference: the symbiotic habits replace the free-living ones in the benthic phase. The tropical serpulid *Spirobranchus giganteus*, an obligate symbiont which builds its tubes on the surface of living haerematypic corals, instead of bore or excavate the coral skeleton (Marsden 1987, Hunte et al. 1990a, b, Marsden et al. 1990), may well illustrate this point. *S. giganteus* is a dioecious species, which has external fertilisation and a planktonic larval phase of 9 to 12 days long. These planktonic larvae are attracted by certain coral species whereas they do not respond to certain others. Despite it was suggested that commensals' larval settlement should occur on the bottom, with a subsequent juvenile migration towards the respective hosts (Davenport 1966a), it seems more likely that host-recognition by settling larvae is a widespread trend among symbiotic polychaetes (parasites included, see the corresponding sections below). Moreover, the planktonic larvae of symbiotic polychaetes may also be attracted by their adult conspecifics, as it occurs in *S. giganteus*. In summary, the life-cycle of this species consists of a symbiotic adult stage with limited mobility and a free-living planktonic phase, which is in fact responsible for dispersion.

This scheme may vary depending on the species. For example, in the nereidid *Nereis fucata*, the life-cycle is complicated with an additional free-living benthic stage. The gravid heteronereis leave the hosts and spawn freely in the water column from late Spring to early Summer (Gilpin-Brown 1969, Goerke 1971). Unexpectedly, the planktotrophic larvae settle directly on the soft bottom, rather than on their hosts, and the juveniles live in tubes inside the bottom sediment during several months. During this phase, they feed on detritus and small benthic animals, exactly like their free-living related species. However, 4 months old juveniles start to develop the ability to recognise the substrate vibrations produced by the hermit crab shell bouncing on the bottom (Gilpin-Brown 1969). The development of the life-cycle is completed when a hermit crab reaches the area inhabited by the pseudo free-living juveniles and triggers their characteristic host-entering

behaviour (see the corresponding section above). Host-entering occurs more intensively in Spring, due to the increasing number of “emptied” host shells after the release of gravid heteroneris.

Some commensals tend to simplify their life-cycles by reducing, or even eliminating, the free-living pelagic stage. In these cases, the adult symbionts are the responsible for dispersal. Known examples of this strategy occur, for example, among the histriobdellids, which possess internal fertilisation and whose eggs directly develop inside cocoons attached to the host (e.g. *Histriobdella homari* in Haswell 1913). Conversely, other commensals tend to increase the complexity of their life-cycles by having an intermediate host (or hosts). The best known example of such complex life-cycle occurs probably in the scaleworm *Arctonoe vittata*. This species is also one of the most widely studied commensal species, whose behaviour, population ecology and reproductive biology has been reported in detail (Davenport 1950, Palmer 1968, Dimock & Dimock 1969, Wagner et al. 1979, Britayev & Smurov 1985, Britayev et al. 1989), allowing to reconstruct the main traits of its life-cycle (Britayev 1991). In the Northwest part of the Sea of Japan (Vostok Bay) this species is associated with several host from different taxa (i.e. the starfish *Asterias amurensis*, the limpet *Acmaea pallida* and, more accidentally, with the sea cucumber *Stichopus japonicus* and the starfish *Aphelasterias japonica*). The spawned eggs are poor in yolk so that the fertilisation gives rise to planktotrophic larvae. After a long pelagic phase, settlement occurs on all above-mentioned hosts, with the main flow of settling larvae being addressed to *A. amurensis*, and the low number of successfully settled larvae occurring on *A. pallida* (Fig 13). However, the later remain during the whole life on their host limpets, whereas the former may have diverse destinations: the initial starfish individual will be the definitive hosts for some of them, while some others will be forced to leave it and to relocate on other host-individuals (i. e. starfish of the same species, or of *A. japonica*, but also the limpets or the sea cucumbers). Undoubtedly, intraspecific competition plays the most important role in these relocation processes.

The limpets are probably more “suitable” hosts than the starfish for *A. vittata*. However, both the high infestation prevalence and the limited available space on the limpet tend to reduce juvenile’s survival. It should be taken into account that the species shows a strong intraspecific aggressive behaviour. However, as a result of the large surface of the host starfish, the amount of aggressive interactions between the symbionts from the same host individual may be significantly reduced. It is thus possible for recently settled juveniles to survive sharing the same host starfish with a large adult. However, if several young specimens settle on the same host, the number of negative interactions between them, as well as that of aggressive actions of the large adult (if present), became higher together with young’s growth (Britayev et al., 1989). The final result is that some symbionts (usually the smallest) are obliged to leave the host and move then to another one. In this case, the starfish *A. amurensis* may be regarded as an intermediate host, whereas, at least for some symbionts, *A. pallida* acts as the definitive one. In fact, we may speculate that the complex life-cycle of *Arctonoe vittata* has an additional interest in that it may probably illustrate how some symbiotic (i.e. parasitic) life-cycles including different hosts may have evolved as a result of symbionts’ intraspecific competition.

PARASITIC POLYCHAETES

Parasites are often specially adapted to facilitate their specialised way of life (Margalef 1980). Thus, a low degree or the lack of specialisation has been interpreted as a sign of an evolutively recent change to parasitic life (Clark 1956). A strict parasitic relationship often implies some degree of co-evolution. In fact, the hosts may even be able to support the presence of their parasites, the infested populations attaining a certain level of equilibrium in normal, non-stressed conditions (Margalef 1980). Endoparasitic relationships tend to be more strict than ectoparasitic relationships. Most ectoparasites are, indeed, haematophagous, dermatophagous or secretophagous. The endoparasites inhabit the tissues or the body cavities of the hosts. As we have included within the commensals those symbiotic polychaetes lacking clear parasitic characteristics, the following sections will refer to the polychaete species with known described morphological or behavioural parasitic trends.

TAXONOMICAL DISTRIBUTION OF PARASITIC POLYCHAETE SPECIES

81 polychaete species belonging to 13 different families are reported to be involved in 253 different parasitic relationships (Tables 6, 8 and 9; Fig 15A). Parasitic polychaetes are thus present in about 15% of known polychaete families and about 0.5% of known species, which is far from being the highest figure for the presence of commensals (see the above corresponding section).

Probably one of the most striking facts arising from the comparison between classic papers, such as those by Paris (1955) and Clark (1956), and the present review is that some of the typical examples of parasitic polychaetes have now been excluded from this category, and included in the commensals. Clearly this is due to increased knowledge of the characteristics of the involved associates. *Histiobdella homari* and *Ophryotrocha geryoncola*, together with species of the genus *Iphitime*, were reported as ectoparasites of the branchial chambers of crustaceans by the above classic authors. More recent studies, however, demonstrated that *H. homari* behave more as a cleaning symbiont than as a parasite (Jennings & Gelder 1976), whereas the relationships between crabs and *Iphitime* spp. (Hartnoll 1962, Pilger 1971, Abelló et al. 1988, Comely & Ansell 1989) and *Ophryotrocha* spp. (Gaston & Benner 1981, Martin et al. 1991) may be regarded as commensalisms. In fact, these worms feed on material captured or attracted by the host, and their presence did not negatively affect the gills of the host.

The highest number of polychaete species considered, to some degree, as parasites belong to the family Spionidae (38%) which are, in fact, boring species. This family also includes the highest number of relationships (52%), which suggests that most of the parasitic spionid species have a low degree of specificity. In other words, the same species may frequently bore (and infest) many different hosts. However, the symbiotic associations involving boring polychaete species (spionids, but also the so-called parasitic species of the families Caobangidae and Sabellidae) show very peculiar characteristics and their main trends will be analysed in separate sections.

Most of the polychaetes that have been reported, in principle, as real parasites are obligatory symbionts (45%), whereas only 30% are permanent parasites (Table 6). Parasitic polychaetes mainly belong to the family Oeonidae (about 24%). These worms are internal parasites and, with the exception of *Oligognathus bonelliae* (parasitic on the echiuroid *Bonellia viridis*) and *Pholadiphilia turnerae* (parasitic on the bivalve *Xyloredo ingolfia*), all their hosts are other polychaetes (Table 6). The parasitic oeonids apparently show a high degree of specificity: of the 19 known species, 16 are known to infest a single host. This trend may be explained, however, by their extreme rarity which gives rise to the fact that most species are only known from a single original record.

The syllids are the second most well represented family within the “non-boring” parasites (14%). Members of this family have been mainly reported from sponge hosts, the most representative parasitic syllid being the cosmopolitan species *Haplosyllis spongicola*. The remaining polychaete families include only one or two parasitic species. Among them, the highly specialised families Calamizidae (2 species) and Ichtyotomidae (1 species) are entirely parasitic.

MARINE TAXA HARBOURING PARASITIC POLYCHAETES

The parasitic polychaetes infest 186 different host species included in 16 groups of organisms (Table 6, 8 and 9; Fig 13B). With the exception of 3 fishes and 1 plant, all remaining host species are benthic invertebrates. Gastropod and bivalve molluscs showed the highest percentage of species harbouring parasitic polychaetes (29% and 23%, respectively). Thus, they are involved in most of the parasitic relationships (28% and 31%, respectively). With the exception of the oeonid *Pholadiphilia turnerae*, all parasitic polychaetes infesting gastropods and bivalves belong either to the caobangids or to the spionids. Similarly, the host cirripeds and bryozoans, a few of the host sponges and cnidarians, and the host seagrass are also infested by spionids.

The next most common host groups (each one representing about 16% of the host species) are the sponges and the polychaetes themselves. The former are mainly parasitised by syllids, particularly *Haplosyllis spongicola* and *Branchisyllis oculata*. The latter are infested by the parasitic oeononids (with the exception of *Pholadiphilia turnerae*), 2 calamizids, 1 iphitimid and 1 syllid. The host polychaete species belong to the families Aphroditidae, Eunicidae, Onuphidae, Terebellidae, Spionidae, Ampharetidae, Syllidae, Nereidae and Sabellidae.

SPECIFICITY AMONG PARASITIC POLYCHAETES

It is very difficult to analyse the degree of specificity among parasitic polychaetes. The analysis of the available data seems to point to a clear monoxenous pattern. More than half of the parasitic polychaete species (about 69%) infest a single host species, while the figure rises to 91% if those infesting 2 or 3 different host species are included. However, this monoxenous pattern is clearly biased by the virtual absence, in most cases, of data other than the original citation. As new data are reported, the host spectrum tends to increase. This may be the case of the oeononid *Labrorostratus parasiticus*. This species, with 6 known host polychaete species (up to 9 if we assume that the specimens described by San Martín & Sardá 1986 as *Labrorostratus* sp. are indeed *L. parasiticus*), is certainly the most frequently reported and the one with most recent citations. *L. parasiticus* is also the only oeononid known from more than one host polychaete. According to our interpretation, the latter may be a direct consequence of the former. A certain degree of specificity in the parasitic habits of *L. parasiticus* can be assumed, as all known hosts belong to the family Syllidae ([Table 6](#)).

Polyxenous relationships are mainly present within the syllids parasitising sponges (i.e. *Branchisyllis oculata* and *Haplosyllis spongicola*). However, the apparently polyxenous behaviour of *H. spongicola* (it has been reported from as many as 21 different host sponges) must be interpreted with care. The external morphology of this species is very well adapted to its life style and appears to be relatively simple. However, two different morphologies have been reported (viz. different arrangements of cirri, different shapes of setae) and are considered either as belonging to different subspecies, *H. spongicola spongicola* and *H. spongicola tentaculata* (Imajima 1966), as different growth stages of the same species (San Martín 1984) or, even, as different species, *H. spongicola* and *H. tentaculata* (Lee & Rho 1984). The existence of different colourings has been related to the colour of the host sponge (San Martín 1984, Magnino & Gaino in press). In light of the above, we suggest that the possible existence of a hidden sibling or pseudosibling species complex is still open for this species.

After the above-mentioned syllids, the number of host species parasitised by the same polychaete species sharply decreases: two species, *Ichthyotomus sanguinarius* and *Sphaerodorium flavus*, parasitise 3 host species, whereas only *Pholadiphilia turnerae* parasitises 2 host species. It must be pointed out, however, that these parasitic species closely resemble the behaviour of *Labrorostratus parasiticus* in that the taxonomic status of their respective hosts is always very close. All hosts are sponges for *H. spongicola*, fishes (species of conger) for *I. sanguinarius*, ophiuroids for *S. flavus* and pholadid bivalves for *P. turnerae*.

INFESTATION CHARACTERISTICS AND INTRA-HOST DISTRIBUTION PATTERNS OF PARASITIC POLYCHAETES

The known prevalences of infestation by non-boring parasitic polychaetes are extremely low: 0.2% within 28,604 hosts examined for *Labrorostratus luteus* (Uebelacker 1978), 0.05% within more than 6,000 hosts examined for *Labrorostratus* sp. (San Martín & Sardá 1986), and a maximum of 4% for *Arabella endonata* but with only 25 hosts examined (Emerson 1974). Probably, the infestation prevalence for *A. endonata* could not be accurately predicted from the small host sample examined and a decrease in prevalence could be expected with an increase in the amount of hosts examined. However, Emerson (1974) pointed out that several hundred of the host polychaete

Diopatra ornata from a population located in the vicinity of the type locality were examined and none of the specimens were infested.

Infestation intensities have been more often reported than prevalences (Table 7). A regular pattern of distribution seems to characterise most of the known parasitic relationships involving polychaetes, with each host harbouring only one single adult parasite. This statement can not be easily confirmed due to lack of information on the incidence of parasitic relationships involving polychaetes. However, the presence of one parasite in each host in the most frequently reported species, *Labrorostratus parasiticus*, supports the hypothesis of a regular distribution for all related species. The presence of two parasites on the same host specimen was reported for *Haplosyllis spongicola* on a eunicid host (as *H. cephalata* in Treadwell 1909), for *Ichthyotomus sanguinarius* (one male and one female, see Fig 20C) on an eel host (Eisig 1906, Fauvel 1923) and for *Calamyas amphictenicola* (also one male and one female) on its ampharetid host (Franzén 1982).

Although less frequently, an aggregated distribution has also been reported for parasitic polychaetes (Table 7). The aggregates always seem to be connected to the reproduction of the involved species, with the exception of the parasitic syllids *Brachiosyllis oculata* and *Haplosyllis spongicola*. The highest known number of parasites (more than twenty thousand) inside a single host has been reported for *H. spongicola* (Bacescu 1971). However, *B. oculata*, *Proceraea* sp. and some of the endoparasitic oeononids also show numerous individuals inside a single host (Table 7). In *B. oculata*, the high densities were surprisingly supported by the host sponges with no apparent effect on them (Pawlik 1983). In *Proceraea* sp., the aggregated distribution occurs only within the juveniles, the mature adult phase being probably free-living (Britayev et al. unpubl.). In the oeononids *Notocirrus spiniferus* (Allen 1952) and *Arabella endonata* (Emerson 1974) the individuals were juveniles showing many different developmental stages. Amaral (1977) reported that two adult individuals of *Labrorostratus prolificus* showed traces of asexual reproduction (stolons) coexisting with their numerous juvenile stages. Conversely, there was not additional information about the several individuals of *Veneriservia pygoclava* found inside its aphroditid host.

LOCATION OF PARASITIC POLYCHAETES ON THEIR HOSTS

Most parasitic polychaetes are endoparasites (Fig 16), either inhabiting the tissues of their hosts (e.g. *Alciopina parasitica*, *Dorvillea sociabilis*, *Branchiosyllis exilis*, *Autolytus penetrans*, *Myrianida pinnigera*, *Typosyllis extenuata*), the peri-intestinal blood sinus (e.g. *Haematocleptes terebellidis*), the coelomic cavities (e.g. *Ophryotrocha puerilis*, *Veneriservia pygoclava*, *Oligognathus bonelliae*, most oeononids parasitising polychaetes), the aquiferous system (e.g. *Haplosyllis spongicola*), the hydrothecae (e.g. *Proceraea* sp.) or special galls formed by the host because of the presence of the parasite (e.g. *Ophiuricola cynips*). With the exception of *A. penetrans* and the last three species, no special morphological, structural or behavioural reactions to the presence of the parasites in their hosts has been described.

Wright & Woodwick (1977) described the blisters formed by the small syllid *Autolytus penetrans* on the hydrocorall *Allopora californica*. This worm apparently penetrated the surface of the host resulting in a hyperplasia of cellular and calcareous material which produce a characteristic vermiform mound. The blisters may be located almost anywhere on the living hydrocoral with no specific association with the coral polyps. This species was not originally described as parasite. In fact, there were no indications of any damage to the host - other than the blisters themselves - linked to the presence of the symbiont, but also any profit was suggested. Although this species does not actually bore, its blisters closely resemble those of the polydorids. In this case, however, the blister lining had cellular, instead of muddy, make up (Wright & Woodwick 1977).

The induction of special modifications in host sponges by *H. spongicola* apparently depends on the morphology of its hosts. If the sponge canals are larger than the parasite, it may be located inside these canals without inducing special modifications in the host (Bacescu 1971, Pansini & Daglio 1981, Tsurumi & Reiswig 1977, Magnino & Gaino in press). However, it may directly suck the sponge-bacteria tissues by inserting the pharynx through the canal walls, as was observed in the host reef bacteriosponge *Aplysina cauliformis* (Tsurumi & Reiswig 1977) (Fig 17B). Where

the canals are smaller than the parasite, *H. spongicola* directly penetrates into the sponge tissues, living inside them and often inducing malformations in the host sponge. The formation of a thick protective epithelial layer surrounding the zone inhabited by the worms has been mentioned for the sponge *Rhizaxinella pyrifera* (Uriz 1978) (Fig 17A) and *Aaptos* cf. *aaptos* (T.A. Britayev personal observations).

According to Ludwig (1905), the galls produced by *O. cynips* are rather large and partly protrude into the coelomic cavity of the host ophiuroid *Ophioglypha tumulosa*. In the host hydroid *Abietinaria turgida*, there is a single large mature adult *Proceraea* sp. per colony, inhabiting a thin hyaline tube attached to the axis of the host branches (Britayev et al. unpubl.). Conversely, a large number of juveniles of this parasite occurs inside modified hydrothecae from the same colony (Fig 17C, Table 7). The modified hydrotheca consist of a basal jug-like part (as in uninhabited ones) and a distal cylindrical part, which is the result of the polyp's response to the presence of the worm. Moreover, the presence of the parasite leads to morphological changes in the polyp, which lengthens its body during the initial stages of infestation (when the hydrothecae are shared with the parasite). At a further stage polyps are totally absent from the infested hydrothecae. Finally, the worms leave the hydrothecae and build mucous tubes attached to the stem or branches of the colony to continue their development until the adult stage being then able to leave the colony.

The oeonid *Pholadiphila turnerae* can be considered as an ectoparasite, as it inhabits the mantle (infrabranchial) cavity of the host bivalve (Dean 1992). The ectoparasitic polychaetes, however, tend to live more or less intimately attached to different parts of the host's body (see Fig 20). They may simply live on the host's surface (e.g. *Sphaerodorum flavus*), inside tubes attached to the host surface (e.g. the species of the genus *Procerastea*), attached to an external appendix (e.g. a parapodial cirrus in *Haplosyllis spongicola* as *H. cephalata*) or penetrating the host tissues (e.g. the body wall in *Asetocalamyzas laoncola* and *Parasitosyllis claparede*, the branchiae in *Calamyzas amphictenicola*, the fins in *Ichthyotomus sanguinarius*). *Branchiosyllis oculata* has been mentioned as living inside the canals of *Speciospongia vesparium* (Pearse 1932, Westinga & Hoetjes 1981), but has been more often found living (and feeding) on the external surface of the remaining sponge host species (see Table 6). It was found often embedded in a trench in the sponge ectosome (excavated by the setae), with their long dorsal cirri extending outward onto the sponge surface (Pawlik 1983). Moreover, *B. oculata* is morphologically adapted for dwelling on sponge surface and even takes on the colouring of some of its hosts. Thus, it can be considered a specialised ectoparasite.

RELATIONSHIPS BETWEEN HOST AND PARASITIC POLYCHAETE CHARACTERISTICS

It is commonly accepted, and is implicit in the definition of a parasitic relationship, that the parasitic organisms must be smaller than their hosts. Most parasitic associations involving polychaetes are so. However, some exceptions can be found within the oeonids. Some parasitic species are not smaller than their free-living relatives (e.g. *Notocirrus* spp., *Drilonereis* spp.), some other species are similarly sized or even larger than their hosts (Fig 16). In these cases, the species involved would probably be closer to a predator than to a real parasite. In the case of *Pholadiphila turnerae*, the fact that the mere presence of the large worm in the branchial cavity causes significant stress to the host, as it hinders water flow, was the basis for considering the relationship parasitic (Dean 1992).

The feeding activity of *Haplosyllis spongicola* apparently caused a decrease in the growth rate of host sponge *Verongula reisi* (Reiswig 1973). On the other hand, the *H. spongicola* population inhabiting another closely related host sponge, *Aplysina cauliformis*, was reproductively active at all times of the year, and was thus qualified as a "good" parasite (*sensu* Ricklefs 1990) by Tsurumi & Reiswig (1997). The same authors mentioned that there was no correlation between the timing of sexual reproduction in *H. spongicola* and *A. cauliformis*. However, because of its continuous grazing and removal of host biomass, the syllid certainly must have an impact, though of unknown significance, upon both sexual and asexual reproduction of the host sponge (Tsurumi & Reiswig 1997). In *Proceraea* sp., growth from late larva to juvenile is

accompanied by mouth and gut development but also by the disappearance of polyps from the infested hydrotheca. Moreover, juveniles from empty hydrothecae were observed inserting their heads into thecae openings from neighbouring polyps. Not surprisingly, pigment granules characteristic of the hydroid were observed in the polychaete intestine. All these observations strongly support that the polychaetes feed on the hydroid tissues, and so are real parasites (Britayev et al. unpubl.). As a consequence of the parasite's feeding activity that causes a significant reduction in the number of active polyps per colony, we suggest that considerable stress, affecting the overall well-being of the infested host, should be expected. A very close feeding habit was described for *Procerastea halleziana* living on the hydroid host *Tubularia indivisa*. The worm lives in hyaline tubes attached to the host branches and was observed to suck the contents of the gastro-vascular cavity of its host after piercing the basis of the hydroid polyps exteriorly (Caullery 1925). On the basis of this observation (and lack of specific information), we have considered all remaining species of *Procerastea* from hydroid hosts to be parasites (see [Table 6](#)).

ADAPTATIONS OF POLYCHAETES TO THE PARASITIC MODE OF LIFE

Morphological adaptations in parasitic polychaetes

As a general rule, endoparasites show a reduction or specialisation of locomotive appendages and mouth parts, and they are usually smaller than their free-living relatives (Clark 1956). However, endoparasitic polychaetes often undergo nothing but the most trivial changes. Unfortunately, several factors prevent the development of a satisfactory hypothesis: first, these parasites' rarity and second, the fact that we know practically nothing on their life-histories.

Reductions in the setal pattern of the endoparasitic oeononids ([Fig 18](#)) are seen in the species *Drilonereis benedicti* which has no emergent setae and in the two species of *Haematocleptes*, which possess several slender, distally pointed setae rather than the typical limbate setae of the oeononids. In *Drilograthus capensis*, the setae are completely absent and only a single stout pointed aciculum, often projecting through the skin, is present on each parapodium. Moreover, study of the jaw apparatus of all endoparasitic oeononid species ([Fig 19](#)), shows that they tend to have smaller jaws. This tendency can be related to some extent to a more specialised parasitic mode of life. The mandibles are well-developed in the free-living oeononids, as well as in the parasitic *Notocirrus spiniferus*, *Arabella iricolor*, *A. endonata* and *Drilograthus capensis*. Conversely, they are only small plates in *Labrorostratus*, *Haematocleptes* and *Oligograthus*, and are completely lacking in the parasitic species of *Drilonereis*. The free living oeononids, like the parasitic *Notocirrus* and *Arabella*, possess 5 pairs of well-developed maxillae whereas the parasitic *Drilonereis* possess 4. In the remaining parasitic genera, the maxillae consist of 3 pairs of unidentate hooks in *Oligograthus* while in *Drilograthus*, *Labrorostratus* and *Haematocleptes* they are 2 pairs of small cuticular pieces. Free-living oeononids and both free-living and parasitic species of *Notocirrus* and *Drilonereis* possess a pair of long, slender maxillary carriers with a third carrier attached ventrally. The paired maxillary carriers show a different degree of fusion in *Labrorostratus* and *Haematocleptes* than in *Drilograthus*, *Oligograthus* and the parasitic species of *Arabella*, with the third carrier retained in the former two genera and lost in the latter three. The maxillae and maxillary carriers of the single known species of *Drilograthus*, *D. capensis*, were considered vestigial (Day 1960, 1967). However, they closely resembled those of the young *Notocirrus spiniferus* found living as parasite in *Diopatra cuprea*, which were considered incompletely developed (Pettibone 1957). Whether the jaw apparatus of *D. capensis* corresponds to a young developing specimen or to an adult with highly modified jaws is impossible to assess. However, the shape of the jaw apparatus and the size of the worm (3 mm long for only 60 segments) suggest that the single known specimen was not adult.

Besides the structural changes in the jaw apparatus that may be more or less subjectively related to a progressive adaptation to the endoparasitic mode of life, little is known on the possible sources of food for the endoparasitic oeononids and, thus, on the real significance of the above-mentioned smallness in jaws. Emerson (1974) mentioned that the *Diopatra ornata* females

harbouring *Arabella endonata* contained significantly fewer oocytes than the uninfested females. This author suggested that the gametes may represent the major food source for the later growth stages of the parasite, when it has a fully functional jaw apparatus and digestive tract, and that smaller or juvenile parasites lacking jaws could survive by either direct consumption of the coelomic fluid or absorption of dissolved nutrients from it. Moreover, gamete consumption by adults may also provide additional space within the coelomic cavity of the host for the parasites at the earlier stages.

Surprisingly, it is within the ectoparasitic polychaetes where we find the highest degree of structural and behavioural adaptations to their peculiar mode of life. An exception, however, are those temporary ectoparasites which are not at all modified, such as *Myrianida pinnigera* which feeds on the body fluids of ascidians, or the capitellids *Capitomastus lividus* and *Capitella ovincola* which parasitise the egg-masses of *Loligo* (Table 6).

The mouth parts of *Pholadiphila turnerae* are small, like those of the endoparasitic oeononids (Fig 19), with well-developed mandibles and 3 pairs of maxillar plates, which suggests reliance on the host for nutrition (Dean 1992). Although their maxillae are less modified than those of several endoparasitic oeononids, the slender, short (but not broad) maxillary carrier with indications of tripartite end (which strongly suggests fusion of the original priognat carrier) are believed to be the consequence of a parasitic lifestyle (Dean 1992). Possible food sources within the pholad mantle cavity may be the gill filaments, the mucous coat on these filaments or perhaps partly digested material within the pholad's food-storing caecum. The setal arrangement of *P. turnerae* is the same as in all oeononid species (free-living or endoparasitic). However, its acuminate setae and strong spines may be an adaptation to its parasitic mode of life, affording strong purchase against the body of its mollusc host. These setae are more highly developed than those seen in other parasitic oeononids, being more robust, more numerous and extending out much further from the parapodia which may be a consequence of the ectoparasitic habit of the species (Fig 18).

The ectoparasitic sphaerodorids of the species *Sphaerodorum flavus* feed on the epithelium of their host ophiuroids and, as its regeneration is not possible, they may even kill the hosts if the wounds are too big (Ockelman, personal communication). This association, together with that between *P. turnerae* and the pholadid mollusc and those of the temporary ectoparasites, are probably the simplest relationships developed by ectoparasitic polychaetes. Otherwise, there is a progressively increasing gradient in intimacy in host/parasite relationships.

Haplosyllis cephalata, which has been thought identical to *H. spongicola* (San Martín 1984), was found attached to a parapodial cirrus of the host eunicid, which had been swallowed and occupied most of the pharyngeal cavity of the parasite. However, no special modifications of the mouth, pharynx or pharyngeal cavity seem to be present in this species. *Asetocalamyzas laoncola* penetrates the body wall of the host terebellid using its large everted pharynx, which was distended after penetrating the host body (Tzetlin 1985), allowing the parasite to keep firmly attached to the host (Fig 20A). A more specialised pharynx can be found in *Parasitosyllis clapparede* (Potts 1912). The pharynx projects from the pharynx-sheath and resembles an elongated vase with a short stem, the rim of which is embedded in the host body while the stem communicates posteriorly with the proventriculum (Fig 20B). Except in this posterior region, the pharynx is enormously thickened and composed of at least four layers of chitin. Anteriorly, these chitinous layers run far into the host, bending round at right angles as they enter the host body. As they penetrate, these layers become thinner and thinner so that it is soon extremely difficult to distinguish between the tissues of parasite and host. The lumen of the pharynx is narrow anteriorly and there is a cushion muscle posteriorly. A narrow duct can be observed apparently communicating the pharynx with the proventriculum, which would serve for the passage of fluids absorbed from the host. The other known species of calamyzid, *Calamyzas amphictenicola*, possesses a buccal sucker and a specialised eversible pharynx with stylet-shaped sucker tube to penetrate the branchiae of its host ampharetid (Arwidsson 1932, Paris 1955, Fauvel 1959, Hartmann-Schröder 1971).

Certainly, the highest degree of specialisation occurs in the single known ichthyotomid species *Ichthyotomus sanguinarius* (Eisig 1906). Its peristomium, with the subterminal mouth, forms an oral cone that is capable of being protracted beyond the prostomium and retracted to form a cup-shaped oral sucker by which it fixes on the skin of the host fins (Fig 20C). The ventral cirri

have spinning glands opening at their tips, serving also to attach to the host. The muscular pharynx has a pair of articulating, scissorlike jaws, each formed by a distal spoonlike stylet provided with recurved teeth, a middle articulating joint and a bifurcated basal stem for muscle attachment (Fig 20D). When the oral cone is protracted, the stylets project from the opening, pierce the skin of the eel and attach firmly. In such a way, the worm cuts the blood capillaries of the host and uses its muscular pharynx to suck the host blood. The blood passes into dorsal and ventral haemophilic pharyngeal glands and into the gut, which is enlarged with diverticula extending into the parapodia. The modifications of this species are not only morphological but physiological. Effectively, like the mosquito, it has developed an anticoagulant to facilitate its feeding mode. Moreover, the circulatory apparatus and branchiae are absent. According to Eisig (1906), the fact that the eel's blood remains always liquid and constantly flows towards the gut diverticula may enable the tissues of the parasite to breathe.

Behavioural adaptations in parasitic polychaetes

Probably the only study reporting behavioural aspects of a parasitic polychaete is about *Branchiosyllis oculata* on different sponge hosts (Pawlik 1983) (Table 6). This author reported a series of data which define this species as a specialised parasite apparently well-adapted to living on the surface of its hosts. By means of a combined effect of parapodial muscular contractions and the claw-like hooks of the setae (Fig 20E), the worm may either keep itself firmly attached to the host tissues or advance across the sponge's surface. The long dorsal cirri appear to have a mechanosensory function. Touching the worm cirri produced a rapid reaction: a writhing backward motion (to dislodge setae) followed by a rapid forward advance. Hooked setae are also present in other parasitic syllids such as *Haplosyllis spongicola* (see Fig 11C) and the species of *Procerastea* (Figs 20F, 20G, 20H). Although *H. spongicola* may use its setae as *B. oculata* does (i.e. to move on and inside its host sponges), the species of *Procerastea* more probably use their setae to move back and forth along their tubes and to keep themselves attached to the branches of their host hydroids when feeding.

The colour of the gut contents and body of *B. oculata* on the sponges *Cinachyra alloclada*, *Speciospongia othella* and *Tedania ignis* was yellow, brownish-black and red, respectively, each the same colour as its sponge host. Worms from the remaining host species had uncoloured bodies with the gut contents varying from brown to grey. When transferring uncoloured worms to the red *T. ignis*, they were observed to have taken on red gut-contents a few hours after transplantation. This was considered a clear demonstration of the fact that the polychaete feeds on sponge tissue. In addition, transplanted autotomised worms regenerated their posterior setigers with pigmentation identical to that of *B. oculata* found on the surrogate sponges, while their anterior setigers did not show any detectable change in colour. This provided evidence that the polychaetes incorporate sponge pigments into their body tissues, although only the pigments of some species were incorporated. The worms having the same colour as the sponges they inhabit may have a distinct antipredatory advantage as the uncoloured worms were much more readily eaten by fishes under laboratory conditions.

Life-cycle and reproductive adaptations in parasitic polychaetes

It seems evident that a parasitic mode of life should lead to modifications in the life-cycle of parasites as they adapt to their particular mode of life. However, little is known on the developmental and reproductive cycles of parasitic polychaetes. In *Ichthyothomus sanguinarius* and *Calamyzas amphictenicola*, male and female individuals have been reported on the same host. The former has a hypertrophied genital apparatus (Eisig 1906), whereas the latter has aflagellate spermatozoa (Franzén 1982). There is not a clear relationship between the hypertrophy of the genital apparatus and the parasitic mode of life or the presence of heterosexual pairs. Conversely, the aflagellate spermatozoa have extremely low motility. In this case, the relationship of low motility

with male and female individuals always being found close together seems clear, as the spermatozoa do not need to swim to reach the eggs.

Fully mature specimens carrying eggs or sperm have not been reported for the solitary endoparasitic oeononids such as *Labrorostratus parasiticus*, while some specimens were reported as free-living among algae. On the basis of this slender evidence Caullery & Mesnil (1916) suggested that infestation took place when the parasites were extremely young, that adults left the host as they approached sexual maturity and that they spawned outside it. If this theory is general among solitary endoparasitic oeononids, it would explain the retention by some of them of characteristics of free-living species of the family (Clark 1956). According to this author, however, what is more inexplicable and puzzling than the lack of morphological specialisation, is how the endoparasitic habit was ever evolved in these worms, particularly if there is no substantial reduction in size.

Occasionally, however, the size of endoparasitic oeononids is much smaller than that of their hosts. In these cases, the existence of endoparasitic juvenile stages, very abundant in a single host, together with the presence of asexually reproductive adults inside the host body (Amaral 1977) suggest two different strategies of dispersion. In the first case, we may assume an adult free-living reproductive phase. Then, the initial infestation would be accomplished by larvae (probably pelagic), whereas the host infestation would progress as a result of successive cycles of asexual multiplication of the parasites inside it. The final step in the infestation would be the release of adults that would reach maturity as free-living forms. In the second case, we may assume an absence of the sexual reproductive phase. Although the infestation inside the host could progress the same as in the first strategy, the infestation of new hosts would be undertaken by direct migration of the stolons released from the first infested host after entirely consuming the available host resources. This second strategy involves a more contagious distribution of both host and parasite populations. In theory, the two strategies could coexist in the same species. The asexual phase would lead to the infestation of hosts from the same population while the sexual phase would allow the colonisation of new host populations. Unfortunately, the low incidence of these parasites and poor knowledge of their life-histories do not permit satisfactory general extrapolations.

In the case of the parasitic syllid *Proceraea* sp., a first approach to the initial infestation phases suggested that the infestation may occur through planktonic larvae reaching the colony and subsequently penetrating the hydrothecae. However, three different reasons lead Britayev et al. (unpubl.) to discard this strategy: 1) the penetration of the well-defended thecae by the delicate larvae of the worm seems very difficult, 2) that the larvae have no ciliary cover but a small apical tuft strongly suggests the absence of a pelagic larval phase, and 3) there is only one parasite per host hydrothecae. Therefore, these authors suggested that the female *Proceraea* sp. (*Sacconereis*) take care of their offspring by directly laying their eggs inside the hydrothecae. Thus, both a reliable shelter and fresh food are provided for the initial developmental stages of the parasite. This behaviour closely resembles that of the ichneumonid insects that lay their eggs inside the body of other insects and keep them alive to supply their larvae with fresh food. This, in turn, leads to the observed clustered distribution of commensals among the host colonies and also favours the presence of a high number of commensals infesting each host colony. Accordingly, swimming fertilised females are probably responsible for commensal dispersion from one host colony to another.

In *Branchiosyllis oculata*, the fact that adult worms removed from the host sponges had little capacity to relocate their original host or to locate a new sponge suggested that sponge selection and colonisation was carried out solely by larvae (possible swimming or crawling) (Pawlik 1983). However, all adults were morphologically identical and were able to survive after being experimentally relocated to different host sponges. Thus, it appeared unlikely that recruitable larvae were more specifically adapted to particular sponge species. The same author also pointed out that the differential densities on some host species (particularly high in *Tedania ignis*, intermediate in the coloured species and lower in the colourless species) may result from the combination of two factors: (1) differential recruitment as a result of simple differences of density or accessibility of the host species, or chemical cues and corresponding chemosensitive larvae; (2) differential mortality linked either to worms' colour mimicry, to physical (spicules) or chemical defences of hosts (whether these defences are transferable or not to the worms) or to the inaccessibility of the host to

the potential predators. Differences in infestation intensity within the polychromatic host *Tethya actinia* may indicate that whatever controls host pigmentation may also have a direct effect on *B. oculata* larval recruitment and/or adult survival.

From the two examples reported above, it seems clear enough that an accurate study of a given parasitic relationship (from an ecological, behavioural or even morphological point of view) provide pointers towards a reliable hypothesis on the life-cycle of the symbiont. However, unfortunately, these studies are few and far between.

SYMBIOTIC BORING POLYCHAETES

Usually, boring polychaetes did not show special adaptations other than those allowing them to bore into other organisms with more or less hard structures (mainly of a calcareous nature). The association between them and the bored organisms often appeared to be fortuitous, as the worms might be found boring either into living organisms or non-living substrates. 48 species of polychaetes, belonging to the families Spionidae, Sabellidae, and Cirratulidae have been reported as borers of other living marine organisms ([Tables 8](#) and [9](#)). Some interactions between these boring worms and their hosts, however, seemed to be negative, which lead to the species being labelled as “parasitic” borers. They are pests that drain the energy by causing the host to work harder to keep them away from the interior of the shell, but they are often uninterested in the hosts as such. The host suffers, but is not attacked directly: it just is stressed by a mud-eating worms that are “looking for a home”. This may reflect an old-fashioned view of a “parasitic” association. Hence, although we decided to mention these associations in the present review, we realised that some of the cannot be certainly considered as a real symbionts and, thus, they have been included them in the present specific section. In other cases, there were either no negative interactions described or the nature of the interactions was assessed by behavioural observations and some benefits were suggested or even demonstrated, enabling classification of the worms as “commensal” borers. There are a few quantitative studies on infestations by boring polychaetes: the known data on intensities and prevalences re summarised in [Table 10](#). The two types of interactions involving boring polychaetes (i.e. parasitic and commensalistic) will be reviewed in the following three sections.

Parasitic boring polychaetes

The most common parasitic boring polychaetes are, certainly, the spionids ([Table 8](#)). Among them, the species of *Polydora* and related genera are the only one able to bore (Blake 1969, 1980, 1996, Blake & Evans 1973). However, little is known concerning the initial steps of their establishment in the calcareous habitats (but see Hopkins 1958), and the physical (linked to the modified setae of the 5th setiger) or chemical (a not-yet identified acidic substance) mechanisms of burrow expansion are still a matter of controversy (Haigler 1969, Blake & Evans 1973, Zottoli & Carriker 1974, Sato-Okoshi & Okoshi 1993).

We also know little about how the polydorids interact with their hosts and most polydorids that live in molluscs do not really harm their hosts. However, other worms may make different kinds of burrows (viz. U-shaped, branched, cylindrical) ([Fig 21](#)), which may be lined with a variety of parchment-like secretions or with mud or sand grains. When reaching the inner walls of the shells, however, this boring activity often leads the mollusc hosts to react by producing “mud-blisters”, probably the most damaging effect of polydorids. The mud-blisters are masses of mud accumulated on the inner surface of the shell by the recently settled worms ([Figs 21D, 21E](#)). The hosts react by first secreting over the mud a roof of conchiolin and then a layer of nacreous material. The mud-filled chambers formed are occupied by the worms which communicate with the exterior *via* pairs of tubes either at or close to the periphery of the shell. Although it is difficult to evaluate the expenditure of metabolic energy linked to this extraordinary secretion of protective layers (and,

thus, to determine to what extent the life of the mollusc might be affected), the mollusc host may suffer a certain degree of distress (Kent 1979). Additionally, mud-blisters may be so numerous that they lead to the hosts' death. In fact, all this boring activity weakens the shells (Kent 1981) and so makes them less resistant to diseases, other parasites and predators.

The presence of blisters was also reported on the hydrocoral *Allopora californica*. In this case, however, the blisters were formed by the syllid *Autolytus penetrans*, which apparently penetrated the surface of the host resulting in a hyperplasia of cellular and calcareous material (Wright & Woodward 1977). However, *A. penetrans* does not actually bore. Although its blisters closely resemble those of the polydorids, they were lined with cells instead of mud. In spite of blisters, there were no indications of any other damage to the coral linked to the presence of the syllid. Therefore, *A. penetrans* was not originally described as parasite. However, two points allowed us to include this relationship among parasitisms (see [Table 6](#)): (a) no apparent profits were reported for the host and (b) the behaviour of the symbiont closely resembles that of a cysticole parasite.

The boring polydorids have been often considered as parasitic organisms from an anthropogenic rather than ecological point of view. As soon as they infest species of molluscs that are cultivated or harvested as a fishery resource (viz. mussels, pearl oysters, edible oysters, scallops), they are immediately viewed as pests (e.g. Haswell 1885, Houlbert & Galaine 1916, Lunz 1940, 1941, Korrington 1951, Landers 1967, Blake & Evans 1973, Tkachuk 1988). However, the polydorids may, although rarely, cause the demise of the cultivated host populations so affect commercial profit. A decrease of mollusc growth-rates linked to the presence of polydorid species has seldom been reported (but see Imajima & Sato 1984 and Mori et al. 1985). However, they may damage the appearance of the shell, making it less attractive to potential consumers and so lowering the market value of the mollusc. In most cases, the shell damage caused by boring species may be linked to their gregarious habits, leading to the presence of large numbers of individuals on the same host ([Table 10](#)).

The boring polydorids may also inhabit other organisms with calcareous structures. In some cases, the interactions with their hosts (e.g. cirriped crustaceans, serpulid polychaetes) closely resembles the interactions established with molluscs ([Table 9](#)). They simply bore into the calcareous parts of these hosts and no further information about the interactions between host and polydorids is available (Radashevsky 1993). Similarly, *Polydora armata* was reported as symbiont with the madreporid *Leptastrea purpurea* by Okuda (1937), but there was no additional information. *Polydora alloporeis* inhabits deep burrows in the coenosteum of the hydrocoral *Allopora californica*, forming large colonies without apparently damaging the host (Light 1970a). Each *P. alloporeis* burrow has two distinctive openings and the worms may be seen in living material with the palpi projecting from one of the openings and the pygidium just visible below the lip of the other.

Probably the most remarkable associations with non-mollusc hosts are, however, those between *Polydora armata* and *P. hoplura* and the bryozoans *Holoporella sardonica*, *Porella concina*, *Schizoporella armata* and *S. auriculata* (Laubier 1958, 1959). The bryozoans are infested throughout their basallayer (usually dead) fixed to the substratum, the worms entering the colony using the existing crevices or breaks. In *H. sardonica*, *P. armata* excavates a dense complex of galleries, some of them reaching the outer surface of the colony. At the beginning, the openings are only made of silt and mucus. Then, the bryozoan builds a thin calcareous layer (about 2 mm high and 0.25 mm in diameter) surrounding the worm tubes ([Fig 22A](#)). In *P. concina*, the initial infestation steps are the same, but there is no trace of galleries inside the colony. The special structures surrounding the polychaete tubes are, in this case, composed of host zooids ([Fig 22B](#)). The tube heights are similar but wider (about 1 mm wide). At the end of these formations, a thin calcareous zone (probably a growing zone) resembles that in *H. sardonica* ([Figs 22A, 22B](#)). In *S. armata* the two types of calcareous formations (with and without zooids) may be found. *Polydora hoplura* was only found infesting *Schizoporella auriculata*. In this case, the calcareous formations surrounding the worm tubes are made of zooids, reaching about 6 mm high. The formations are conical with 4-5 mm at the basis and 0.5-1 mm at the top. A thin calcareous layer of no more than 0.1 mm forms the border of the cones. The infestation of the bryozoan colonies by the polydorids

occurs in two phases. The first one (initial penetration of the colonies) does not differ from the normal excavating habits of the species. The second phase is characterised by a stimulation of the bryozoan to build the calcareous formations. These two points strongly suggest that these relationships may be considered specific parasitisms (closer to cysticole behaviour). Besides that, we may speculate on a possible cleaning behaviour of the worm, which could benefit the host and so lead to reallocate these relationships between the commensalisms (see *Polydora glycymerica* and *Dipolydora rogeri* on the next section).

Parasitic polydorids were also reported from non-calcareous organisms ([Table 9](#)). *Polydora cornuta* forms cysts in the eelgrass *Zostera marina* (Michaelis 1978). Any sponge with a substantial, firm body appears to be a suitable habitat for the hermaphroditic species *Boccardia androgyna* (Read 1975). The worm inhabits U-shaped mud-lined tubes within the sponges and a large mud-filled cavity may be formed if the sponge species has soft tissue with little spongine material. Finally, *Polydora wobberi* causes structural damage to the colony of the gorgonian *Lophogorgia* sp. (Light 1970b). The worm lives in U-shaped burrows along short branches which arise from the bases of the coelenterate colonies. The burrows open to the exterior at the tips of short stubby branches of the gorgonian which are about 20-30 cm in length (the longer uninfested branches may reach 70 cm in length). The final result is that the woody central stems of the gorgonian are entirely missing in infested branches. However, it seems not to seriously affect the overall well-being of the host.

A situation similar to that of the shell-boring polydorids was described for the sabellids *Pseudopotamilla reniformis* boring in *Placopecten magellanicus* (Blake 1969) and *Pseudofabricia* sp. in *Haliotis rufescens* (Oakes & Fields 1996). *P. reniformis* inhabits large ridges on the inside of the shell, which appear to be the response of the scallop to occasional penetration of the inside of the shell by the worm. The inside of the ridges is filled by mud and worm tubes. The large size of *P. reniformis* and the possibility of high infestation intensities ([Table 10](#)) qualifies this worm as a potential menace to the scallop. The very small specimens of *Pseudofabricia* sp. form cylindrical burrows at the outer part of the abalone shell's edge. As the result of their activity, the shell becomes very weak and porous, which prevents the abalone from enlarging its shell horizontally. Even a heavy infestation by *Pseudofabricia* sp. is generally not life-threatening for the host. It is, however, a very serious problem for the commercial exploitation of abalones, significantly decreasing their growth rate and hence causing additional costs and reducing profits.

The species of the fresh-water caobangid polychaetes (reviewed by Jones 1974), which are currently included within the family Sabellidae (Fitzhugh 1989, Fauchald & Rouse 1997) are exclusive inhabitants of mollusc shells ([Table 9](#)). Little is known of the life-history of the *Caobangia* species since most of them are known only from dried specimens in museums. The worms bore into shells of both gastropods and bivalve molluscs in Asian rivers. The adult burrows are restricted to the collumellar area of the snails (i.e. the thicker calcareous region of the shell), although encapsulated metamorphosing larvae were encountered all over the shell. The bore holes, mainly located in the apex of the snail shell, weaken this portion, which causes a truncated profile ([Figs 23A, 23B](#)). The burrows, lined with a thin secreted membrane, never connect with one another and are teardrop-shaped. In the case of boring bivalve shells, the worms were distributed throughout the available surface.

Cirratulids of the genus *Dodecaceria* are well-known boring polychaetes ([Table 9](#)). Although some of them may be pests in bivalves of commercial value such as *Placopecten magellanicus*, they are not particularly specific (or, perhaps, not specific at all). They bore into virtually any kind of calcareous substrata (e.g. live or dead mollusc or barnacle shells, encrusting coralline algae) without showing any apparent preference for a given species. Moreover, some species of this genus cannot be considered as strict borers. *D. fewkesi*, for example, forms its own free tubes, whereas *D. concharum* also occurs as a cryptofaunal nestler (i.e. it is commonly found between the internal ribs of dead barnacle shells in *Laminaria* holdfasts and occurs in protected cracks and crevices in shells). *D. concharum* may also be able to build a tube of sorts, but it seems that it is more probably creating just a smooth lining in already built burrows. In fact, Evans (1969) found North American populations of *D. concharum* to be "a secondary borer (i.e. occupying and adapting vacant burrows of primary borers, but unable to make a burrow of its own), whereas

Gibson & Clark (1976: 659) found that “in the laboratory ... adults or asexually produced individuals of *D. caulleryi* [= *D. concharum*] fail to make burrows in pieces of smooth rock or smooth *Lithothamnion*. Small holes made in the surface with a needle were sometimes temporarily occupied but a definitive burrow was never made in them”. Moreover, it was pointed out that worms in a dish with detritus will make a kind of tube and secrete a calcium layer sticking it together and corresponding to the lining of the tube (Gibson & Clark 1976, M.E. Petersen personal communication). In fact, the impact of borers or nestlers with some boring ability such as the species of *Dodecaceria*, would probably be higher on molluscs with exposed shells (e.g. scallops or oysters) than on those which are normally buried in the substratum (e.g. *Arctica islandica*). It should be mentioned that, in Danish waters, *D. concharum* occurs in shells of *A. islandica* previously excavated by the sponges of the genus *Cliona*. Usually, these are shells of dead molluscs, but probably *D. concharum* also occurs in live ones, if they are not buried in the sediment and have been attacked by *Cliona* spp. first (M. E. Petersen personal communication). However, this association has not been attributed to a worm / sponge symbiosis, but to the fact that shells that are older and partly decalcified by the sponge (i.e. “softer”) are probably easier to excavate than fresh ones. The behaviour of some *Dodecaceria* species as “secondary borers” may also contribute to explain their occurrence on sponge-excavated calcareous substrates. In the Mediterranean, specimens of *Dodecaceria* sp. have also been observed inhabiting calcareous substrates (i.e. encrusting coralline algae) previously excavated by *Cliona viridis* (D. Martin personal observations).

COMMENSAL BORING POLYCHAETES

One of the best known commensal borers is the spionid *Polydora commensalis*, which bores into snail shells occupied by numerous species of hermit-crabs ([Table 9](#)). Studies on its boring activity revealed that larvae mainly settle on the inner surface of the shells near the outer edge (Radashevsky 1989). Growing worms relocate themselves on the columella, enlarging their tubes along the columella toward the shell apex. As a consequence, all tube openings of *P. commensalis* are located along the columellar side (near the inner lip) of the opening of the shell occupied by the host hermit crabs. Occasionally, the worms excavate shallow channels along the columella, and some tubes can be found in the umbilicus of the shell. The tubes of large gravid females may even reach the top of the columella. The tubes are coiled within the sediment that fills the apex of the infested shell. Occasionally, the worm tubes are covered by a thin arched calcareous “roof” of unknown origin, covering the galleries on the inner surface of the hermit host’s shell (Radashevsky 1989). Each host shell is usually inhabited by one large female and several smaller males and juveniles, whose tube openings are characteristically non-visible externally. Besides that, simultaneous hermaphroditism has also been reported for *P. commensalis* and, in the case of death of the female, the remaining largest individual becomes a female (Radashevsky 1989). The worms have been observed feeding either by removing suspended particles from the branchial (respiratory) current of the hermit crabs or by removing particles attached to the setae on the legs of the hermit crabs (Dauer 1991). When feeding as suspension feeders, worms held the frontal surface of their palps directly in the branchial current of the crab, and constantly contacted the legs of its host with the abfrontal and lateral surfaces of the palps (which are very short).

Polydora glycymerica may be also considered as a specialised commensal borer (Radashevsky 1993). The inner walls of the long and wide U-shaped burrow are lined with silt, its two openings being located at the posterior end of the shell, in the region of the mollusc siphons. This position is closely related to the feeding mode: projecting out of the burrow, the worms expose their palps and catch suspended particles from the water current produced by the mollusc. Similar behaviour may be assumed for *Boccardia acus*, whose burrows are also U-shaped and usually follow the curve of the host’s shell growth lines. The borings are not lined with sand apart from a sand-grain partition at the short, U-shaped external chimneys. As the host cockle lies buried just beneath the sediment surface, the worm extends out through the external chimneys around the bivalve siphons (Read 1975). This is the easiest way to contact with the water column just over the

sediment, but also the closeness of the siphons may allow the worm to feed on the water current produced by the host.

A particularly curious relationship occurs between *Polydora rogeri* and the boring sponge *Cliona celata* (Martin 1996). Both organisms bore into calcareous algae, but the sponge may develop at different growth stages, progressively overgrowing the calcareous excavated substrate (Rosell & Uriz 1991). At the papillate stage of growth, only the papillae of the sponge protrude from the calcareous substrate and the tops of the polychaete tubes were observed protruding from the surface of the algae. The external part of the polydorid tube was formed by fine sediment grains embedded in an organic matrix, whereas the linear internal parts were only formed by the organic matrix. Internal tubes passed through the calcareous algae and the sponge body (choanosome) until an appropriate portion of an aquiferous canal of the sponge was reached. Then, the tubes disappeared, being replaced by the sponge canals (Figs 24A, 24B). In encrusting and massive sponge specimens with almost no trace of visible calcareous substrate within the sponge surface, the anterior ends of the polychaete tubes were also observed directly protruding from the sponge surface. The polychaetes tend to place the openings of their tubes near the inhalant papillae of the sponge. Thus, their feeding activity can be favoured by the inhalant flow originated by the filtering activity of the host. Moreover, the sponge offers physical protection to the worm when the calcareous algae have completely disappeared (i.e. massive stage). The ability of the polychaetes to manipulate relatively large particles (either to feed or to build its tubes) may favour the filtering activity of the sponge by cleaning the area around the inhalant papillae, thus preventing the collapse of their orifices. Moreover, the polychaetes do not disturb the normal progress of the host through successive growth stages and the aquiferous canal occupied by the polydorid does not collapse. If the canal belongs to the exhalant system, water flow would contribute to the discharge of worm faeces, while faeces **would** be used as food by the sponge if the canal belongs to the inhalant system. In light of the above, the association between *P. rogeri* and *C. viridis* was tentatively considered as a mutualism (Martin 1996).

SPECIFICITY IN THE SYMBIOTIC RELATIONSHIPS INVOLVING BORING POLYCHAETES

The analysis of the available data (Tables 8 and 9) on the specificity of the relationships between boring polychaetes and their hosts seems to display a generic monoxenous pattern. About 37% of the polychaetes infest a single host species, this figure becoming 63% if borers infesting 2 or 3 host species are included. It must be pointed out, however, that some species are reported on 10 to 19 different hosts and are, thus, clearly polyxenous. On the other hand, studies enabling the exact degree of specificity to be assessed are virtually lacking, although stimulating (but inconclusive) hypotheses may be found throughout the literature. It should be taken into account that more than half (53%) parasitic boring polychaetes are facultative symbionts, boring also into non-living substrata (Tables 8 and 9). Often, the appraisal of their interactions is tentative, as in the case of defining caobangids s parasites. There are no studies on the possible costs to the hosts arising from the infestation of these worms (other than the weakening of the shell); additionally, only one species of *Caobangia* was reported on a single host (probably the single specimen known), while the remaining were reported on 2 to 9 different hosts (Table 8). In fact, in the rivers, snails and bivalves are the most common and, often, the only available sources of calcareous substrates for these worms. However, the caobangids have also been found boring into empty shells of dead molluscs. Although there are no real observations, it was assumed that they might bore into non-living substrates such as calcareous limestone outcrops which, it was though, could serve as populational reservoirs allowing the infestation of new molluscs.

Among "parasitic" *Polydora* species, there are a few observations suggesting a certain degree of specificity in the relationships with their hosts. Ramberg & Schram (1982) observed that the shells of the gastropod *Littorina littorea* smaller than 10 mm were never infested by *P. ciliata*. As the gastropod host did not become mature until it reached this size, it was suggested that larvae of *Polydora ciliata* may be guided to the snail by some substance which the snails secrete into the water. However, this was not supported by data. The existence of chemical cues in the interaction

between the polydorids infesting bryozoans was suggested by Laubier (1959) on the basis of two facts: i) the worm seems to control the height of the calcareous formations induced in the host colony, this height being always the same (on average); ii) even in colonies where the polydorids can not be currently found, the calcareous formations remain open, the bryozoan apparently being unable to close them. Finally, the special configuration of the prostomium (markedly projected forward), the presence of interbranchial septa and the reduced pygidium led Light (1970b) to suggest that *Polydora wobberi* could be a highly specialised parasitic borer.

Within the commensal boring polychaetes, little is known about the specificity of the relationships. *Polydora commensalis*, for example, is known to be associated with as many as 9 different species of hermit crabs (Table 9). This is habitually related to a lack of specificity. However, adult *P. commensalis* have never been found free-living and, although it was demonstrated that the species can be experimentally induced to burrow in shells that can never be occupied by hermit crabs (i.e. bivalve shells) this has never been reported in natural conditions. Conversely, the association of *Polydora glycymeris* and the burrowing bivalve *Glycymeris yessoensis* may be considered as a rare example of a high degree of specificity within commensal boring polydorids. Despite the intensive research carried out on this species, it was always found in the shells of *G. yessoensis*, with the exception of a very few localised cases where it was boring into the shell of another clam, *Anadara broughtoni* (Radashevsky 1989).

Food availability, sheltering or avoidance of stagnation were suggested as factors cementing the relationship between *Polydora commensalis* and the host hermit crabs (Hatfield 1965). When the host leaves an infested shell, the worms then have nutrient granules in the stomach wall to ensure their survival. Although these absences are necessarily temporary, they imply that the shell could be re-occupied by a different host individual or even by a different hermit crab species. Since the polydorids are, in principle, sedentary, and their feeding mode always incurs the added risk of being attacked by the host, we may assume that the crabs are able to recognise the worms as associates, such as in other polychaetes commensal with hermit crabs (e.g. *Nereis fucata*, Gilpin-Brown 1969). There are no studies on this particular aspect of the relationship, but some very interesting questions arise from the possibility of a chemically mediated recognition: Are the possible hosts “genetically” adapted to recognise the presence of the symbionts? Have the symbionts developed behavioural adaptations to solve the problem of host exchange (e.g. a delay in the start of feeding activity at the beginning of each new host occupancy, till the recognition of the commensal and the “permission” to feed)? Is the behaviour of the symbiont the same, independently of the re-occupation of the shell by the same or a different host species? Additional questions re posed by the fact that shells covered by the hydroid *Hydractinia echinata* were more heavily infested by *P. commensalis* (Andrews 1891a, b): May the hydroid be a third associated symbiont? How could the presence of the hydroid favour that of the worm? All these questions remain open, making the symbiotic relationships involving *P. commensalis* a very interesting subject for further research.

The relationship between *Polydora rogeri* and its host sponge *Cliona viridis* was considered endemic to the NW Mediterranean, as it was only known from the type locality (Martin 1996). *C. viridis* is a widely distributed species (Rosell & Uriz 1991, Rosell 1996) but the presence of its associated worm had not been previously reported. On the other hand, *Polydora armata*, the species most closely resembling *P. rogeri*, is a cosmopolitan polydorid which was reported to bore in calcareous algae from the same area in the NW Mediterranean. These algae were, however, non-excavated by *C. viridis* (Martin 1987). The behaviour of *P. rogeri* inhabiting calcareous algae excavated by papillate specimens of *C. viridis* appears not to differ greatly from that of other coralline-boring species of *Polydora*. The main difference, and indeed that characterising the association and supporting its specificity, is that the symbiotic association is still maintained when the sponge progresses to the encrusting and massive stages, with almost no trace of visible calcareous matrix. The association between *P. rogeri* and *C. viridis* has only been considered from a descriptive point of view, based on dead specimens. Further morphological and experimental studies are required before its exact nature may be assessed. Morphological aspects that might be addressed are, for example, both the cellular organisation and the aquiferous system structure of the sponge around the worm tubes. Experiments could also usefully analyse the substratum

preferences (excavated calcareous algae versus others) during larval settlement of polychaetes, or assess the possible differences in growth rates (from alpha to gamma stages) of infested and non-infested sponges.

THE WAY FORWARD

Over the last forty years, the information on symbiotic polychaetes has grown enormously. This review has attempted to give an overview of the current state of knowledge. What is clear, from this review, is that the relationships involving symbiotic polychaetes are often remarkably complex and this may be true no matter the approach we use to analyse them (i.e. taxonomical, biological, physiological, ecological, behavioural). Our understanding of the interactions between the symbiotic polychaetes and their hosts is still pitifully inadequate. In this final section, therefore, we shall conclude by suggesting avenues of further research which, in the next few years, could help to redress this shortfall.

One of the most troublesome facts dealing with many symbiotic polychaetes is their rarity. We cannot change this and, unfortunately, we will still leave the acquisition of new information on many species (either already known or not yet described) to chance. This may be the case of the parasitic oeonids, which are known, for the most part, only from the original descriptions. In fact, there are many interesting hypothesis arising from the comparison of all trends that characterise each known relationship involving the parasitic oeonids. These hypotheses are necessarily open and cannot be convincingly refuted or validated if no new data on the relationships are reported. However, a few additional information, more than a single mention, may provide relevant data. The host-specificity (i.e. it always infests syllids) characterising *Labrorostratus parasiticus* may be a good example.

The rarity of parasites also difficulties the evaluation of their role in natural communities. We may expect, however, that changes in the environmental conditions affecting a given community would lead to an increase of the number of parasites, so that they would significantly affect the natural "economy" of biocoenosis. In fact, symbionts has been often regarded as "curiosities of the nature", but the few known studies on the biology and behavioural trends of some target species clearly demonstrated their significance in the economy of marine communities (e.g. cleaners such as *Histiobdella homari* or *Arctonoe vittata*, defenders such as *Arctonoe vittata* or *Spirobranchus giganteus*). A different concept of "economy" comes from an anthropomorphic point of view. In this case, the species boring on shells of commercially exploited organisms may play a relevant role. Although these species are common in "healthy" cultures, the possibility of unpredictable outbreaks of their number, followed by harming commercial farms, might not be excluded (e.g. the undescribed boring sabellid in Oakes & Fields 1996). Besides that, the impact of borers on their host populations may significantly contribute to regulate the number of the latter, subsequently leading to community perturbations.

Most symbiotic polychaetes are known from dead specimens and their quality of symbionts has been either proposed after directly finding them on their respective hosts or inferred from some widely accepted "symbiotic attributes". As a consequence, we often know little about the nature of most associations. Although, in practice, it is difficult to obtain unequivocal demonstrations of all factors affecting a given interaction, the few known examples of symbiotic associations whose nature has been studied in deep revealed a more complex network of relationships than expected, these associations being apparently more bi-directional than unidirectional (e.g. Dimock & Dimock 1969, Wargner et al. 1979, Britayev 1991, Radashevsky 1993, Martin 1996). A significant step forward would be, therefore, to look at the nature of the associations on the basis of direct observations of living organisms (i.e. *in situ* or under experimentally controlled situations). This approach may provide information, for example, on host/symbiont colour matching. In fact, the source of this colour matching is also a matter of controversy by itself. Whether a symbiont acquire its host's colour by feeding on the host or as a response to any stimuli coming from the host will substantially contribute to make a decision on the exact nature of a given association. A closely related matter of study, which is also relevant to assess the nature of a given association may be,

thus, the type of trophic relationship established between a host and its symbiont(s). We may also pinpoint that, often, a symbiont is not alone on its host. A very interesting direction for further research will be, thus, to study the interactions (i.e. competition, predator-prey) between different symbionts (i.e. from the same or from different species) co-inhabiting on the same host individual (i.e. the association as a "microcosm"). A major problem may be that, often, it is difficult to obtain enough living partners to undertake experimental essays, but also, that the experimentally observed trends must be completed with the inference of their functional role in natural symbiotic populations.

Today, biologists have a number of new and interesting tools at their disposal and new and exciting techniques are being developed continually (in particular, we are all aware of the potential of electron microscopy or molecular biology). It is certain that such tools and techniques will be employed to great benefit in the area of polychaete symbiotic relationships. These approaches should not, however, be pursued to the exclusion of more established techniques because these still have a valuable contribution to make. Faunistic and systematic studies based on classical morphological characters are still fundamental in localising and describing new associations. The elegant review on symbiotic polynoids by Pettibone (1993) may be a good example of this. Moreover, it should be taken into account that remote areas, such as bathyal bottoms (e.g. Kirkegaard & Billet 1980, Martin et al. 1982, Emson et al. 1993), cold-seep sites (e.g. Miura 1988, Miura & Laubier 1990) or hydrothermal vents (e.g. Pettibone 1984a, b, Miura & Hashimoto 1991, Miura & Ohta 1991) are becoming more and more accessible to scientists. The limiting conditions of these environments are probably connected with the diversity of new symbiotic associations found there. The functionality of these associations, as well as the development of both host and symbiont life-cycles, are interesting fields still open to further research.

Although the polychaetes are probably one of the most widely studied group of marine benthic organisms, the basic information on descriptive ecology (e.g. spatial distribution, bathymetric distribution, seasonality, population structure and dynamics) is still lacking for most known symbiotic polychaetes and, consequently, for the ecological unit formed by the host/symbiont partnership. Symbiotic associations involving polychaetes may serve as useful models to study biological interactions among marine organisms. The associations could be analysed as elementary "biocoenosis", which included a reduced number of species and relationships. In that way, the biotic interactions (intra- and interspecific) could be studied and analysed with a less expenses. Moreover, symbiotic associations are "natural" sample units to study distribution patterns (Palmer, 1968). As all (or, at least, most) commensals are found on the hosts, each host is the basic habitat unit for a given commensal. Therefore, changes or variations in the commensal's distribution are likely to be of ecological interest. The symbionts may serve as a convenient model of distribution, being then possible to generalise on the basis of the main trends described from the association.

Finally, despite several examples where chemically mediated host-symbiont relationships are known to exist because behavioural responses of both partners have been demonstrated, there are no-one where any details of their chemical nature are understood. In this respect, polychaete physiology lags behind that of almost all other invertebrate groups. The habitat restrictions imposed to a symbiont by its intimate association with its host is probably at the basis of most suggested roles of chemical cues in symbiotic associations. The first, classical role is the host-recognition behaviour by adult symbiotic polychaetes, which is involved in the specificity of the response of the symbionts to their hosts. The few studies on this subject are now considered as classic papers but, in fact, the origin of the host-factors, its chemical nature, the way of reaching the symbiont and how the symbionts detect them are basically unknown for most symbiotic associations involving polychaetes. Among other roles, chemical cues may be also involved in: 1) location of host during larval settlement, 2) sex-specific recognition when heterosexual pairs of symbiont inhabit the same host individual, 3) hosts' reproduction triggering symbionts' reproduction, and 4) symbiont recognition by hosts. Molecular tools such as the biochemical and chromatographic techniques, which are employed in purification and structural analysis of chemicals have advanced significantly, so the identification of the substance (or substances) involved in the maintaining and regulation of symbiotic associations are today easier than ever. Chemical characterisation of cues may be a way to clarify the different patterns of symbiont specificity (i.e. if the host shared or

differed in the nature of the attractants). But we cannot forget the possibility of hidden sibling species-complex, being involved in non-specific relationships. Once the existence of this problem has been demonstrated is the way then open for analysis using a variety of modern techniques. Fine morphological studies using electron microscopy, molecular techniques such as protein electrophoresis and RNA/DNA sequencing may provide answers to questions on sibling species involved in symbiotic associations.

Certainly, we are not providing a complete list of shortcomings connected with the study of symbiotic associations involving polychaetes in this necessarily brief, conclusive section. A good final epilogue would probably be that, no matter the scientific field used to approach the symbiotic polychaetes, there are so many open questions that the efforts devoted will be always rewarded.

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REFERENCES

- Abelló, P. 1985. *Iphitime cuenoti* (Polychaeta: Iphitimidae), commensale des crabes en Méditerranée. *Rapports de la Commission Internationale pour l'Exploration de la Mer Méditerranéenne* **29**, 5 only.
- Abelló, P., Sardá, R. & Masalles, D. 1988. Infestation of some Mediterranean Brachyuran crabs by the Polychaete *Iphitime cuenoti*. *Cahiers de Biologie Marine* **29**, 149-162.
- Abelló, P., Villanueva, R. & Gili, J.M. 1990. Epibiosis in deep-sea crab populations as indicator of biological and behavioural characteristics of the host. *Journal of the Marine biological Association of the United Kingdom* **70**, 687-695.
- Achari, G.P. Kumaraswamy 1974[1977]. On the polychaete *Gattyana deludens* Fauvel Associated with the hermit crab *Diogenes diogenes* Herbst and *D. custos* Fabricius. *Journal of the Marine Biological Association of India* **16**, 839-843.
- Addicot, J.F. 1984. Mutualistic interactions in population and community processes. In *A new ecology. Novel approaches to interactive systems*, P.W. Preece, C.N. Slobodchikoff & W.S. Gaud (eds.), New York: Willey-Interscience Publ. (John Willey and Sons), pp. 438-453.
- Ajeska, R.A. & Nybakken, J. 1976. On *Halosydna brevisetosa* commensal with *Melibe leonina*?? *The Veliger* **19**, 19-26.
- Al-Ogily, S.M. & Knight-Jones, E.W. 1981. *Circeis paguri* the spirorbid Polychaete associated with the hermit crab *Eupagurus bernhardus*. *Journal of the Marine biological Association of the United Kingdom* **61**, 821-826.
- Allen, E.J. 1915. Polychaeta of Plymouth and the South Devon coast including a list of the Archiannelida. *Journal of the Marine biological Association of the United Kingdom* **10**, 592-646.
- Allen, E.J. 1921. Regeneration and reproduction of the syllid *Procerastea*. *Philosophical Transactions of the Royal Society of London* **211**, 131-177.
- Allen, M.J. 1952. An example of Parasitism among Polychaetes. *Nature* **169**, 197 only.
- Alós, C. 1988. Anélidos poliquetos de Cabo de Creus (Alt Empordà). Doctoral Thesis, Universitat de Barcelona.
- Alós, C. 1989. Adiciones a la fauna de Anélidos Poliquetos de la península Ibérica: familia Syllidae. *Cahiers de Biologie Marine* **30**, 329-337.
- Alós, C., Campoy, A. & Pereira, F. 1982. Contribución al conocimiento de los Anélidos Poliquetos endobiontes de Esponjas. *Actas Simposium Ibérico de Estudio del Bentos Marino* **3**, 139-159.
- Alvå, V. & Jangoux, M. 1989. Sur les symbioses entre Polychètes et Ophiures avec la description d'un nouveau cas de commensalisme. In *Echinodermes: Actuels et Fossiles. Actes du VIe Séminaire International sur les Echinodermes*, M.B. Régis, A. Segui, C. Frasson, P. Escoubet & A. Riva (eds.), Aix-Marseille III: CERAM; Faculté des Sciences et Techniques de Saint-Jérôme; Foundation Océanographique Ricard, pp. 185-192.
- Amaral, A.C.Z. 1977. Um poliqueto endoparasita, *Labrorostratus prolificus* sp. nov. em Nereídeo. *Boletim do Instituto Oceanográfico, Sao Paulo* **26**, 285-292.
- Amoureux, L., Josef, G. & O'Connor, B. 1980. Annélides Polychètes de l'éponge *Fasciospongia cavernosa* Schmidt. *Cahiers de Biologie Marine* **21**, 387-392.
- Andrews, E.A. 1891a. A commensal annelid. *American Naturalist* **24**, 25-35.
- Andrews, E.A. 1891b. Report upon the Annelida Polychaeta of Beaufort, North Carolina. *Proceedings of the United States National Museum* **14**, 277-302.
- Arvanitidis, C. & Koukouras, A. 1994. Polychaete fauna associated with the coral *Cladocora caespitosa* (L.) in the eastern Mediterranean. *Mémoires du Muséum national d'Histoire natural (zoologie), Paris* **162**, 347-353.
- Arwidsson, I. 1933. *Calamyzas amphictenicola*, ein ektoparasitischer Verwandter der Sylliden. *Zoologiska Bidrag fran Uppsala* **14**, 153-218.
- Augener, H. 1914. Polychaeta II, Sedentaria. *Fauna Südwest-Australia* **5**, 1-170.
- Augener, H. 1922. Results of Dr. E. Mjöberg's Swedish scientific expeditions to Australia 1910-13. 33. Polychaeten. *Kungliga Svenska vetenskapsakademiens handlinga* **63**, 1-49.
- Bacescu, M. 1971. Les Spongiaires: un des plus intéressants biotopes benthiques marins. *Rapports de la Commission Internationale pour l'Exploration de la Mer Méditerranéenne* **20**, 239-241.
- Bailey-Brock, J.H. 1985. Polychaetes from Fijian coral reefs. *Pacific Science* **39**, 195-220.
- Barel, C.D.N. & Kramers, P.G.N. 1977. A survey of the echinoderm associates of the North-East Atlantic area. *Zoologische Verhandelingen. Leiden* **156**, 1-159.

- Bartel, A.H. & Davenport, D. 1956. A technique for the investigation of chemical responses in aquatic animals. *British Journal of Animal Behaviour* **4**, 117-119.
- Beauchamp, P. de & Zachs, I. 1913. Esquisse d'une monographie bionomique de la plage de Terrénès. *Mémoires de la Société de Zoologie Française* **26**, 197-237.
- Bellan, G. 1959. Repartition biogéographique et bionomique de quelques annélides polychètes de la Méditerranée et du proche océan. *Recueil des Travaux de la Station Marine d'Endoume* **Bull. 17 Fasc. 29**, 127-172.
- Bellan, G. 1964. Contribution à l'étude systématique, bionomique et écologique des Annélides Polychètes de la Méditerranée. *Recueil des Travaux de la Station Marine d'Endoume* **Bull. 33 Fasc. 49**, 1-371.
- Belloni, S. & Mori, M. 1985. Presenza di *Iphitime cuenoti* (Annelida: Iphitimidae) in Mar Ligure. *Nova Thalassia* **7**, 402.
- Ben-Eliahu, M.N. 1975b. Polychaete cryptofauna from rims of similar intertidal vermetid reefs on the Mediterranean coast of Israel and in the Gulf of Elat: Nereidae (Polychaeta Errantia). *Israel Journal of Zoology* **24**, 177-191.
- Ben-Eliahu, M.N. 1975a. Polychaete cryptofauna from rims of similar intertidal vermetid reefs on the Mediterranean coast of Israel and in the Gulf of Elat: Sabellidae (Polychaeta Sedentaria). *Israel Journal of Zoology* **24**, 54-70.
- Ben-Eliahu, M.N. 1976. Polychaete cryptofauna from rims of similar intertidal vermetid reefs on the Mediterranean coast of Israel and in the Gulf of Elat: Serpulidae (Polychaeta Sedentaria). *Israel Journal of Zoology* **25**, 103-119.
- Beneden, P.J.van 1853. Note sur une larve d'annelide d'une forme toute particulière, rapportée avec doute aux serpules. *Bulletin de l'Académie Royale de Bruxelles* **20**, 69-72.
- Beneden, P.J.van 1858. Histoire naturelle d'un animal nouveau désigné sous le nom d'*Histriobdella*. *Bulletin de l'Académie Royale de Bruxelles* **5**, 270-302.
- Beneden, P.J.van 1869. Le commensalisme dans le Règne Animal. *Proceedings of the Royal Irish Academy* **28**, 621-636.
- Berkeley, E. 1924. On a new case of commensalism between echinoderm and annelid. *Canadian Field Naturalist* **38**, 193 only.
- Berkeley, E. & Berkeley, C. 1941. On a collection of Polychaeta from Southern California. *Bulletin of the Southern California Academy of Sciences* **40**, 16-60.
- Berkeley, E. & Berkeley, C. 1942. North Pacific Polychaeta, chiefly from the west coast of Vancouver Island, Alaska and Bering Sea. *Canadian Journal of Science* **20**, 183-208.
- Berkeley, E. & Berkeley, C. 1948. *Canadian Pacific Fauna*. Toronto: Fisheries Research Board of Canada.
- Berkeley, E. & Berkeley, C. 1950. Notes on Polychaeta from the coast of western Canada. IV. Polychaeta Sedentaria. *Annals and Magazine of Natural History* **3**, 50-69.
- Blake, J.A. 1969. Systematics and ecology of shell-boring polychaetes from New England. *American Zoologist* **9**, 813-820.
- Blake, J.A. 1971. Revision of the genus *Polydora* from the East coast of North America. *Smithsonian Contributions to Zoology* **75**, 1-32.
- Blake, J.A. 1980. *Polydora* and *Boccardia* species (Polychaeta: Spionidae) from western Mexico, chiefly from calcareous habitats. *Proceedings of the Biological Society of Washington* **93**, 947-962.
- Blake, J.A. 1983. Polychaetes of the family Spionidae from South America, Antarctica, and adjacent seas and islands. In *Biology of the Antarctic Seas XIV. Antarctic Research Series. Vol. 39 (3)*, L. Kornicker (ed.), Washington D.C.: American Geophysical Union, pp. 205-288.
- Blake, J.A. 1990. A new genus and species of Polychaeta commensal with a deep-sea thyasirid clam. *Proceedings of the Biological Society of Washington* **103**, 681-686.
- Blake, J.A. 1993. New genera and species of deep-sea polychaetes of the family Nautiliniellidae from the Gulf of Mexico and the Eastern Pacific. *Proceedings of the Biological Society of Washington* **106**, 147-157.
- Blake, J.A. 1994. Introduction to the Annelida. In *Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel. The Annelida part 1*, J.A. Blake, B. Hilbig & P.H. Scott (eds.), Santa Barbara, California: Santa Barbara Museum of Natural History, pp. 39-113.
- Blake, J.A. 1996. Family Spionidae Grube, 1850. Including a review of the genera and species from California and a revision of the genus *Polydora* Bosc, 1802. In *Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel. The Annelida part 3*, J.A.

- Blake, B. Hilbig & P.H. Scott (eds.), Santa Barbara, California: Santa Barbara Museum of Natural History, pp. 81-224.
- Blake, J.A. & Evans, J.W. 1973. *Polydora* and related genera as borers in mollusc shells and other calcareous substrates. *The Veliger* **15**, 235-249.
- Blake, J.A. & Kudenov, J.D. 1978. The spionidae (Polychaeta) from Southeastern Australia and adjacent areas with a revision of the genera. *Memories of the national Museum of Victoria* **39**, 171-280.
- Blake, J.A. & Woodwick, K.H. 1971. New species of *Polydora* (Polychaeta: Spionidae) from the coast of California. *Bulletin of the Southern California Academy of Sciences* **70**, 72-79.
- Boucher, D.H., James, S. & Keeler, K.H. 1982. The ecology of mutualism. *Annual Review of Ecology and Systematics* **13**, 315-347.
- Brettey, J. & Campbell, A. 1985. Occurrence of *Histriobdella homari* (Annelida: Polychaeta) on the american lobster in the Canadian maritimes. *Canadian Journal of Zoology* **63**, 392-395.
- Brightwell, L.R. 1951. Some experiments with the common hermit crab (*Eupagurus bernhardus* Linn.) and transparent univalve shells. *Proceedings of the Zoological Society of London* **121**, 279-283.
- Britayev, T.A. 1981. Two new species of commensal polynoids (Polychaeta: Polynoidae) and bibliography on polychaetes, symbionts of Coelenterata. [In Russian]. *Zoologicheski Zhurnal* **60**, 817-824.
- Britayev, T.A. 1989. The symbiotic Polychaetes: Morphology, Ecology and Distribution. In *Symbiosis among marine animals*, V.A. Sveshnicov (ed.), Moscow: A.N. Severtzov Institute, Russian Academy of Sciences, pp. 60-74.
- Britayev, T.A. 1991. Life cycle of the symbiotic scaleworm *Arctonoe vittata* (Polychaeta: Polynoidae). *Ophelia Suppl.* **5**, 305-312.
- Britayev, T.A. 1993. *Pilargis berkeleyae* (Polychaeta, Pilargidae) as a commensal of a sedentary polychaete *Chaetopterus cautus* (Chaetopteridae). [In Russian]. *Zoologicheski Zhurnal* **72**, 147-151.
- Britayev, T.A. & Fahrutdinov, R.R. 1994. Pontoniin shrimps associated with molluscs at the coast of South Vietnam. [In Russian]. In *Hydrobionts of South Vietnam*, D.S. Pavlov & J.N. Sbikin (eds.), Moscow: Nauka, pp. 128-145.
- Britayev, T.A. & Memmy, M.P. 1989. Symbiotic association between the pelagic polychaete *Hipponoe gaudichaudi* (Polychaeta, Amphinomidae) and goose barnacles (Cirripedia, Lepadomorpha). [In Russian]. *Zoologicheski Zhurnal* **68**, 30-35.
- Britayev, T.A. & Smurov, A.V. 1985. The structure of a population of symbionts and related biological features, *Arctonoe vittata* (Polychaeta, Polynoidae) taken as an example. [In Russian]. *Zhurnal obschey Biologii* **46**, 355-366.
- Britayev, T.A. & Zamyshliak, E.A. 1996. Association of the commensal scaleworm *Gastrolepidia clavigera* (Polychaeta: Polynoidae) with holothurians near the coast of South Vietnam. *Ophelia* **45**, 175-190.
- Britayev, T.A., Ivashchenko, N.I. & Litvinov, E.G. 1977. Peculiarities of the commensal complex in the polychaete *Arctonoe vittata*. [In Russian]. *Biologiya Morya* **1978**, 76-78.
- Britayev, T.A., Smurov, A.V., Adrianov, A.V., Bazhin, A.G. & Rhzavsky, A.V. 1989. Ecology of symbiotic Polychaete *Arctonoe vittata* according to the peculiarity of starfish *Asterias ratbunae* ecology. [In Russian]. In *Symbiosis among marine animals*, V.A. Sveshnicov (ed.), Moscow: A.N. Severtzov Institute, Russian Academy of Sciences, pp. 102-127.
- Buzhinskaya, G.N. 1967. On the ecology of the Polychaetous Annelids of the Possjet Bay (the Sea of Japan). [In Russian]. *Isseldovaniya Fauni Moorei* **5**, 78-124.
- Buzhinskaya, G.N. 1971. New and interesting species of polychaete worms of the Possjet Bay of the Sea of Japan. [In Russian]. *Isseldovaniya Fauni Moorei* **8**, 123-145.
- Buzhinskaya, G.N., Obut, A.M. & Potin, V.V. 1980. Errantiate polychaetes (Polychaeta, Errantia) of the coral reefs and islands of the Indian and Pacific oceans (based on the material of the "KALLISTO" expedition of 1974, 1975) [In Russian]. In *Biology of Coral Reefs*, Moscow: USSR Academy of Sciences; Inst. Mar. Biol. Far E. Sci. Centre, pp. 225-256.
- Campoy, A. 1982. Fauna de España. Fauna de Anélidos Poliquetos de la Península Ibérica. *Publicaciones de la Universidad de Navarra. Serie Zoológica* **7**, 1-400.
- Cañete, J.I., Gallardo, V.A., Enríquez, S. & Baltazar, M. 1993. *Harmothoe brevipalpa* Begström, 1916 (Polynoidae), poliqueto asociado a los tubos de dos especies de poliquetos frente a la Bahía de Concepción, Chile. *Boletín de la Sociedad de Biología de Concepción, Chile* **64**, 43-46.
- Cannon, L.R.G. & Jennings, J.B. 1987. Occurrence and nutritional relationships of four

- ectosymbiotes of the freshwater crayfishes *Cherax dispar* Riek and *Cherax punctatus* Clark (Crustacea: Decapoda) in Queensland. *Australian Journal of Marine and Freshwater Research* **38**, 419-427.
- Carrasco, F.D. 1974. Spionidae (Polychaeta) provenientes de la Bahía de Concepción y lugares adyacentes. *Boletín de la Sociedad de Biología de Concepción, Chile* **48**, 185-201.
- Carthy, J.D. 1958. *An introduction to the behaviour in invertebrates*. London: George Allen & Unwin.
- Carton, Y. 1966b. Specificite parasitaire de *Sabelliphilus sarsi*, parasite de *Spirographis spallanzani*. 1. Intérêt de son étude dans la taxonomie de divers sabellidae. *Archives de Zoologie Expérimentale et Générale* **107**, 428-442.
- Carton, Y. 1966a. Etude du comportement et de la specificite parasitaire de *Sabelliphilus sarsi* Claparède, copepode parasite de *Spirographis spallanzani* Viviani. *Bulletin du Museum National d'Histoire Naturelle Paris* **37**, 807-817.
- Carton, Y. 1967. Specificite parasitaire de *Sabelliphilus sarsi*, parasite de *Spirographis spallanzani*. 2. Reactions histologiques des hôtes lors des contaminations expérimentales. *Archives de Zoologie Expérimentale et Générale* **108**, 387-411.
- Carton, Y. 1968b. Specificite parasitaire de *Sabelliphilus sarsi*, parasite de *Spirographis spallanzani*. 4. Etude biochimique des hotes et de leurs secretions. *Archives de Zoologie Expérimentale et Générale* **109**, 269-286.
- Carton, Y. 1968a. Specificite parasitaire de *Sabelliphilus sarsi*, parasite de *Spirographis spallanzani*. 3. Mise en evidence d'une attraction biochimique du Copepode par l'Annelide. *Archives de Zoologie Expérimentale et Générale* **109**, 123-144.
- Caullery, M. 1914. *Labidognathus parasiticus* n. g. n. sp. Cas nouveau d'endoparasitisme évolutif chez les Eunicien. *Compte Rendu de la Société de Biologie de Paris* **77**, 490-493.
- Caullery, M. 1925. Schizogenese et schizogamie de *Procerastea halleziana* Malaquin. Parasitism de ce Syllidien sur les Tubulaires. *Bulletin de la Société Zoologique de France* **50**, 204-208.
- Caullery, M. & Mesnil, F. 1916. Notes biologiques sur les mares à *Lithothamnion* de la Hague. 1. Presentation d'un *Labrostratus parasiticus* S.J., parasite interne d'*Odonthosyllis ctenostoma* Clap. *Bulletin de la Société Zoologique de France* **40**, 160-161.
- Cazaux, C. 1968. Etude morphologique du developpement larvaire d'annelides polychetes (Basin d'Arcachon). I. Aphroditidae, Chrysopetalidae. *Archives de Zoologie Expérimentale et Générale* **109**, 477-543.
- Clark, R.B. 1956. *Capitella capitata* as a commensal, with a bibliography of parasitism and commensalism in the polychetes. *Annals and Magazine of Natural History* **12**, 433-448.
- Comely, A. & Ansell, A.D. 1988. Invertebrate associates with the sea-urchin *Echinus sculentus* L. from the Scottish West Coast. *Ophelia* **28**, 111-137.
- Comely, C.A. & Ansell, A.D. 1989. The occurrence of the Eunicid polychaetes *Iphitime cuenoti* Fauvel and *I. paguri* Fage & Legendre in crabs from the Scottish West coast. *Ophelia* **31**, 59-76.
- Cordero, E.H. 1927. Un nuevo Arquianélido, *Stratiadrilus platensis*, n. sp., que habita sobre *Aegla laevis* (Latr.). Nota preliminar. *Physis, Revista Soc. Argentina ciencias naturales* **8**, 574-578.
- Cram, A. & Evans, S.M. 1980. Shell entry behaviour in the commensal ragworm *Nereis fucata*. *Marine Behaviour and Physiology* **7**, 57-64.
- Cuenot, L. 1912. Contribution a la faune du Bassin d'Arcachon. Echinodermes. *Bulletin de la Station Biologique d'Arcachon* **14**, 17-1227.
- Dales, R.P. 1957. Interrelations of organisms. A. Commensalism. In *Treatise on marine ecology and palaeoecology* (Ed. J.W. Hedgpeth). *Memorials of the Geological Society of America* **67**, 391-412.
- Dauer, D.M. 1974. Polychaete fauna associated with Gulf of Mexico sponges. *Florida Scientist* **36**, 192-196.
- Dauer, D.M. 1991. Functional morphology and feeding behavior of *Polydora commensalis* (Polychaeta: Spionidae). *Ophelia Suppl.* **5**, 607-614.
- Davenport, D. 1950. Studies in the physiology of commensalism. I. The polynoid genus *Arctonoë*. *Biological Bulletin of the marine biological Laboratory, Woods Hole* **98**, 81-93.
- Davenport, D. 1953b. Studies in the physiology of commensalism. IV. The polynoid genera *Polynoe*, *Lepidasthenia* and *Harmothoe*. *Journal of the Marine biological Association of the United Kingdom* **32**, 273-288.
- Davenport, D. 1953a. Studies in the physiology of commensalism. III. The polynoid genera *Acholoe*, *Gattyana*, and *Lepidasthenia*. *Journal of the Marine biological Association of the United Kingdom* **32**, 161-173.

- Davenport, D. 1954. Notes on the early stages of the commensal polynoid *Acholoe astericola* (delle Chiaje). *Journal of the Marine biological Association of the United Kingdom* **33**, 123-127.
- Davenport, D. 1955. Specificity and behaviour in symbiosis. *Quarterly Review of Biology* **30**, 29-46.
- Davenport, D. 1966b. The experimental analysis of behaviour in symbioses. In *Symbiosis. I. Associations of Microorganisms, Plants and Marine Organisms*, S.M. Henry (ed.), New York: Academic Press, pp. 381-429.
- Davenport, D. 1966a. Echinoderms and the control of behavior in associations. In *Physiology of Echinodermata*, R.A. Boolootian (ed.), New York: Academic Press/John Wiley and Sons, pp. 145-156.
- Davenport, D. & Hickok, J.F. 1951. Studies in the physiology of commensalism. 2. The polynoid genera *Arctonoe* and *Halosydna*. *Biological Bulletin of the marine biological Laboratory, Woods Hole* **100**, 71-83.
- Davenport, D. & Hickok, J.F. 1957. Notes on the early stages of the facultative commensal *Podarke pugettensis* (Polychaeta, Hesionidae). *Annals and Magazine of Natural History* **10**, 625-631.
- Davenport, D., Camougis, G. & Hickok, J.F. 1960. Analysis of the behaviour of commensals in host-factor. I. A hesionid polychaete and pinnotherid crab. *Animal Behaviour* **8**, 209-218.
- Day, J.H. 1960. The Polychaete fauna of South Africa. Part 5. Errant species dredged off Cape coasts. *Annales of the South African Museum* **45**, 261-373.
- Day, J.H. 1962. Polychaeta from several localities in the western Indian Ocean. *Proceedings of the Zoological Society of London* **139**, 627-656.
- Day, J.H. 1967. A monograph on the Polychaetes of Southern Africa. Part 1. Errantia. *Trustees of the British Museum (Natural History)* **656**, 1-656.
- Day, J.H. 1973. Polychaeta collected by U.D. Gaikwad at Ratnagiri, south of Bombay. *Zoological Journal of the Linnean Society* **52**, 337-361.
- Dean, H.K. 1992. A new arabellid polychaete living in the mantle cavity of deep-sea wood boring bivalves (family Pholadidae). *Proceedings of the Biological Society of Washington* **105**, 224-232.
- Desportes, I., Laubier, L. & Theodorides, J. 1977. Présence d'*Ophriotrocha geryoncola* (Esmark) (Polychète, Dorvilleidae) en Méditerranée Occidentale. *Vie et Milieu* **27**, 131-133.
- Devaney, D.M. 1967. An ectocommensal polynoid associated with Indo-pacific echinoderms, primarily ophiuroids. *Occasional Papers of the Bernice Pauahi Bishop Museum* **23**, 287-304.
- Devaney, D.M. 1974. Shallow water Echinoderms from British Honduras, with a description of a new species of *Ophiocoma* (Ophiuroidea). *Bulletin of Marine Science* **24**, 122-164.
- DeVantier, L.M., Reichelt, R.E. & Bradbury, R.H. 1985. Does *Spirobranchus giganteus* protect host *Porites* from predation by *Acanthaster planci*: predator pressure as a mechanism of coevolution? *Marine Biology* **32**, 307-310.
- Dimock Jr, R.V. 1974. Intraspecific aggression and the distribution of a symbiotic polychaete on its host. In *Symbiosis in the sea*, W.B. Vernberg (ed.), Columbia: University of South Carolina Press, pp. 29-44.
- Dimock Jr, R.V. & Davenport, D. 1971. Behavioral specificity and the induction of host recognition in a symbiotic polychaete. *Biological Bulletin of the marine biological Laboratory, Woods Hole* **141**, 472-484.
- Dimock Jr, R.V. & Dimock, J.G. 1969. A possible "defense" response in a commensal polychaete. *The Veliger* **12**, 65-68.
- Ditlevsen, H. 1917. *Annelids. I.* Copenhagen: H. Hagerup.
- Eckelbarger, K.J. 1978. Metamorphosis and settlement in the Sabellariidae. In *Settlement and metamorphosis of marine invertebrate larvae*, F.S. Chia & M.E. Rice (eds.), New York: Elsevier, pp. 127-144.
- Eisig, H. 1906. *Ichthyotomus sanguinarius*, eine auf Aalen schmarotzende Annelide. *Fauna und Flora des Golfes von Neapel* **28**, 1-300.
- Emerson, R.R. 1974. A new species of polychaetous annelid (Arabellidae) parasitic in *Diopatra ornata* (Onuphidae) from Southern California. *Bulletin of the Southern California Academy of Sciences* **73**, 1-4.
- Emson, R.H., Young, C.M. & Paterson, G.L.J. 1993. A fire worm with a sheltered life: studies of *Benthoscolex cubanus* Hartman (Amphinomidae), an internal associate of the bathyal sea-urchin *Archeopneustes hystrix* (A. Agassiz, 1880). *Journal of Natural History* **27**, 1010-1028.
- Essenberg, C. 1918. The factors controlling the distribution of the Polynoidae of the Pacific coast of North America. *University of California Publications in Zoology* **18**, 171-238.
- Estcourt, I.N. 1967. Burrowing polychaete worms from a New Zealand estuary. *Transactions of the*

- Royal Society of New Zealand* **9**, 65-78.
- Euders, H.E. 1905. Notes on the commensals found in the tube of *Chaetopterus pergamentaceus*. *American Naturalist* **34**, 1-3.
- Fage, L. 1936. Sur l'association d'un annélide polychète *Lumbriconereis flabellicola* n. sp. et d'un madrépore *Flabellum pavoninum distinctum* E. et H. *Comptes Rendues du XIIe Congrès International de Zoologie* **1**, 941-945.
- Fage, L. & Legendre, R. 1925. Sur une Annélide Polychète (*Iphitime cuenoti* Fauv.) commensale des crabes. *Bulletin de la Société Zoologique de France* **50**, 219-225.
- Fage, L. & Legendre, R. 1933. Les anélides polychètes du genre *Iphitime*. A propos d'une espèce nouvelle commensale des pagures, *Iphitime paguri*. *Bulletin de la Société Zoologique de France* **58**, 299-305.
- Fauchald, K. 1970. Polychaetous annelids of the families Eunicidae, Lumbrineridae, Iphitimidae, Arbellidae, Lysaretidae and Dorvilleidae from western Mexico. *Allan Hancock Monographs in marine Biology* **5**, 1-335.
- Fauchald, K. 1977. Polychaete worms, definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County Science Service* **28**, 1-190.
- Fauchald, K. 1992. A review of the genus *Eunice* (Polychaeta: Eunicidae) based upon type material. *Smithsonian Contributions to Zoology* **523**, 1-422.
- Fauchald, K. & Jumars, P.A. 1979. The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology: An Annual Review* **17**, 193-284.
- Fauvel, P. 1913. Quatrième note préliminaire sur les Polychètes provenant des campagnes de l'“Hirondelle” et de la “Princesse-Alice”, ou déposées dans le Musée Océanographique de Monaco. *Bulletin de l'Institut Océanographique (Foundation Albert 1er, Prince de Monaco)* **270**, 1-80.
- Fauvel, P. 1914. Un Eunicien énigmatique *Iphitime cuenoti* n. sp. *Archives de Zoologie Expérimentale et Générale* **53**, 34-37.
- Fauvel, P. 1923. Faune de France. Polychètes Errantes. *Faune de France* **5**, 1-488.
- Fauvel, P. 1959. Classe des Annélides Polychètes. Annelida Polychaeta (Grube, 1851). In *Traité de Zoologie. Anatomie, Systématique, Biologie*, P.P. Grassé (ed.), Paris: Masson et Cie, pp. 13-196.
- Fox, R.S. & Ruppert, E.E. 1985. Shallow-water marine benthic macroinvertebrates of South Carolina, species identification, community composition and symbiotic associations. *The Belle W. Baruch Library in Marine Sciences* **14**, 1-130.
- Franzén, Å. 1982. Ultrastructure of the biflagellate spermatozoon of *Tomopteris helgolandica* Greef, 1879 (Annelida, Polychaeta). *Gamete Research* **6**, 29-37.
- Frith, D.W. 1976. Animals associated with sponges at North Hayling, Hampshire. *Zoological Journal of the Linnean Society* **58**, 353-362.
- Fuehr, I.M. 1971. A new histriobdellid on a marine isopod from South Africa. *South African Journal of Science* **67**, 325-326.
- Gaikwad, U.D. 1993. Some ecological observations on commensal behaviour of polychaetes, *Loimia medusa* and *Lepidasthenia tubicola*. *Journal of Ecobiology* **5**, 143-145.
- Gallardo, V.A. 1967. Polychaeta from the bay of Nha Trang, South Viet Nam. *Scientific Researches on the Marine Invertebrates of South China Sea and the Gulf of Thailand, 1959-1961. NAGA report* **4**, 35-279.
- Ganapati, P. & Radhakrishna, Y. 1962. Inquilinism between a new hesionid polychaete and a holothuria *Molpadia* sp. *Current Science* **31**, 382-383.
- Gardiner, S.L. 1976. Errant Polychaete Annelids from North Carolina. *The Journal of the Elisha Mitchell Scientific Society* **91**, 77-220.
- Gaston, G.R. & Benner, D.A. 1981. On Dorvilleidae and Iphitimidae (Annelida: Polychaeta) with a redescription of *Eteonopsis geryoncola* and a new host record. *Proceedings of the Biological Society of Washington* **94**, 76-87.
- George, J.D. & Hartmann-Schroeder, G. 1985. *Polychaetes: British Amphinomida, Spintherida and Eunicida. Synopses of the British Fauna (New Series). Vol. 32*. London: Linnean Society of London and Estuarine and Brackish-Water Sciences Association.
- Gerber, H.S. & Stout, J.F. 1968. Sensory basis of the symbiotic relationship of *Arctonoe vittata* (Grube) (Polychaeta, Polynoidae) to the keyhole limpet *Diodora aspera*. *Physiological Zoology* **41**, 169-179.
- Gibbs, P.E. 1969. Aspects of polychaete ecology with particular reference to commensalism. *Philosophical Transactions of the Royal Society of London* **255**, 443-458.
- Gibbs, P.E. 1971. The polychaete fauna of the Solomon Islands. *Bulletin of the British Museum of*

- Natural History* **21**, 101-211.
- Gilpin-Brown, J.B. 1969. Host-adoption in the commensal polychaete *Nereis fucata*. *Journal of the Marine biological Association of the United Kingdom* **49**, 121-127.
- Glasby, C.J. 1994. A new genus and species of polychaete *Bollandia antipathicola* (Nereidoidea, Syllidae), from black coral. *Proceedings of the Biological Society of Washington* **107**, 615-621.
- Goerke, H. 1971. *Nereis fucata* (Polychaeta, Nereidae) als kommensale von *Eupagurus bernhardus* (Crustacea, Decapoda) Entwicklung einer population und verhalten der art. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven* **13**, 79-81.
- Goerke, H. 1977b. *Nereis fucata* (Nereidae) - kommensalismus: Nahrungserwerb. *Publikationen zu wissenschaftlichen filmen* **59**, 3-11.
- Goerke, H. 1977a. *Nereis fucata* (Nereidae) - Kommensalismus: Eindringen in das Gehäuse von *Eupagurus bernhardus*. Film E 1891 des IWF, Gottingen 1977. *Publikationen zu wissenschaftlichen filmen* **58**, 3-12.
- Gravier, C. 1900. Sur le commensalisme de l'*Eunice harasii* Audouin et M.-Edwards et de l'*Ostrea edulis* L. *Bulletin du Museum National d'Histoire Naturelle Paris* **6**, 415-417.
- Gravier, C. 1905b. Sur les genres *Lepidasthenia* Malmgren et *Lepidametria* Webster. *Bulletin du Museum National d'Histoire Naturelle Paris* **11**, 181-184.
- Gravier, C. 1905a. Sur un Polynoidien (*Lepidasthenia digueti* n. sp.) commensal d'un *Balanoglossus*. *Comptes Rendues de l'Academie des Sciences de Paris* **140**, 875-878.
- Gravier, C. 1918. Note sur une Actinie (*Thoractis*) et un Annélide Polychète (*Hermadion fauveli*) commensaux d'une éponge silicieuse (*Sarcostegia oculata*). *Bulletin de l'Institut Océanographique (Foundation Albert 1er, Prince de Monaco)* **334**, 1-20.
- Guille, A. 1965. Contribution a l'étude de la systématique et l'écologie d'*Ophiotrix quinquemaculata* d. Ch. *Vie et Milieu* **15**, 243-308.
- Haigler, S.A. 1969. Boring mechanism of *Polydora websteri* inhabiting *Crassostrea virginica*. *American Zoologist* **9**, 821-828.
- Hamond, R. 1966. The Polychaeta of the coast of Norfolk. *Cahiers de Biologie Marine* **7**, 383-436.
- Hanley, J.R. 1984. A new host and locality records of the commensal *Adyte crinoidicola* (Polychaeta, Polynoidae). *The Beagle, Records of the Northern territory Museum of Arts and Sciences* **1**, 87-92.
- Hanley, J.R. 1989. Revision of the scaleworm genera *Arctonoe* Chamberlin and *Gastrolepidia* Schmarda (Polychaeta, Polynoidae) with the erection of a new subfamily, Arctonoinae. *The Beagle, Records of the Northern territory Museum of Arts and Sciences* **6**, 1-34.
- Hanley, J.R. 1992. Checklist of scaleworms (Polychaeta: Polynoidae) from Hong Kong. In *The marine flora and fauna of Hong Kong and southern China III. Proceedings of the Fourth International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 11-29 April 1989*, B. Morton (ed.), Hong Kong: Hong Kong University Press, pp. 361-369.
- Hanley, J.R. 1993. Scaleworms (Polychaeta: Polynoidae) of Rottnest Island, Western Australia. In *Proceedings of the Fifth International Marine Biological Workshop: The Marine Flora and Fauna of Rottnest Island, Western Australia*, F.E. Wells, D.I. Walker, H. Kirkman & R. Lethbridge (eds.), Perth: Western Australian Museum, pp. 305-320.
- Hanley, J.R. & Burke, M. 1988. A new genus and species of commensal scaleworm (Polychaeta, Polynoidae). *The Beagle, Records of the Northern territory Museum of Arts and Sciences* **5**, 5-15.
- Hanley, J.R. & Burke, M. 1989. A new genus and species of commensal scaleworm (Polychaeta, Polynoidae) from Broome, Western Australia. *The Beagle, Records of the Northern territory Museum of Arts and Sciences* **6**, 97-103.
- Hanley, J.R. & Burke, M. 1990. Scaleworms (Polychaeta: Polynoidae) of Albany, Western Australia. In *Proceedings of the Third International Marine Biological Workshop: The Marine Fauna of Albany, Western Australia*, F.E. Wells, D.I. Walker, H. Kirkman & R. Lethbridge (eds.), Perth: Western Australia Museum, pp. 203-236.
- Hanley, J.R. & Burke, M. 1991a. A new genus and species of scaleworm (Polychaeta, Polynoidae) from the Cascade Plateau, Tasman Sea. *The Beagle, Records of the Northern territory Museum of Arts and Sciences* **8**, 97-102.
- Hanley, J.R. & Burke, M. 1991b. Polychaeta Polynoidae: Scaleworms of the Chesterfield Islands and Fairway Reefs, Coral Sea. In *Résultats des Campagnes MUSORSTOM, Vol. 8*, A. Crosnier (ed.), *Mémoires du Muséum national d'Histoire naturel*, (A) **151**, 9-82.
- Harrington, N.R. 1897. On nereids commensal with hermit crabs. *Transactions of the New York Academy of Science* **16**, 214-221.

- Harrison, L. 1928. On the genus *Stratiodrilus* (Archiannelida: Histriobdella) with a description of a new species from Madagascar. *Records of The Australian Museum* **16**, 116-121.
- Hartman, O. 1941. New species of polychaetous annelids from Southern California. *Allan Hancock Pacific Expedition* **7**, 159-171.
- Hartman, O. 1942. The polychaetous Annelida. Report on the scientific results of the Atlantis Expedition to the West Indies under the joint auspices of the University of Havana and Harvard University. *Memorias de la Sociedad Cubana de Historia Natural* **16**, 89-104.
- Hartman, O. 1948. The polychaetous annelids of Alaska. *Pacific Science* **2**, 1-58.
- Hartman, O. 1951. The littoral marine Annelids of the Gulf of Mexico. *Publications of the Institute of Marine Sciences* **2**, 7-124.
- Hartman, O. 1952. *Iphitime* and *Ceratocephala* (Polychaetous annelids) from California. *Bulletin of the Southern California Academy of Sciences* **51**, 9-20.
- Hartman, O. 1954. Marine annelids from the northern Marshall Islands. *United States Geological Survey Professional Papers* **260 Q**, 615-644.
- Hartman, O. 1966. Polychaetous annelids of the Hawaiian Islands. *Occasional Papers of the Bernice Pauahi Bishop Museum* **23**, 163-252.
- Hartman, O. 1968. *Atlas of the errantiate polychaetous annelids from California*. Los Angeles: Allan Hancock Foundation, University of Southern California.
- Hartman, O. & Boss, K.J. 1965. *Antonbruunia viridis*, a new inquiline annelid with dwarf males, inhabiting a new species of pelecypod, *Lucinia fosteri* in the Mozambique channel. *Annals and Magazine of Natural History* **13**, 177-186.
- Hartman, O. & Fauchald, K. 1971. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic Areas. Part II. *Allan Hancock Monographies in Marine Biology* **6**, 1-327.
- Hartmann-Schröder, G. 1960. Polychaeten aus dem Roten Meer. *Kieler Meeresforschungen* **16**, 69-125.
- Hartmann-Schröder, G. 1971. Annelida, Borstenwürmer, Polychaeta. In *Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Maermalen und nach ihrer Lebensweise*, M. Dahl & F. Peus (eds.), Jena: Gustav Fischer Verlag, pp. 1-594.
- Hartmann-Schröder, G. 1978. Einige Sylliden-Arten (Polychaeta) von Hawaii und aus dem Karibischen Meer. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* **75**, 49-61.
- Hartmann-Schröder, G. 1981. *Hololepidella alba* n. sp. (Polynoidae: Polychaeta), a commensal with the crown-of-thorns starfish from Mactan, Cebu. *The Philippine Scientist* **18**, 10-14.
- Hartmann-Schröder, G. 1983. Zur Kenntnis einiger Foraminiferengehäuse bewohnender Polychaeten aus dem Nordostatlantik. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* **80**, 169-176.
- Hartmann-Schröder, G. 1984. Zwie neue kommensalische Polychaeten der Gattung *Hololepidella* Willey (Polynoidae) von der Philippinen. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* **81**, 63-70.
- Hartmann-Schröder, G. 1985. *Polynoe caeciliae* Fauvel (Polynoidae), ein mit Korallen assoziierter Polychaet. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* **82**, 31-35.
- Hartmann-Schröder, G. 1989. *Polynoe thouarellicola* n. sp. aus der Antarktis, assoziiert mit Hornkorallen, und Wiederbeschreibung von *Polynoe antarctica* Kinberg, 1858 (Polychaeta, Polynoidae). *Zoologische Anzeiger* **3/4**, 205-221.
- Hartmann-Schröder, G. 1991. *Syllis onkylochaeta* sp.n., ein korallenfressender Polychaet (Syllidae) aus dem Korallenaquarium des Löbbecke-Museums. *Helgoländer Meeresuntersuchungen* **45**, 59-63.
- Hartmann-Schröder, G. 1992. Drei neue Polychaeten-arten der familien Polynoidae und Syllidae von Neu-Kaledonien, assoziiert mit einer verkalteten Hydrozoe. *Helgoländer Meeresuntersuchungen* **46**, 93-101.
- Hartmann-Schröder, G. 1993. *Haplosyllis xeniaecola*, ein neuer Polychaet (Syllidae) von der Molukken (Indonesien). *Helgoländer Meeresuntersuchungen* **47**, 305-310.
- Hartnoll, R.G. 1962. *Iphitime cuenoti* Fauvel (Eunicidae), a polychaete new to Brithish waters. *Annals and Magazine of Natural History* **5**, 93-96.
- Haswell, W.A. 1885. On a destructive parasite of the rock-oyster (*Polydora ciliata* and *P. polybranchia* n. sp.). *Proceedings of the Linnean Society of New South Wales* **10**, 273-275.
- Haswell, W.A. 1900. On a new Histriobdellid. *Quarterly Journal of Microscopical Science* **43**, 299-335.

- Haswell, W.A. 1913. Notes on the Histriobdellidae. *Quarterly Journal of Microscopical Science* **59**, 197-226.
- Hatfield, P.A. 1965. *Polydora commensalis* Andrews - Larval developpement and observations on adults. *Biological Bulletin of the marine biological Laboratory, Woods Hole* **128**, 356-368.
- Hendler, G. & Meyer, D.L. 1982. An association of a polychaete, *Branchiosyllis exilis*, with an ophiuroid, *Ophiocoma echinata*, in Panama. *Bulletin of Marine Science* **32**, 736-744.
- Henry S.M. (ed.) 1966. *Symbiosis. I. Associations of Microorganisms, Plants and Marine Organisms*. New York & London: Academic Press.
- Hermans, C.O. 1969. The systematic position of the Archiannelida. *Systematics and Zoology* **18**, 85-102.
- Hickok, J.F. & Davenport, D. 1957. Further studies in the behavior of commensal polychaetes. *Biological Bulletin of the marine biological Laboratory, Woods Hole* **113**, 397-406.
- Hilbig, B. 1994. 9. Family Hesionidae Sars, 1862. In *Taxonomic atlas of the benthic fauna of the Santa Barbara Basin and western Santa Barbara Channel. Vol. 4 - The Annelida part 1. Oligochaeta and Polychaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae)*, J.A. Blake & B. Hilbig (eds.), Santa Barbara: Santa Barbara Museum of Natural History, pp. 243-269.
- Hopkins, S.H. 1958. The planktonic larvae of *Polydora websteri* Hartman (Annelida, Polychaeta) and their settling on oysters. *Bulletin of Marine Science of the Gulf and Caribbean* **8**, 268-277.
- Hornell, J. 1891. Report on the polychaetous annelids of the L.M.B.C. district. *Proceedings and Transactions of the Liverpool Biological Society* **5**, 223-268.
- Horst, R. 1915. On new and little-known species of Polynoinae from the Netherland's East-Indies. *Zoologische Mededeelingen Leiden* **1**, 2-20.
- Houlbert, C. & Galaine, C. 1916. Sur le chambrage des huiters et l'infection possible desc chambers parle fait d'une Annelide tubicole parasite de la coquille (*Sclerocheilus*). *Comptes Rendues de l'Academie des Sciences de Paris* **162**, 54-56.
- Hove, H.A. ten 1970. Serpulinae (Polychaeta) from the Caribbean. 1. The genus *Spirobranchus*. *Studies on the Fauna of Curaçao and Caribbean Islands* **32**, 14-19.
- Hove, H.A. ten 1989. Serpulinae (Polychaeta) from the Caribbean: IV *Pseudovermilia madracicola* sp.n., a symbiont of corals. *Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen* **123**, 135-144.
- Hove, H.A. ten 1994. Serpulidae (Annelida: Polychaeta) from the Seychelles and Amirante Islands. In *Oceanic reefs of the Seychelles. Cruise reports Neth. Indian Ocean Programm II*, J. van der Land (ed.), Leiden: National Natural Museum of Leiden, pp. 107-116.
- Humann, P. 1992. *Reef creature identification. Florida, Caribbean, Bahamas*. Orlando: Vaughan Press.
- Hunte, W., Colin, B.E. & Marsden, J.R. 1990a. Habitat selection in the tropical polychaete *Spirobranchus giganteus*. 1. Distribution on corals. *Marine Biology* **104**, 87-92.
- Hunte, W., Marsden, J.R. & Conlin, B.E. 1990b. Habitat selection in the tropical polychaete *Spirobranchus giganteus*. III. Effects of coral species on body size and body proportions. *Marine Biology* **104**, 101-107.
- Imajima, M. 1966. The Syllidae (polychaetous annelids) from Japan. IV. Syllinae. *Publications of the Seto Marine Biological Laboratory* **14**, 219-252.
- Imajima, M. & Hartman, O. 1964. The Polychaetous Annelids from Japan. Pt. I. *Allan Hancock Foundation Special Publication* **26**, 1-237.
- Imajima, M. & Sato, W. 1984. A new species of *Polydora* (Polychaeta: Spionidae) collected from Abashiri Bay, Hokkaido. *Bulletin of the National Science Museum of Tokyo, Series A* **10**, 57-62.
- Izuka, A. 1912. The errantiate Polychaeta of Japan. *Journal of the College of Science, Imperial University of Tokyo* **30**, 1-262.
- Jamieson, B.G.M., Afzelius, B.A. & Franzén, Å. 1985. Ultrastructure of the acentriolar, aflagellate spermatozoa and the eggs of *Histriobdella homari* and *Stratiodrilus novaehollandiae* (Histriobdellidae, Polychaeta). *Journal of Submicroscopical Cytology* **17**, 363-372.
- Jangoux, M. 1987. Diseases of Echinodermata. III. Agents Metazoans (Annelida to Pisces). *Diseases in Aquatic Organisms* **3**, 59-83.
- Jennings, J.B. & Gelder, S.R. 1976. Observations on the feeding mechanism, diet and digestive physiology of *Histriobdella homari* van Beneden 1858: An aberrant polychaete symbiotic with North American and European lobsters. *Biological Bulletin of the marine biological Laboratory, Woods Hole* **151**, 489-517.
- Jensen, K. & Bender, K. 1973. Invertebrates associated with snail shells inhabited by *Pagurus bernhardus* (L.) (Decapoda). *Ophelia* **10**, 185-192.

- Jensen, R.A. & Morse, D.E. 1984. Intraspecific facilitation of larval recruitment: gregarious settlement of the polychaete *Phragmatopoma californica* (Fewkes). *Journal of Experimental Marine Biology and Ecology* **54**, 677-684.
- Jones, M.L. 1974. On the Caobangidae, a new family of Polychaeta, with redescription of *Caobangia billeti* Giard. *Smithsonian Contributions to Zoology* **175**, 1-55.
- Jones, S. 1964. Notes on animal associations. The starfish *Pentaceros hedemanni* and the hesionid polychaete *Podarke angustifrons*. *Journal of the Marine Biological Association of India* **6**, 249-250.
- Kent, R.M.L. 1979. The influence of heavy infestations of *Polydora ciliata* on the flesh content of *Mytilus edulis*. *Journal of the Marine biological Association of the United Kingdom* **59**, 289-297.
- Kent, R.M.L. 1981. The effect of *Polydora ciliata* on the strength of *Mytilus edulis*. *Journal du Conseil Permanent International pour l'Exploration de la Mer* **39**, 252-255.
- Kirkegaard, J.B. 1977. A new species of *Iphitime* (Polychaeta: Iphitimidae) living under the tail of *Hyas* (Crustacea: Decapoda) in the oslo fjord. In *Essays of Polychaetous annelids in memory of Dr. Olga Hartman*, D.J. Reish & K. Fauchald (eds.), Los Angeles: Allan Hancock Foundation, University of Southern California Press, pp. 199-209.
- Kirkegaard, J.B. & Billett, D. 1980. *Eunoe laetmogonensis*, a new species of polynoid worm, commensal with the bathyal holothurian *Laetmogone violacea*, in the North-East Atlantic. *Steenstrupia* **6**, 101-109.
- Koch, H. 1846. Einige Worte zur Entwicklungsgeschichte von Eunice, mit einem Nachwort von A. Koelliker. *Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft für die Gesamten Naturwissenschaften* **8**, 1-31.
- Korringa, P. 1951. The shell of *Ostrea edulis* as a habitat: observations on the epifauna of oysters living in the Oosterchelde, Holland, with some notes on polychaete worms occurring there in other habitats. *Archives néerlandaises de zoologie* **10**, 32-152.
- Koukouras, A., Russo, A., Voultsiadou-Koukoura, E., Dounas, C. & Chintiroglou, C. 1992. Relationship of sponge macrofauna with the morphology of their hosts in the North Aegean sea. *Internationale Revue der gesamten Hydrobiologie* **77**, 609-619.
- Koukouras, A., Russo, A., Voultsiadou-Koukoura, E., Arvanitidis, C. & Stefanidou, D. 1996. Macrofauna associated with sponge species of different morphology. *P.S.Z.N. I: Marine Ecology* **17**, 569-582.
- Kudenov, J.D. 1975. The occurrence of the Polynoid *Harmothoe cf lunulata* from the tube of the Maldanid *Axiiothella rubrocincta* (Polychaeta). *Research Notes of the Pacific Marine Station of California* **34**, 42-43.
- Lande, R. & Reish, D.J. 1968. Seasonal occurrence of the commensal polychaetous annelid *Ophryodromus pugettensis* on the starfish *Patiria miniata*. *Bulletin of the Southern California Academy of Sciences* **67**, 104-111.
- Landers, W.S. 1967. Infestation of the hard clam, *Mercenaria mercenaria*, by the boring polychaete worm, *Polydora ciliata*. *Proceedings of the National Shellfisheries Association* **57**, 63-66.
- Lang, K. 1949. A contribution to the morphology of *Stratioidrilus platensis* Cordero (Histiobdellidae). *Arkiv för Zoologi* **42A**, 1-30.
- Laubier, L. 1958. Contribution à la faunistique de coralligène. I. Quelques particularités biologiques de *Polydora armata* Langerhans. *Vie et Milieu* **9**, 412-415.
- Laubier, L. 1959. Contribution à la faunistique de coralligène. III. Deux spionidiens inquilins sur des bryozoaires chilostomides. *Vie et Milieu* **10**, 347-349.
- Laubier, L. 1960. Une nouvelle sous-espèce de Syllidien: *Haplosyllis depressa* Augener ssp. nov. *chamaeleon*, ectoparasite sur l'octocoralliaire *Muricea chamaeleon* Von Koch. *Vie et Milieu* **11**, 75-87.
- Laubier, L. 1973. Découverte d'une annélide polychète de l'Atlantique boréal dans l'étage bathyal de Méditerranée occidentale. *Vie et Milieu* **23**, 255-261.
- Lee, J.-W. & Rho, B.-J. 1994. Systematic studies on Syllidae (Annelida, Polychaeta) from the South Sea and the East Sea in Korea. *The Korean Journal of Systematic Zoology* **10**, 131-144.
- Light, W.J. 1970b. A new spionid (Annelida: Polychaeta) from the Gulf of California. *Bulletin of the Southern California Academy of Sciences* **69**, 74-79.
- Light, W.J. 1970a. *Polydora alloporis*, new species, a commensal spionid (Annelida, Polychaeta) from a Hydrocoral off Central California. *Proceedings of the California Academy of Sciences (Fourth Series)* **37**, 459-472.
- López, E., San Martín, G. & Jiménez, M. 1996. Syllinae (Syllidae, Annelida, Polychaeta) from Chafarinas Islands (Alborán Sea, W. Mediterranean). *Miscel.lània Zoològica* **19**, 105-118.

- Ludwig, H. 1905. Ein endoparasitischer Chaetopod in einer Tiefsee Ophiure. *Zoologische Anzeiger* **29**, 397-399.
- Lunz, G.R. 1940. The annelid worm *Polydora* as an oyster pest. *Science* **92**, 310.
- Lunz, G.R. 1941. *Polydora*, a pest in South Carolina oysters. *The Journal of the Elisha Mitchell Scientific Society* **57**, 273-283.
- Lützen, J. 1961. Sur une nouvelle espèce de Polychète, *Sphaerodoridium commensalis* n. gen., n. spec. (Polychaeta Errantia, famille des Sphaerodoridae) vivant en commensal de *Terebellides stroemi* Sars. *Cahiers de Biologie Marine* **2**, 409-416.
- MacNae, W. & Kalk, M. 1962. The fauna and flora of sand flats at Inhaca Island, Mocambique. *Journal of Animal Ecology* **31**, 93-128.
- Magnino, G. & Gaino, E. Submitted. *Haplosyllis spongicola* (Polychaeta, Syllidae) associated with two species of sponges from East Africa (Tanzania, Indian Ocean). *P.S.Z.N. I: Marine Ecology*.
- Marenzeller, E. 1874. Zur Kenntnis der adriatischen Anneliden. *Sitzungsberichte der Kaiserliche Akademie der Wissenschaften Wien, Mathematisch-Naturwissenschaftliche Klasse* **69**, 407-478.
- Marenzeller, E. 1902. Süd-japanische Anneliden. III. *Denskschriften der Akademie der Wissenschaften Wien, Mathematisch-naturwissenschaftliche Klasse* **72**, 563-582.
- Marenzeller, E. 1904. Steinkorallen. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee- Expedition auf dem Dampfer 'Valdivia' 1898-1899* **7**, 261-318.
- Marenzeller, E. 1895. *Phalacrostemma cidariophilum*, eine neue Gattung und Art der Hermelliden. *Anzeiger, Akademie der Wissenschaften, Wien (mathematische naturwissenschaften Klasse)* **32**, 191-192.
- Margalef, R. 1980. *Ecología*. Barcelona: Ediciones Omega S.A.
- Margolis, L., Esch, G.W., Holmes, J.C., Kuris, A.M. & Schad, G.A. 1982. The use of ecological terms in parasitology (report of a committee of the American Society of Parasitologists). *Journal of Parasitology* **68**, 131-133.
- Marsden, J.R. 1987. Coral preference behaviour by planktotrophic larvae of *Spirobranchus giganteus corniculatus* (Serpulidae: Polychaeta). *Coral Reefs* **6**, 71-74.
- Marsden, J.R. 1992. Reproductive isolation in two forms of the serpulid polychaete, *Spirobranchus polycerus* (Schmarda) in Barbados. *Bulletin of Marine Science* **51**, 14-19.
- Marsden, J.R., Conlin, B.E. & Hunte, W. 1990. Habitat selection in the tropical polychaete *Spirobranchus giganteus*. II. Larval preferences for corals. *Marine Biology* **104**, 93-99.
- Martin, D. 1987. La comunidad de Anélidos Poliquetos de las concreciones de algas calcáreas del litoral Catalán. Caracterización de las especies. *Publicaciones del Departamento de Zoología de Barcelona* **13**, 45-54.
- Martin, D. 1996. A new species of *Polydora* (Polychaeta, Spionidae) associated with the excavating sponge *Cliona viridis* (Porifera, Hadromerida) in the North Western Mediterranean sea. *Ophelia* **45**, 159-174.
- Martin, D. & Alvà, V. 1988. *Sphaerodorum ophiurophoretos* n. sp., une nouvelle espèce de Sphaerodoridae (Annelida, Polychaeta) commensal sur *Amphipholis squamata* (Echinodermata, Ophiuridae). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* **58**, 45-49.
- Martin, D., Abelló, P. & Cartes, J. 1991. A new species of *Ophryotrocha* (Polychaeta: Dorvilleidae) commensal in *Geryon longipes* (Crustacea: Brachyura) from the Western Mediterranean Sea. *Journal of Natural History* **25**, 1-14.
- Martin, D., Rosell, D. & Uriz, M.J. 1992. *Harmothoe hyalonemae* sp. nov. (Polychaeta, Polynoidae), an exclusive inhabitant of different Atlanto-Mediterranean species of *Hyalonema* (Porifera, Hexactinellida). *Ophelia* **35**, 169-185.
- McGinitie, G.E. & McGinitie, N. 1949. *Natural history of marine animals*. New York: McGraw-Hill.
- McIntosh, W.C. 1900. *A monograph of the British Annelida. II. Polychaeta, Amphinomidae to Sigalionidae*. London: Ray Society.
- Mesnil, F. & Caullery, M. 1922. L'appareil maxillaire d'*Histriobdella homari*; affinités des Histiobdellides avec les Euniciens. *Comptes Rendues de l'Academie des Sciences de Paris* **174**, 913-917.
- Mettam, C. 1980. On the feeding habits of Aphrodita aculeata and commensal polynoids. On the Feeding Habits of Aphrodita aculeata and Commensal Polynoids, a Short Note. *Journal of the Marine biological Association of the United Kingdom* **60**, 833-834.
- Michaelis, H. 1978. Zur morphologie und oekologie von *Polydora ciliata* und *Polydora ligni* (Polychaeta, Spionidae). *Helgoländer Meeresuntersuchungen* **31**, 102-116.
- Millot, N. 1953. A remarkable association between *Ophionereis reticulata* (Say) and *Harmothoe lunulata* (Delle Chiage). *Bulletin of Marine Science* **3**, 96-99.

- Miura, T. 1988. A new species of the genus *Protomystides* (Annelida, Polychaeta) associated with a vestimentiferan worm from the Hatsushima cold-seep site. *Proceedings of the Japanese Society of Systematics and Zoology* **38**, 10-14.
- Miura, T. & Hashimoto, J. 1991. Two new branchiate scale-worms (Polynoidae: Polychaeta) from the hydrothermal vent of the Okinawa Trough and the volcanic seamount off Chichijima Island. *Proceedings of the Biological Society of Washington* **104**, 166-174.
- Miura, T. & Hashimoto, J. 1993. *Mytilidiphila*, a new genus of nautiliniellid polychaetes living in the mantle cavity of deep-sea mytilid bivalves collected from the Okinawa Trough. *Zoological Science* **10**, 169-174.
- Miura, T. & Laubier, L. 1989. *Nautilina calyptogenica*, a new genus and species of parasitic polychaete on a vesicomid bivalve from the Japan Trench, representative of a new family Nautilinidae. *Zoological Science* **6**, 387-390.
- Miura, T. & Laubier, L. 1990. Nautiliniellid polychaetes collected from the Hatsushima Cold-seep site in Sagami Bay, with descriptions of new genera and species. *Zoological Science* **7**, 319-325.
- Miura, T. & Ohta, S. 1991. Two polychaete species from the deep-sea hydrothermal vent in the Middle Okinawa Trough. *Zoological Science* **8**, 383-387.
- Miura, T. & Shirayama, Y. 1992. *Lumbrineris flabellicola* (Fage, 1936), a Lumbrinerid Polychaete associated with a Japanese haermatypic coral. *Benthos Research* **43**, 23-27.
- Mohammad, M.-B.M. 1972. Infestation of the pearl oyster *Pinctada margaritifera* (Linné) by a new species of *Polydora* in Kuwait, Arabian sea. *Hydrobiologia* **39**, 463-477.
- Monticelli, F.S. 1892. Notizia preliminare intorno ad alcuni inquilini degli Holothuroidea del Golfo di Napoli. *Monitore di Zoologia Italiani* **3**, 248-256.
- Moore, J.P. 1905. New species of polychaetes from the North Pacific, chiefly from Alaskan waters. *Proceedings of the Academy of Natural Sciences of Philadelphia* **57**, 525-554.
- Moore, J.P. 1908. Some polychaetous annelids of the North Pacific of North America. *Proceedings of the Academy of Natural Sciences of Philadelphia* **60**, 321-364.
- Moore, J.P. 1910. The polychaetous annelids dredged by the U.S.S. 'Albatross' off the coast of southern California in 1904. II. Polynoidae, Aphroditidae and Segaleonidae. *Proceedings of the Academy of Natural Sciences of Philadelphia* **62**, 328-402.
- Moore, P.G. & Gorzula, S.J. 1973. A note on the commensal eunicean *Ipitime paguri* Fage and Legendre (Polychaeta) in the Firth of Clyde. *Journal of Natural History* **7**, 161-164.
- Morgado, E.H. & Amaral, A.C.Z. 1981. Anelídeos poliquetos associados a um briozoário. III. Polynoidae. *Boletim do Instituto Oceanográfico, Sao Paulo* **30**, 91-96.
- Morgado, E.H. & Amaral, A.C.Z. 1981a. Anelidos poliquetos associados a um briozoario I. Euniceidae, Lumbrineridae, Lysaretidae e Dorvilleidae. *Iheringia* **60**, 33-54.
- Morgado, E.H. & Amaral, A.C.Z. 1981b. Anelídeos poliquetos associados a um briozoário. II. Palmyridae. *Boletim do Instituto Oceanográfico, Sao Paulo* **30**, 87-89.
- Morgado, E.H. & Amaral, A.C.Z. 1984. Anelídeos poliquetos associados ao briozoário *Schizoporella unicornis* (Johnston). IV. Phyllodocidae e Hesionidae. *Revista Brasileira de Biologia Curitiba* **2**, 49-54.
- Morgado, E.H. & Amaral, A.C.Z. 1985. Anelídeos poliquetos associados ao briozoário *Schizoporella unicornis* (Johnston). V. Syllidae. *Revista Brasileira de Biologia* **3**, 219-227.
- Mori, K., Sato, W., Nomura, T. & Imajima, M. 1985. Infestation of the Japanese scallop *Pecten (Patinopecten) yessoensis* by the boring polychaetes, *Polydora* on the Okhotsk Sea coasts of Hokkaido, especially Abashiri waters. *Bulletin of the Japanese Society of Scientific Fisheries* **51**, 27-41.
- Mori, M. & Belloni, S. 1985. Distribution, abundance and infestation of *Ophryotrocha geryonicola* (Annelida: Dorvilleidae) in *Geryon longipes* (Crustacea: Decapoda: Geryonidae) of Ligurian bathyal bottoms. *Oebalia* **11**, 277-287.
- Moyano, H.I.G., Carrasco, F.D. & Gacitua, S. 1993. On Chilean species of the genus *Stratiodrillus* Haswell, 1900 (Polychaeta, Histiobdellidae). *Boletín de la Sociedad de Biología de Concepción, Chile* **64**, 147-157.
- Newell, G.E. 1954. The marine fauna of Whitstable. *Annals and Magazine of Natural History* **7**, 321-350.
- Núñez, J., Brito, M.C. & Ocaña, O. 1991. Anelídeos poliquetos de Canarias: familia Amphinomidae. *Cahiers de Biologie Marine* **32**, 469-476.
- Oakes, F.R. & Fields, R.C. 1996. Infestation of *Haliotis refescens* shells by a sabellid polychaete. *Aquaculture* **140**, 139-143.
- Okuda, S. 1934. On a tubicolous polychaete living in commensal with a pycnogonid. *Annotations on*

- Zoology, Japan* **14**, 437-439.
- Okuda, S. 1936a. Description of two polychaetous annelids found in burrows of an apodous holothurian. *Annotations on Zoology, Japan* **15**, 410-415.
- Okuda, S. 1936b. Japanese commensal polynoids. *Annotations on Zoology, Japan* **15**, 561-571.
- Okuda, S. 1937. Spioniform polychaetes from Japan. *Journal of the Faculty of Science, Hokkaido Imperial University, Series 6, Zoology* **5**, 217-254.
- Okuda, S. 1950. Notes on some commensal polychaetes from Japan. *Annotations on Zoology, Japan* **24**, 49-53.
- Orton, J.H. 1923. Some new commensals from the Plymouth District. *Nature* **112**, 861.
- Orton, J.H. & Smith, C. 1935. Experiments with *Amphitrite* and its commensals. *Annals and Magazine of Natural History ser. 10* **16**, 644-645.
- Overstreet, R.M. 1983. Metazoan symbionts of crustaceans. In *The Biology of Crustacea*, A.J. Provenzano Jr. (ed.), New York-London: Academic Press, pp. 155-250.
- Paiva, P.C. & Nonato, E.F. 1991. On the genus *Iphitime* (Polychaeta: Iphitimidae) and description of *Iphitime sartorae* sp. nov. a commensal of brachyuran crabs. *Ophelia* **34**, 209-215.
- Palmer, J.B. 1968. An analysis of the distribution of a commensal polynoid on its hosts. Ph.D. Thesis, University of Oregon.
- Pansini, M. & Daglio, S. 1980-1981. Osservazioni sull'inquilinismo di Policheti erranti in alcune demosponge del litorale ligure. *Bollettino del Museo del Istituto de Biologia dell'Universita di Genova* **48-49**, 55-60.
- Paris, J. 1955. Commensalisme et parasitisme chez les annélides polychètes. *Vie et Milieu* **6**, 525-536.
- Pascual, M., Núñez, J. & San Martín, G. 1996. *Exogone* (Polychaeta: Syllidae: Exoginae) endobiontics of sponges from the Canary and Madeira Islands with description of two new species. *Ophelia* **45**, 67-80.
- Pawlik, J.R. 1983. A sponge-eating worm from Bermuda: *Branchiosyllis oculata* (Polychaeta, Syllidae). *P.S.Z.N. I: Marine Ecology* **4**, 65-79.
- Pawlik, J.R. 1988. Larval settlement and metamorphosis of sabellariid polychaetes, with special reference to *Phragmatopoma lapidosa*, a reef-building species, and *Sabellaria floridensis*, a non-gregarious species. *Bulletin of Marine Science* **43**, 41-60.
- Pearse, A.S. 1932. Inhabitants of certain sponges at Dry Tortugas. *Carnegie Institut of Washington, Papers of Torugas Laboratory* **28**, 117-124.
- Pérès, J.-M. 1949. Sur un cas nouveau de parasitisme chez les Polychètes. *Bulletin de l'Institut Océanographique (Foundation Albert 1er, Prince de Monaco)* **46 number 945**, 1-4.
- Petersen, M.E. & Britayev, T.A. 1997. A new genus and species of polynoid scaleworm commensal with *Chaetopterus appendiculatus* Grube from the Banda Sea (Annelida: Polychaeta), with a review of commensals of Chaetopteridae. *Bulletin of Marine Science* **60**, 261-276.
- Pettibone, M.H. 1953. *Some scale-bearing polychaetes of Puget Sound and adjacent waters*. Seattle: University of Washington Press.
- Pettibone, M.H. 1954. Marine polychaete worms from Point Barrow, Alaska, with additional records from the North Atlantic and North Pacific. *Proceedings of the United States National Museum* **103**, 203-356.
- Pettibone, M.H. 1955. New species of polychaete worms of the family Polynoidae from east coast of North America. *Journal of the Washington Academy of Sciences* **45**, 119-126.
- Pettibone, M.H. 1956. Some polychaete worms of the families Hesionidae, Syllidae, and Nereidae from the coast of North America, West Indies, and Gulf of Mexico. *Journal of the Washington Academy of Sciences* **46**, 281-294.
- Pettibone, M.H. 1957. Endoparasitic polychaetous annelids of the family Arabellidae with descriptions of new species. *Biological Bulletin of the marine biological Laboratory, Woods Hole* **113**, 170-187.
- Pettibone, M.H. 1961. New species of polychaete worms from the Atlantic ocean, with a revision of the Dorvilleidae. *Proceedings of the Biological Society of Washington* **74**, 167-186.
- Pettibone, M.H. 1963. *Marine polychaete worms of the New England region. 1. Families Aphroditidae through Trochochaetidae*. Washington: Smithsonian Institution.
- Pettibone, M.H. 1969a. Review of some species referred to *Scalissetosus* McIntosh (Polychaeta, Polynoidae). *Proceedings of the Biological Society of Washington* **82**, 1-30.
- Pettibone, M.H. 1969b. Remarks on the North Pacific *Harmothoe tenebricosa* Moore (Polychaeta, Polynoidae) and its association with asteroids (Echinodermata, Asteroidea). *Proceedings of the Biological Society of Washington* **82**, 31-42.
- Pettibone, M.H. 1969c. The genera *Polyeunoa* McIntosh, *Hololepidella* Willei, and three new genera

- (Polychaeta, Polynoidae). *Proceedings of the Biological Society of Washington* **82**, 43-62.
- Pettibone, M.H. 1969d. *Australaugenira pottsi*, new name for *Polynoe longicirrus* Potts, from the Maldiv Islands (Polychaeta: Polynoidae). *Proceedings of the Biological Society of Washington* **82**, 519-524.
- Pettibone, M.H. 1969e. Revision of the Aphroditoid Polychaetes of the Family Eulephthidae Chamberlin (= Eulepidinae Darboux; = Pareulepididae Hartman). *Smithsonian Contributions to Zoology* **41**, 1-44.
- Pettibone, M.H. 1970. Polychaeta Errantia of the Siboga Expedition. Part IV. Some additional polychaetes of the Polynoidae, Hesionidae, Nereidae, Goniadidae, Eunicidae, and Onuphidae, selected as new species by the late Dr. Hermann Augener with remarks on other related species. In *Siboga-Expeditie Uitkomsten op Zoologisch, Botanisch, Oceanographisch en Geologisch gebied verzameld in Nederlandsch Oost-Indië 1899-1900*, M. Weber, L.F.de Beaufort & J.H. Stock (eds.), Leiden: E.J. Brill, pp. 199-270.
- Pettibone, M.H. 1975. Review of the genus *Hermenia* with a description of a new species (Polychaeta: Polynoidae: Lepidonotinae). *Proceedings of the Biological Society of Washington* **88**, 233-248.
- Pettibone, M.H. 1977. Review of *Halosydropsis* and related genera (Polychaeta: Polynoidae: Lepidonotinae). In *Essays on Polychaetous annelids in memory of Dr. Olga Hartman*, D.J. Reish & K. Fauchald (eds.), Los Angeles: University of South California Press, pp. 39-62.
- Pettibone, M.H. 1982. Annelida. Polychaeta. In *Synopsis and classification of living organisms*, S.P. Parker (ed.), New York: McGraw-Hill Book Company, pp. 3-43.
- Pettibone, M.H. 1983. *Minusculisquama hughesi*, a new genus and species of scale-worm (Polychaeta: Polynoidae) from Eastern Canada. *Proceedings of the Biological Society of Washington* **96**, 400-406.
- Pettibone, M.H. 1984a. A new scale-worm commensal with deep-sea mussels on the Galapagos hydrothermal vent (Polychaeta: Polynoidae). *Proceedings of the Biological Society of Washington* **97**, 226-239.
- Pettibone, M.H. 1984b. Two new species of *Lepidonotopodium* (Polychaeta: Polynoidae: Lepidonotopodinae) from hydrothermal vents off the Galapagos and East Pacific Rise at 21°N. *Proceedings of the Biological Society of Washington* **97**, 849-863.
- Pettibone, M.H. 1986a. A new scale worm commensal with deep-sea mussels in the seep-sites at the Florida Escarpment in the Eastern Gulf of Mexico (Polychaeta: Polynoidae: Branchipolynoidae). *Proceedings of the Biological Society of Washington* **99**, 444-451.
- Pettibone, M.H. 1986b. Review of the Iphioninae (Polychaeta: Polynoidae) and revision of *Iphione cimex* Quatrefages, *Gattyana deludens* Fauvel, and *Harmothoe iphionelloides* Johnson (Harmothoinae). *Smithsonian Contributions to Zoology* **428**, 1-43.
- Pettibone, M.H. 1989a. A new species of *Benhamipolynoe* (Polychaeta: Polynoidae: Lepidasteniinae) from Australia, associated with the unattached stylasterid coral *Conopora adeta*. *Proceedings of the Biological Society of Washington* **102**, 300-304.
- Pettibone, M.H. 1989b. Revision of the Aphroditoid Polychaetes of the family Acoetidae Kinberg (= Polyodontidae Augener) and reestablishment of *Acoetes* Audouin and Milne-Edwards, 1832, and *Euarche* Ehlers, 1887. *Smithsonian Contributions to Zoology* **464**, 1-138.
- Pettibone, M.H. 1990. New species and new records of scaled polychaetes (Polychaeta: Polynoidae) from the axial seamount caldera of the Juan de Fuca Ridge in the Northeast Pacific and the East Pacific Ocean off Northern California. *Proceedings of the Biological Society of Washington* **103**, 825-838.
- Pettibone, M.H. 1991a. Polynoids commensal with gorgonian and stylasterid corals, with a new genus, new combinations, and new species (Polychaeta: Polynoidae: Polynoinae). *Proceedings of the Biological Society of Washington* **104**, 688-713.
- Pettibone, M.H. 1991b. Polynoid polychaetes commensal with antipatharian corals. *Proceedings of the Biological Society of Washington* **104**, 714-726.
- Pettibone, M.H. 1993. Scaled polychaetes (Polynoidae) associated with ophiuroids and other invertebrates and review of species referred to *Malmgrenia* McIntosh and replaced by *Malmgeniella* Hartman, with descriptions of new taxa. *Smithsonian Contributions to Zoology* **538**, 1-92.
- Pettibone, M.H. 1996. Revision of the scaleworm genera *Acholoe* Claparède, *Arctonoella* Buzhinskaja, and *Intoshella* Darboux (Polychaeta, Polynoidae) with the erection of the new subfamily Acholoinae. *Proceedings of the Biological Society of Washington* **109**, 629-644.
- Pfannenstiel, H.D., Grothe, C. & Kegel, B. 1982. Studies on *Ophryotrocha geryoncola* (Polychaeta, Dorvilleidae). *Helgoländer Meeresuntersuchungen* **35**, 119-125.

- Pilger, J. 1971. A new species of *Iphitime* (Polychaeta) from *Cancer antennarius* (Crustacea: Decapoda). *Bulletin of the Southern California Academy of Sciences* **70**, 84-87.
- Potts, F.A. 1910. Polychaeta of the Indian ocean. Pt. 2. The Palmyridae, Aphroditidae, Polynoidae, Acoetidae and Sigalionidae. *Transactions of the Linnaeus Society of Zoology, series 2* **16**, 325-353.
- Potts, F.A. 1912. A new type of parasitism in the Polychaeta. *Proceedings of the Cambridge Philosophical Society* **16**, 409-413.
- Potts, F.A. 1915. The fauna associated with the crinoids of a tropical coral reef; with species reference to its colour variations. *Papers from the Tortugas Laboratory, Carnegie Institution* **8**, 71-96.
- Rabaud, E. 1939. *Nereis fucata* Sav. et la notion de commensalisme. *Bulletin de biologie de la France et de Belgique* **73**, 293-302.
- Radashevsky, V.I. 1988. Morphology, ecology, reproduction and larval development of *Polydora uschakovi* (Polychaeta, Spionidae) in the Peter the Great Bay of the Sea of Japan. [In Russian]. *Zoologicheski Zhurnal* **67**, 870-878.
- Radashevsky, V.I. 1989. Ecology, sex determination, reproduction and larval development of commensal Polychaetes *Polydora commensalis* and *Polydora glycymerica* in the Japanese Sea. [In Russian]. In *Simbiosis in marine animals*, V.A. Sveshnicov (ed.), Moscow: A.N. Severtzov Institute, Russian Academy of Sciences, pp. 137-164.
- Radashevsky, V.I. 1993. Revision of the genus *Polydora* and related genera from the North West Pacific (Polychaeta, Spionidae). *Publications of the Seto Marine Biological Laboratory* **36**, 1-60.
- Radashevsky, V.I. 1996. Morphology, ecology and asexual reproduction of a new *Polydorella* species (Polychaeta: Spionidae) from the South China Sea. *Bulletin of Marine Science* **58**, 684-693.
- Rainer, S.F. 1973. *Polydora* and related genera (Polychaeta: Spionidae) from Otago waters. *Journal of the Royal Society of New Zealand* **3**, 345-564.
- Ramberg, J.P. & Schram, T.A. 1982. A systematic review of the Oslofjord species of *Polydora* Bosc and *Pseudopolydora* Czerniavsky, with some new biological and ecological data (Polychaeta: Spionidae). *Sarsia* **68**, 233-247.
- Read, G.B. 1975. Systematics and biology of polydorid species (Polychaeta: Spionidae) from Wellington Harbour. *Journal of the Royal Society of New Zealand* **5**, 395-419.
- Reise, K. & Ax, P. 1979. A meiofaunal "thiobios" limited to the anaerobic sulfide system of marine sand does not exist. *Marine Biology* **54**, 225-237.
- Reish, D.J. 1957. The life history of the polychaetous annelid *Neanthes caudata* (delle Chiaje), including a summary of development in the family Nereidae. *Pacific Science* **11**, 216-228.
- Reiswig, H.M. 1973. Population dynamics of Jamaican Demospongiae. *Bulletin of Marine Science* **23**, 191-226.
- Rhode, K. 1981. The nature of parasitism. In *Australian Ecology Series: Ecology of marine parasites*, H. Heatwole (ed.), St. Lucia: University of Queensland Press, pp. 4-5.
- Ricketts, E.F., Calvin, J., Hedgpeth, J.W. & Phillips, D.W. 1985. *Between Pacific tides*. Stanford: Stanford University Press.
- Ricklefs, R.E. 1990. *Ecology*. New York: W.H. Freeman.
- Riser, N.W. 1982. Observations on some poorly known syllid polychaetes from the Gulf of Maine. *Canadian Journal of Zoology* **60**, 105-111.
- Rosell, D. 1996. Systematics, biology and ecology of Mediterranean excavating sponges. Doctoral Thesis, Universitat de Barcelona, Barcelona.
- Rosell, D. & Uriz, M.J. 1991. *Cliona viridis* (Schmidt, 1862) and *Cliona nigricans* (Schmidt, 1862) (Porifera, Hadromerida): Evidence which shows they are the same species. *Ophelia* **33**, 45-53.
- Rossi, M.M. 1984. A new genus and species of Iphitimid parasitic in an Aphroditid (Polychaeta), with an emendation of the family Iphitimidae. *Bulletin of the Southern California Academy of Sciences* **83**, 163-166.
- Rozbaczylo, N. & Cañete, J.I. 1993. A new species of scale-worm, *Harmothoe commensalis* (Polychaeta: Polynoidae), from mantle cavities of two Chilean clams. *Proceedings of the Biological Society of Washington* **106**, 666-672.
- Ruff, R.E. 1991. A new species of *Bathynoe* (Polychaeta: Polynoidae) from the Northeast Pacific Ocean commensal with two species of deep-water asteroids. *Ophelia* **5**, 219-230.
- Ruff, R.E. 1995. 3. Family Polynoidae Malmgren, 1867. In *Taxonomic atlas of the benthic fauna of the Santa Barbara Basin and western Santa Barbara Channel. Vol. 5 - The Annelida part 2. Polychaeta: Phyllodocida (Syllidae and scale-bearing families) Amphinomida and Eunicida*, J.A. Blake, B. Hilbig & P.H. Scott (eds.), Santa Barbara: Santa Barbara Museum of Natural

- History, pp. 105-166.
- Rullier, F. 1972. Annélides polychètes de Nouvelle-Calédonie recueillies par Y. Plessis et B. Salvat. *Expédition Française sur les Récifs Coralliens de la Nouvelle-Calédonie* **6**, 1-169.
- Rullier, F. 1974. Quelques annelides polychètes de Cuba recueillies dans des éponges. *Travaux du Muséum d'Histoire Naturelle Grigore Antipa* **14**, 9-77.
- Rullier, F. & Amoureux, L. 1979. Campagne de la Calypso au large des côtes Atlantiques de l'Amérique du Sud (1961-1962). I. 33. Annélides Polychètes. *Annales do Instituto de Oceanografia* **55**, 145-206.
- Rzhavsky, A.V. & Britayev, T.A. 1988. Specific features of colonies of *Circeis armoricana* (Spirorbidae, Polychaeta) on hermit crabs on the East Kamchatka coast. [In Russian]. *Zoologicheski Zhurnal* **61**, 17-22.
- Saint-Joseph, A.de 1888. Les Annelides polychètes des côtes de Dinard, pt. 2. *Annals of Scientia Naturae* **5**, 141-338.
- San Martín, G. 1984. Estudio biogeográfico, Faunístico y sistemático de los poliquetos de la familia sílidos (Syllidae, Polychaeta) en Baleares. Doctoral Thesis, Universidad Complutense.
- San Martín, G. & Sardá, R. 1986. Sobre la presencia de un Arabélido (Polychaeta: Arabellidae) parásito de Sílicos (Polychaeta: Syllidae), del género *Labrorostratus* en las costas españolas. *Boletín de la Real Sociedad Española de Historia Natural (Sección Biología)* **82**, 141-146.
- San Martín, G., Ibarzábal, D., Jiménez, M. & López, E. 1997. Redescription of *Haplosyllides floridana* Augener, 1924 (Polychaeta, Syllidae, Syllinae), with notes on morphological variability and comments on the generic status. *Bulletin of Marine Science* **60**, 364-370.
- Sardá, R. 1984. Estudio sobre los Poliquetos de las zonas mediolitoral e infralitoral de la región del Estrecho de Gibraltar. Doctoral Thesis, Universidad de Barcelona.
- Sato-Okoshi, W. & Okoshi, K. 1993. Microarchitecture of scallop and oyster shells infested with boring *Polydora*. *Nippon Suisan Gakkaishi* **59**, 1243-1247.
- Simon, J.L. 1967. Behavioral aspects of *Histriobdella homari*, an annelid commensal of the American lobster. *Biological Bulletin of the marine biological Laboratory, Woods Hole* **133**, 450.
- Simon, J.L. 1968. Incidence and behavior of *Histriobdella homari* (Annelida: Polychaeta), a commensal of the American lobster. *Bioscience* **18**, 35-36.
- Southern, R. 1914. Archannelida and Polychaeta, in Clare Island survey, pt. 47. *Proceedings of the Royal Irish Academy, Dublin* **31**, 1-160.
- Southward, E.C. 1956. On some polychaetes of the Isle of Man. *Annals and Magazine of Natural History* **12**, 257-279.
- Spies, R.B. 1977. Reproduction and larval development of *Flabelliderma commensalis* (Moore). In *Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman*, D.J. Reish & K. Fauchald (eds.), Los Angeles: The Allan Hancock Foundation, University of Southern California, pp. 323-345.
- Spooner, G.M., Wilson, D.P. & Trebble, N. 1957. Phylum Annelida. In *Plymouth Marine Fauna*, (), Plymouth: Marine Biological Association U.K., .
- Steinbeck, J. & Ricketts, E.F. 1941. *Sea of Cortez. A leisurely journal of travel and research. With a scientific appendix comprising materials for a source book on the marine animals of the Panamic faunal province*. New York: Viking Press.
- Stewart, W.C. 1970. A study of the nature of the attractant emitted by the asteroid host of the commensal polychaete *Ophiodromus pugettensis*. Dissertation, University of California.
- Stock, J.H. 1986. Cases of hyperassociation in the Copepoda (Herphyllobiidae and Nereicolidae). *Systematics and Parasitology* **8**, 71-81.
- Storch, V. & Niggemann, R. 1967. Auf Echinodermen lebende Polychaeten. *Kieler Meeresforschungen* **23**, 156-164.
- Storch, V. & Rosito, R.M. 1981. Polychaetes from interspecific associations found off Cebu. *The Philippine Scientist* **18**, 1-9.
- Storm, V. 1881. Bidrag til Kundskab om Thronhjemsfjordens Fauna III. *Kongelige Norske videnskabers selskabs skrifter* **1881**, 73-96.
- Thesunov, A.V., Britayev, T.A., Larionov, V.V., Khodkina, I.V. & Tzetlin, A.B. 1989. Notes on commensals of some crinoids from Maldivian coral reefs [In Russian]. In *Symbiosis among marine animals*, V.A. Sveshnicov (ed.), Moscow: A.N. Severtzov Institute, Russian Academy of Sciences, pp. 166-192.
- Thorson, G. 1949. Om eremit kraeften och dens kommensal *Nereis fucata*. *Svensk faunistisk revy* **11**, 93-98.
- Tkachuk, L.P. 1988. Vermins of the Black Sea mussel plantations. *Ekologika Morya* **30**, 60-64.

- Treadwell, A.L. 1909. *Haplosyllis cephalata* as an ectoparasite. *Bulletin of the American Museum of Natural History* **26**, 359-360.
- Treadwell, A.L. 1921. Leodicidae of the West Indian region. *Publications of the Carnegie Institut of Wasington* **15**, 1-13.
- Treadwell, A.L. 1940. A new genus and two new species of polychaetous annelids from Texas and one new species from the Philippine islands. *American Museum Novitates* **1089**, 1-4.
- Tsurumi, M. & Reiswig, M. 1997. Sexual versus asexual reproduction in an oviparous rope-form sponge, *Aplysina cauliformis* (Porifera, Verongida). *Invertebrate Reproduction and Development* **32**, 1-9.
- Tzetlin, A.B. 1985. *Asetocalamyzas laonicola* gen et sp. n., a new ectoparasitic polychaete from the White Sea [In Russian]. *Zoologicheski Zhurnal* **64**, 269-298.
- Tzetlin, A.B. & Britayev, T.A. 1985. A new species of Spionidae (Polychaeta) with asexual reproduction associated with sponges. *Zoologica Scripta* **14**, 177-181.
- Uchida, H. 1975. Ectocommensal polynoids (Annelida, Polychaeta) associated with the echinoderms. *Bulletin of the Marine Park Reservation Stations* **1**, 19-30.
- Uchida, H. 1978. Serpulid tube worms (Polychaeta, Sedentaria) from Japan with the systematic review of the group. *Bulletin of the Marine Park Reservation Stations* **2**, 1-98.
- Uebelacker, J.M. 1978. A new parasitic Polychaetous Annelid (Arabellidae) from the Bahamas. *Journal of Parasitology* **64**, 151-154.
- Uebelacker, J.M. 1982. *Haplosyllis agelas*, a new polychaetous annelid (Syllidae) from the Bahamas. *Bulletin of Marine Science* **32**, 856-861.
- Uriz, M.J. 1983. Monografia I. Contribución a la fauna de esponjas (Demospongia) de Catalunya. *Anales de la Sección de Ciencias del Colegio Universitario de Gerona* **7**, 1-220.
- Uschakov, P.V. 1950. Polychaetes from the Sea of Okothsk. [In Russian]. *Issledovaniya dal'nevostochnykh Morei SSSR* **2**, 140-236.
- Uschakov, P.V. 1955. Polychaetous annelids of the Far Eastern seas of the USSR [In Russian]. *Akademiya Nauk SSSR* **56**, 1-433.
- Uschakov, P.V. 1962. Polychaetous annelids of the family Phyllodocidae and Aphroditidae from the An tarctic and Subantarctic. [In Russian]. *Isseldovaniya Fauni Moorei* **1**, 129-189.
- Uschakov, P.V. 1982. *Fauna of the USSR. 2(1): Polychaetes. Polychaetes of the Suborder Aphroditiformia of the Arctic Ocean and the Northwestern Part of the Pacific, Families Aphroditidae and Polynoidae.* [In Russian]. Moscow: NAUKA, Academy of Sciences of the USSR, Zoological Institute.
- Uschakov, P.V. & Wu, B.L. 1959. The polychaetous annelids of the families Phyllodocidae and Aphroditidae from the Yellow Sea. [In Russian]. *Archives de l'Institut d'Océanologie Sinica* **1**, 1-40.
- Utinomi, H. 1956. On the so-called 'Umi-Utiwa' a peculiar flabellate gorgonacean, with notes on a syllidean polychaete commensal. *Publications of the Seto Marine Biological Laboratory* **5**, 243-250.
- Uzmann, J.R. 1967. *Histriobdella homari* (Annelida: Polychaeta) in the American lobster *Homarus americanus*. *Journal of Parasitology* **53**, 210-211.
- Verrill, A.E. 1881. New England Annelida. Part I. Historical sketch, with annotated lists of the species hitherto recorded. *Transactions of the Conneticut Academy of Arts and Sciences* **4**, 285-324.
- Vila, P.I. & Bahamonde, N. 1985. Two new species of *Stratiodrilus*, *S. aeglaphilus* and *S. pugnaxi* (Annelida: Histiobdellidae) from Chile. *Proceedings of the Biological Society of Washington* **98**, 347-350.
- Voultsiadou-Koukoura, E., Koukouras, A. & Eleftheriou, A. 1987. Macrofauna associated with the sponge *Verongia aerophoba* in the North Aegean Sea. *Estuarine, Coastal and shelf Science* **24**, 265-278.
- Wagner, R.H., Phillips, D.W., Standing, J.D. & Hand, C. 1979. Commensalism or mutualism: attraction of a sea star towards a symbiotic polychaete. *Journal of Experimental Marine Biology and Ecology* **39**, 205-210.
- Webster, H.E. 1879. The Annelida Chaetopoda of New Jersey. *Annual Reports of the New York State Museum of Natural History* **32**, 101-128.
- Webster, H.E. 1879. The Annelida Chaetopoda of the Virginian coast. *Transactions Albany Institute New York* **9**, 202-272.
- Webster, S.K. 1968. An investigation of the commensals of *Cryptochiton stellaris* (Middendorf, 1846) in the Monterey Peninsula area, California. *The Veliger* **11**, 121-125.
- Wesenberg-Lund, E. 1938. *Ophryotrocha gerionicola* (Bidenkap) (= *Eteonopsis geryonicola*

- Bidenkap) refound and redescribed. *Göteborgs K niglich vetenskaps- och vitterhetssamh lles handlingar, Series B* **6**, 1-13.
- Wesenberg-Lund, E. 1941. Notes on the Polychaeta I. 1. *Harmothoe bathydomus* Hj. Ditlevsen refound. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i K benhavn* **105**, 31-32.
- Westheide, W. 1982. *Microphthalmus hamosus* sp. n. (Polychaeta, Hesionidae)- an example of evolution leading from the interstitial fauna to a macrofaunal interspecific relationship. *Zoologica Scripta* **11**, 189-193.
- Westinga, E. & Hoetjes, P.C. 1981. The intrasponge fauna of *Speciospongia vesparia* (Porifera, Demospongiae) at Cura ao and Bonaire. *Marine Biology* **62**, 139-150.
- Wiley, A. 1905. Report on the Polychaeta collected by Professor Herdman, at Ceylon, in 1902. *Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar, with supplementary reports upon the Marine Biology of Ceylon, by Other Naturalists. Part IV supplementary report* **30**, 212-324.
- Wiren, A. 1886. *Haematocleptes terebellidis* nouvelle annelide parasite de la famille des euniciens. *Bihang Till K niglga Svenska Vetenskaps-Akademiens Handlingar* **11**, 1-10.
- Wright, J.D. & Woodwick, K.H. 1977. A new species of *Autolytus* (Polychaeta: Syllidae) commensal on a Californian hydrocoral. *Bulletin of the Southern California Academy of Sciences* **76**, 42-48.
- Wu, B.L., Sun, R.P. & Yang, D.J. 1982. On the occurrence of endoparasitic polychaetous annelids in Chinese waters. [In Chinese]. *Oceanologia et Limnologia Sinica* **13**, 201-204.
- Wu, B.L., Sun, R.P. & Yang, D.J. 1985. *Nereidae (Polychaetous Annelids) of the Chinese Coasts*. Berlin: China Ocean Press Beijing.
- Yamamoto, R. & Imajima, M. 1988. A new species of the genus *Spinther* (Polychaeta, Spintheridae) from Japan. *Bulletin of the National Science Museum of Tokyo, Series A* **11**, 129-135.
- Zibrowius, H., Southward, E.C. & Day, J.H. 1975. New observations on a little-known species of *Lumbrineris* (Polychaeta) living on various Cnidarians, with notes on its recent and fossil Scleractinian hosts. *Journal of the Marine biological Association of the United Kingdom* **55**, 83-108.
- Zottoli, R.A. & Carriker, M.R. 1974. Burrow morphology, tube formation and microarchitecture of shell dissolution by the spionid Polychaete *Polydora websteri*. *Marine Biology* **27**, 307-316.

Table 1.- List of commensal polychaete species (boring species excluded). TYPE: Type of relationship (O, obligatory; F, facultative).

COMMENSAL SPECIES	AUTHORITY	HOST GROUP	SPECIES	TYPE	SOURCE
AMPHYNOMIDAE					
<i>Hipponoe gaudichaudi</i>	Aldouin & M. Edwards	Cirriped	<i>Lepas anatifera</i>	O	Paris 1955
“		Cirriped	<i>Lepas anserifera</i>	O	Britayev & Memmy 1989
“		Cirriped	<i>Lepas pectinata</i>	O	Pettibone 1963
“		Cirriped	<i>Lepas</i> sp.	O	Okuda 1950, Day 1967, Nuñez et al. 1991
“		Cirriped	<i>Dosima fascicularis</i>	O	Britayev & Memmy 1989
<i>Benthoscolex cubanus</i>	Hartman	Echinoid	<i>Archeopneustes hystrix</i>	O	Hartman 1942, Emson et al. 1993
<i>Paramphinome pulchella</i>	Sars	Sponge	Unidentified	F	Pettibone 1963
ANTONBRUUNIDAE					
<i>Antonbruunia viridis</i>	Hartman & Boss	Bivalve	<i>Lucinia fosteri</i>	O	Hartman & Boss 1965
OENONIDAE					
<i>Oenone diphyllidis</i>		Sponge	<i>Speciospongia vespera</i>	O	Pearse 1932
CAPITELLIDAE					
<i>Capitella capitata</i>	Fabricius	Decapod	<i>Pinnixia fava</i>	F	Clark 1956
“		Bivalve	<i>Schizothaeus capax</i>	F	Clark 1956
CTENODRILIDAE					
<i>Ctenodrilus serratus</i>	Schmidt	Echinoid	<i>Centrostephanus coronatus</i>	F	Fauchald & Jumars 1979
“		Echinoid	<i>Strongylocentrotus franciscanus</i>	F	Fauchald & Jumars 1979
<i>Ctenodrilus</i> sp.		Holothuroid	<i>Leptosinapta inhaerens</i>	F	Barel & Kramers 1977
“		Holothuroid	<i>Labidoplax digitata</i>	F	Barel & Kramers 1977
“		Holothuroid	<i>Holothuria tubulosa</i>	F	Barel & Kramers 1977
DORVILLEIDAE					
<i>Dorvillea pseudorubrovittata</i>	Berkeley	Polychaete	<i>Phyllochaetopterus prolifica</i>	?	Petersen & Britayev 1997
<i>Ophryotrocha geryonicola</i>	(Esmark)	Decapod	<i>Cancer borealis</i>	O	Wesener-Lund 1938, Gaston & Benner 1981, Pfannestiel et al. 1982
“		Decapod	<i>Geryon quinquedens</i>	O	Gaston & Benner 1981
“		Decapod	<i>Geryon tridens</i>	O	Gaston & Benner 1981
<i>Ophryotrocha mediterranea</i>	Martin, Abelló & Cartes	Decapod	<i>Geryon longipes</i>	O	Desportes et al. 1977, Mori & Belloni 1985, Martin et al. 1991
<i>Ophryotrocha puerilis</i>	Claparede & Metschnikov	Holothuroid	<i>Cucumaria planci</i>	F	Monticelli 1892, Barel & Kramers 1977, Jangoux 1987
EULEPTHIDAE					
<i>Grubeulepis geayi</i>	(Fauvel)	Polychaete	<i>Polyodontes melanotus</i>	F	Day 1962, Pettibone 1969e
EUNICIDAE					
<i>Eunice antennata</i> ?	(Savigny)	Cnidarian	Unidentified Coral	F	Gardiner 1976
<i>Eunice filamentosa</i>	Grube	Sponge	Unidentified (small)	F?	Treadwell 1921
<i>Eunice norvergica</i>	Linnaeus	Cnidarian	<i>Lophelia pertusa</i>	F	Britayev 1981
“		Cnidarian	<i>Madrepora oculata</i>	F	Britayev 1981

<i>Eunice harassii</i>	Aldouin & M. Edwards	Bivalve	<i>Ostrea edulis</i>	F	Gravier 1900
<i>Eunice marovoi</i>	Gibbs	Gastropod	<i>Cerithium vertagus</i>	F	Gibbs 1969, 1971
<i>Eunice pennata</i>	(O.F. Muller)	Cnidarian	<i>Madrepora pertusa</i>	F	Fauchald 1992
“		Cnidarian	Madreporid Coral	F	Fauvel 1923
FAUVELOPSIDAE					
<i>Fauvelopsis olgae</i>	Hartmann-Schröder	Foraminifer	<i>Bathysiphon rusticum</i>	O	Hartmann-Schröder 1983
FLABELLIGERIDAE					
<i>Flabelligera affinis</i>	Sars	Echinoid	<i>Echinus acutus</i>	F	Barel & Kramers 1977
“		Echinoid	<i>Echinus esculentus</i>	F	Fauvel 1923, Clark 1956, Barel & Kramers 1977
“		Echinoid	<i>Psammechinus miliaris</i>	F	Barel & Kramers 1977
<i>Flabelliderma commensalis</i>	(Moore)	Echinoid	<i>Centrostephanus coronatus</i>	O	Spies 1977, Fauchald & Jumars 1979
“		Echinoid	<i>Strongylocentrotus purpuratus</i>	O	Clark 1956
<i>Phalacrostemma cidariophilum</i>	Marenzeller	Echinoid	<i>Cidaris cidaris</i>	O	Marenzeller 1895, Bellan 1964
HISTRIOBDELLIDAE					
<i>Histriobdella homari</i>	Van Beneden	Decapod	<i>Homarus americanus</i>	O	Uzmann 1967, Simon 1967, 1968, Jennings & Gelder 1976, Brettey & Campbell 1985
“		Decapod	<i>Homarus vulgaris</i>	O	Moyano et al. 1993
<i>Stratiodrilus aeglyphilus</i>	Vila & Bahamonde	Decapod	<i>Aegla laevis talcahuano</i>	O	Vila & Bahamonde 1985, Moyano et al. 1993
<i>Stratiodrilus haswelli</i>	Harrison	Decapod	<i>Astacoides madagascariensis</i>	O	Harrison 1928
<i>Stratiodrilus novaehollandiae</i>	Haswell	Decapod	<i>Cherax dispar</i>	O	Moyano et al. 1993
“		Decapod	<i>Cherax punctatus</i>	O	Moyano et al. 1993
<i>Stratiodrilus platensis</i>	Cordero	Decapod	<i>Aegla abtao</i>	O	Gacitua 1992 in Moyano et al. 1993
“		Decapod	<i>Aegla bahamondei</i>	O	Gacitua 1992 in Moyano et al. 1993
“		Decapod	<i>Aegla laevis laevis</i>	O	Cordero 1927
<i>Stratiodrilus pugnaxi</i>	Vila & Bahamonde	Decapod	<i>Parastacus pugnax</i>	O	Vila & Bahamonde 1985, Moyano et al. 1993
<i>Stratiodrilus tasmanicus</i>	Haswell	Decapod	<i>Astacopsis franklinii</i>	O	Haswell 1900, Harrison 1928
<i>Stratiodrilus cirolanae</i>	Führ	Isopod	<i>Cirolana venusticauda</i> var. <i>simplex</i>	O	Führ 1971
<i>Stratiodrilus</i> sp.		Decapod	Unknown	O	Moyano et al. 1993
HESIONIDAE					
<i>Gyptis brevipalpa</i>	Hartmann-Schröder	Polychaete	<i>Glycera robusta</i>	F	Gardiner 1976
“		Holothuroid	<i>Leptosynapta tenuis</i>	F	Gardiner 1976
<i>Gyptis ophiocomae</i>	Storch & Niggemann	Ophiuroid	<i>Ophiocoma scolopendrina</i>	O	Storch & Niggemann 1967
<i>Gyptis vittata</i>	Webster & Benedict	Polychaete	<i>Notomastus lobatus</i>	?	Pettibone 1963, Gardiner 1976
<i>Hesionella maccullochae</i>	Hartman	Polychaete	<i>Lumbrineris brevicirra</i>	F	Hartman 1941
<i>Microphthalmus aberrans</i>	Webster & Benedict	Polychaete	<i>Lysilla alba</i>	F	Pettibone 1963
“		Polychaete	<i>Enoplobranchus sanguineus</i>	F	Pettibone 1963
<i>Microphthalmus hamosus</i>	Westheide	Sipunculid	<i>Sipunculus nudus</i>	F	Westheide 1982
<i>Microphthalmus szcelkowi</i>	Meckzniov	Polychaete	<i>Arenicola marina</i>	F	Reise & Ax 1979
<i>Ophiodromus angusdtifrons</i>	(Grube)	Asteroid	<i>Pentaceros hedemanni</i>	O	Jones 1964
<i>Ophiodromus flexuosus</i>	(Delle Chiaje)	Asteroid	<i>Astropecten aranciacus</i>	F	Barel & Kramers 1977
“		Asteroid	<i>Astropecten bispinosus</i>	F	Barel & Kramers 1977

“		Asteroid	<i>Astropecten platyacanthus</i>	F	Barel & Kramers 1977
“		Asteroid	<i>Astropecten irregularis</i>	F	Barel & Kramers 1977
“		Asteroid	<i>Louidia ciliaris</i>	F	Barel & Kramers 1977
“		Balanoglossid	<i>Balanoglossus</i> sp.	F	Clark 1956
“		Holothuroid	<i>Leptosynapta</i> sp.	F	Barel & Kramers 1977
“		Polychaete	<i>Amphitrite edwardsi</i>	F	Barel & Kramers 1977
“		Polychaete	<i>Euclymene lumbricoides</i>	F	Barel & Kramers 1977
<i>Ophiodromus obscurus</i>	Verrill	Polychaete	<i>Lysilla alba</i>	F	Pettibone 1963
“		Echinoid	<i>Lytechinus</i> sp.	F	Hartman 1951
“		Holothuroid	<i>Thyone</i> sp.	F	Pettibone 1963
<i>Ophiodromus pugettiensis</i>	(Johnson)	Asteroid	<i>Patiria miniata</i>	F	Bartel & Davenport 1956, Davenport et al. 1960, Lande & Reish 1968, Ricketts et al. 1985
“		Asteroid	<i>Louidia foliolata</i>	F	Davenport et al. 1960
“		Asteroid	<i>Louidia magnifica</i>	F	Storch & Rosito 1981
“		Asteroid	<i>Pteraster tessellatus</i>	F	Storch & Niggemann 1967
“		Asteroid	<i>Orcaster occidentalis</i>	F	Steinbeck & Ricketts 1941
“		Asteroid	<i>Pisaster ochraceus</i>	F	Davenport & Hickok 1957, Hickok & Davenport 1957
“		Asteroid	<i>Petalaster foliolata</i>	F	Stewart 1970, Hilbig 1994
“		Holothuroid	<i>Protankyra bidentata</i>	F	Okuda 1936a
“		Decapod	<i>Eupagurus</i> sp.	F	Hickok & Davenport 1957
“		Gastropod	<i>Aletes</i> sp.	F	Storch & Niggeman 1967
“		Bivalve	<i>Chama</i> sp.	F	Storch & Niggeman 1967
“		Echinoid	<i>Clipeaster humilis</i>	F	Storch & Niggeman 1967
<i>Parahesione luteola</i>	(Webster)	Decapod	<i>Upogebia affinis</i>	F	Pettibone 1956
<i>Parasyllidea humesi</i>	Pettibone	Bivalve	<i>Tellina nimphalis</i>	O	Pettibone 1961
IPHYTIMIDAE					
<i>Iphitime cuenoti</i>	Fauvel	Decapod	<i>Liocarcinus depurator</i>	O	Fage & Legendre 1925, 1933, Abelló 1985, Belloni & Mori 1985, Abelló et al. 1988, Comely & Ansell 1889
“					
“		Decapod	<i>Liocarcinus corrugatus</i>	O	Comely & Ansell 1989
“		Decapod	<i>Liocarcinus puber</i>	O	Comely & Ansell 1989
“		Decapod	<i>Carcinus maenas</i>	O	Comely & Ansell 1989
“		Decapod	<i>Cancer pagurus</i>	O	Comely & Ansell 1989
“		Decapod	<i>Hyas araneus</i>	O	Comely & Ansell 1989
“		Decapod	<i>Inachus dorsettensis</i>	O	Comely & Ansell 1989
“		Decapod	<i>Macropipus tuberculatus</i>	O	Abelló 1985, Mori & Belloni 1985, Abelló et al. 1988
“		Decapod	<i>Goneplax rhomboides</i>	O	Fage & Legendre 1925, 1933, Abelló et al. 1988
“		Decapod	<i>Macropodia tenuirostris</i>	O	Fage & Legendre 1927, 1934, Hartnoll 1952
“		Decapod	<i>Maia squinado</i>	O	Fauvel 1914
<i>Iphitime dorderleini</i>	Marenzeller	Decapod	<i>Macrocheria kaempferi</i>	O	Marenzeller 1902
<i>Iphitime hartmanae</i>	Kirkegaard	Decapod	<i>Hyas araneus</i>	O	Kirkegaard 1977
“		Decapod	<i>Hyas coarctatus</i>	O	Kirkegaard 1977
<i>Iphitime holobranchiata</i>	Pilger	Decapod	<i>Cancer antennarius</i>	O	Pilger 1971
<i>Iphitime loxorhynchii</i>	Hertman	Decapod	<i>Loxorhynchus grandis</i>	O	Hartman 1952
<i>Iphitime paguri</i>	Fage & Legendre	Decapod	<i>Eupagurus bernhardus</i>	O	Fage & Legendre 1933, Moore & Gorzula 1973, Comely &

“		Decapod	<i>Eupagurus prideauxi</i>	O	Ansell 1989
<i>Iphitime sartoral</i>	Paiva & Nonato	Decapod	<i>Libinia spinosa</i>	O	Spooner et al. 1957, Comely & Ansell 1989
“		Decapod	<i>Portunus spinicarpus</i>	O	Paiva & Nonato 1991
LUMBRINERIDAE					
<i>Lumbrineris flavellicola</i>	(Fage)	Cnidarian	<i>Acoanthocyathus spiniger</i>	O	Miura & Shirayama 1992
“		Cnidarian	<i>Balanophyllia cellulosa</i>	O	Zibrowius et al. 1975
“		Cnidarian	<i>Balanophyllia</i> sp.	O	Zibrowius et al. 1975
“		Cnidarian	<i>Cariophyllia sarsiae</i>	O	Zibrowius et al. 1975
“		Cnidarian	<i>Cariophyllia smithi</i>	O	Zibrowius et al. 1975
“		Cnidarian	<i>Cariophyllia</i> sp.	O	Zibrowius et al. 1975
“		Cnidarian	<i>Ceratotrochus duodecimcostatus</i>		Zibrowius et al. 1975
“		Cnidarian	<i>Dendrophyllia cornigera</i>	O	Zibrowius et al. 1975
“		Cnidarian	<i>Dendrophyllia cornucopia</i>	O	Zibrowius et al. 1975
“		Cnidarian	<i>Desmophyllum cristagalli</i>	O	Zibrowius et al. 1975
“		Cnidarian	<i>Flavallium majus</i>	O	Zibrowius et al. 1975
“		Cnidarian	<i>Flavellium avicola</i>	O	Zibrowius et al. 1975
“		Cnidarian	<i>Flavellium chumi</i>	O	Marenzeller 1904, Fage 1936, Zibrowius et al. 1975
“		Cnidarian	<i>Flavellium fornasinii</i>	O	Zibrowius et al. 1975
“		Cnidarian	<i>Flavellium inconstans</i>	O	Zibrowius et al. 1975
“		Cnidarian	<i>Flavellium pavonium</i>	O	Zibrowius et al. 1975
“		Cnidarian	Unidentified Hydroids	O	Zibrowius et al. 1975
“		Cnidarian	Scleractinian Coral		Miura & Shirayama 1992
“		Cnidarian	<i>Stephanocyantus mosseleyanus</i>	O	Zibrowius et al. 1975
“		Cnidarian	Zoantharian	O	Zibrowius et al. 1975
<i>Lumbrineris coccinea</i>	(Renier)	Cnidarian	Unidentified Coral	F	Gardiner 1976
NAUTILINIELLIDAE					
<i>Flascarpia alvinae</i>	Blake	Bivalve	Unidentified	?	Blake 1993
<i>Laubierus mucronatus</i>	Blake	Bivalve	Unidentified Mytilid	O	Blake 1993
<i>Mytilidiphila enseiensis</i>	Miura & Hasimoto	Bivalve	Unidentified Mytilid	O	Miura & Hashimoto 1993
<i>Mytilidiphila okinawaensis</i>	Miura & Hasimoto	Bivalve	Unidentified Mytilid	O	Miura & Hashimoto 1993
<i>Natsushima bifurcata</i>	Miura & Laubier	Bivalve	<i>Solemya</i> sp.	O	Miura & Laubier 1990
<i>Nautiliniella caliptogenicola</i>	Miura & Laubier	Bivalve	<i>Calyptogena phaseoliformis</i>	O	Miura & Laubier 1989, 1990
<i>Petrecca thyasira</i>	Blake	Bivalve	<i>Thyasira insignis</i>	O	Blake 1990
<i>Shinkai longipedata</i>	Miura & Ohta	Bivalve	<i>Calyptogena</i> sp.	O	Miura & Ohta 1991
<i>Shinkai sagamiensis</i>	Miura & Laubier	Bivalve	<i>Calyptogena soyoae</i>	O	Miura & Laubier 1990
NEREIDAE					
<i>Cheilonereis cyclurus</i>	(Harrington)	Decapod	<i>Pagurus armatus</i>	O	Harrington 1897, Clark 1956, Hickok & Davenport 1957
“		Decapod	<i>Pagurus branchiomastus</i>	O	Buzhinskaja 1967
“		Decapod	<i>Pagurus ochotoensis</i>	O	Buzhinskaja 1967, Wu et al. 1985
“		Decapod	<i>Pagurus</i> sp.	O	Okuda 1950
<i>Nereis acuminata</i>	Ehlers	Decapod	<i>Clibanarius vittatus</i>	F	Gardiner 1976
<i>Nereis fucata</i>	Savigny	Decapod	<i>Anapagurus laevis</i>	O	Spooner et al. 1957
“		Decapod	<i>Eupagurus bernhardus</i>	O	Spooner et al. 1957, Clark 1956, Gilpin-Brown 1969,

					Jensen & Bender, 1973, Goerke 1971
“		Decapod	<i>Pagurus cuanensis</i>	O	Spooner et al. 1957
“		Decapod	<i>Pagurus prideauxi</i>	O	Clark 1956, Spooner et al. 1957
“		Decapod	<i>Pagurus variabilis</i>	O	Gilpin-Brown 1969
<i>Nereis grayi</i>	Pettibone	Polychaete	<i>Asychis elongatus</i>	O	Pettibone 1982
<i>Perinereis cultrifera</i>	(Grube)	Bivalve	<i>Pteria martensi</i>	F	Okuda 1950
CHRY SOPETALIDAE					
<i>Bhawania goodei</i>	Webster	Sipunculid	<i>Aspidosiphon elegans</i>	F	Gibbs 1969
“		Sipunculid	<i>Cleosiphon aspergillum</i>	F	Gibbs 1969
“		Sipunculid	<i>Phascolosoma albolineatum</i>	F	Gibbs 1969
<i>Bhawania potsiana</i>	(Horst)	Polychaete	<i>Eurithoe complanata</i>	F	Gibbs 1969, 1971
PILARGIDAE					
<i>Ancistrosyllis commensalis</i>	Gardiner	Polychaete	<i>Notomastus lobatus</i>	O	Gardiner 1976
<i>Ancistrosyllis groenlandica</i>	McIntosh	Holothuroid	<i>Molpadia</i> sp.	F	Ganapati & Radhakrishna 1962
<i>Pilargis berkeleyae</i>	Monro	Polychaete	<i>Chaetopterus cautus</i>	F	Buzinskaja et al. 1980, Britayev 1993, Petersen & Britayev 1997
PHYLLODOCIDAE					
<i>Mystides bathysiphonicola</i>	Hartmann-Schröder	Foraminifer	<i>Bathisiphon rusticum</i>	O	Hartmann-Schröder 1983
“		Foraminifer	<i>Bathisiphon</i> sp.	O	Hartmann-Schröder 1983
“		Foraminifer	<i>Hormosina normani</i>	O	Hartmann-Schröder 1983
<i>Protomystides hatsushimensis</i>	Miura	Vetimentiferan	Unidentified	O	Miura 1988
POLYNOIDAE					
<i>Acholoe astericola</i>	(Delle Chiaje)	Asteroid	<i>Astropecten aranciatus</i>	O	Barel & Kramers 1977, D. Martin personal observations
“		Asteroid	<i>Astropecten bispinosus</i>	O	Marenzeller 1874
“		Asteroid	<i>Astropecten hupferi</i>	O	Pettibone 1996
“		Asteroid	<i>Astropecten irregularis</i>	O	McIntosh 1900, Cuenot 1912, Davenport 1953a, Barel & Kramers 1977
“		Asteroid	<i>Astropecten pentacanthus</i>	O	Pettibone 1996
“		Asteroid	<i>Astropecten platyacanthus</i>	O	Barel & Kramers 1977
“		Asteroid	<i>Astropecten</i> sp.	O	Barel & Kramers 1977
“		Asteroid	<i>Louidia ciliaris</i>	O	Davenport 1953a, 1954, Barel & Kramers 1977
<i>Adyte assimilis</i>	(McIntosh)	Echinoid	<i>Echinus esculentus</i>	F	McIntosh 1900, Pettibone 1969a, Barel & Kramers 1977, Comely & Ansell 1988
“		Echinoid	<i>Echinus acutus</i>	F	Barel & Kramers 1977
<i>Alentiana aurantiaca</i>	(Verril)	Cnidarian	<i>Bolocera tuediae</i>	F	Pettibone 1963
<i>Antinoella sarsi</i>	(Malmgren)	Echinoid	<i>Spatangus purpureus</i>	F	Barel & Kramers 1977
<i>Antipathipolyeunoa nuttingi</i>	Pettibone	Cnidarian	<i>Antipathes tanacetum</i>	O	Pettibone 1991b
<i>Arcteobia anticostiensis</i>	(McIntosh)	Polychaete	<i>Pista flexuosa</i>	F	Pettibone 1954, 1963
“		Polychaete	Unidentified Maldanid	F	Pettibone 1954, 1963
<i>Arctonoe fragilis</i>	(Baird)	Asteroid	<i>Evasterias troschelii</i>	O	Davenport & Hickok 1951, Britayev 1991, Ruff 1995
“		Asteroid	<i>Leptasterias aequalis</i>	O	Britayev 1991
“		Asteroid	<i>Leptasterias hexactis</i>	O	Britayev 1991
“		Asteroid	<i>Loidia foliolata</i>	O	Ruff 1995
“		Asteroid	<i>Orthasterias koehleri</i>	O	Britayev 1991

“		Asteroid	<i>Pisaster giganteus</i>	O	Hanley 1989
“		Asteroid	<i>Pisaster ochraceus</i>	O	Britayev 1991
“		Asteroid	<i>Solaster dawsoni</i>	O	Britayev 1991
“		Asteroid	<i>Stylasterias forreri</i>	O	Britayev 1991
<i>Arctonoe pulchra</i>	(Johnson)	Asteroid	<i>Dermasterias imbricata</i>	O	Britayev 1991
“		Asteroid	<i>Louidia foliolata</i>	O	Britayev 1991
“		Asteroid	<i>Pteraster tessellatus</i>	O	Britayev 1991
“		Asteroid	<i>Solaster stimpsoni</i>	O	Britayev 1991
“		Gastropod	<i>Megathura crenulata</i>	O	Britayev 1991
“		Holothuroid	<i>Stichopus californicus</i>	O	Davenport & Hickok 1951, Britayev 1991
“		Holothuroid	<i>Stichopus parvimensis</i>	O	Davenport 1950, Britayev 1991
“		Polychaete	<i>Loimia montagui</i> ?medusa?	O	Britayev 1991, Ruff 1995
“		Polyplacophor	<i>Cryptochiton stelleri</i>	O	Britayev 1991
<i>Arctonoe vittata</i>	(Grube)	Asteroid	<i>Aphelasterias japonica</i>	O	Britayev 1991
“		Asteroid	<i>Asterias amurensis</i>	O	Okuda 1936b, Britayev 1991
“		Asteroid	<i>Asterias rathbunae</i>	O	Britayev et al. 1989, Britayev 1991
“		Asteroid	<i>Crossaster papposus</i>	O	Britayev 1991
“		Asteroid	<i>Dermasterias imbricata</i>	O	Pettibone 1953, Wagner et al. 1979, Britayev 1991, Ruff 1995
“		Asteroid	<i>Evasterias echinosoma</i>	O	Britayev 1991
“		Asteroid	<i>Henricia leviuscula</i>	O	Britayev 1991
“		Asteroid	<i>Leptasterias camtchatica</i>	O	Britayev 1991
“		Asteroid	<i>Louidia foliolata</i>	O	Britayev 1991
“		Asteroid	<i>Pteraster tessellatus</i>	O	Britayev 1991
“		Asteroid	<i>Solaster dawsoni</i>	O	Britayev 1991
“		Asteroid	<i>Solaster endeca</i>	O	Britayev 1991
“		Asteroid	<i>Solaster papposus</i>	O	Barel & Kramers 1977
“		Asteroid	<i>Solaster stimpsoni</i>	O	Britayev 1991
“		Cnidarian	<i>Metridium senile</i>	O	Britayev 1991
“		Echinoid	<i>Cidarina cidaris</i>	O	Britayev 1991
“		Gastropod	<i>Acmaea mitra</i>	O	Britayev 1991
“		Gastropod	<i>Acmaea pallida</i>	O	Britayev 1991
“		Gastropod	<i>Diodora aspera</i>	O	Pettibone 1953, Gerber & Stout 1968, Dimock & Dimock 1969
“		Gastropod	<i>Diodora aspera</i>	O	Hanley 1989, Britayev 1991, Ruff 1995
“		Gastropod	<i>Haliotis kamchatkana</i>	O	Okuda 1936b, Britayev 1991
“		Gastropod	<i>Patelloida</i> sp.	O	Okuda 1936b
“		Gastropod	<i>Puncturella cucullata</i>	O	Britayev 1991
“		Gastropod	<i>Puncturella multistriata</i>	O	Britayev 1991
“		Holothuroid	<i>Parastichopus californicus</i>	O	Britayev 1991
“		Holothuroid	<i>Stychopus japonicus</i>	O	Britayev 1991
“		Polychaete	<i>Neoamphitrite robusta</i>	O	Pettibone 1953, Britayev 1991
“		Polychaete	<i>Neoamphitrite</i> sp.	O	Britayev 1991
“		Polychaete	<i>Thelepus crispus</i>	O	Pettibone 1953, Britayev 1991
“		Polyplacophor	<i>Cryptochiton stelleri</i>	O	Webster 1968, Britayev 1991, Ruff 1995

<i>Asterophyllia carlae</i>	Hanley	Asteroid	<i>Culcita novaeguineae</i>	O	T.A. Britayev personal observations
“		Asteroid	<i>Linckia laevigater</i>	O	Hanley 1989
“		Asteroid	<i>Protoreaster nodosus</i>	O	T.A. Britayev personal observations
“		Asteroid	Unidentified	O	Hanley 1989
“		Crinoid	Unidentified	O	T.A. Britayev personal observations
<i>Australaugenira michelseni</i>	Pettibone	Cnidarian	Unidentified Alcyonarian	F	Pettibone 1969a
“		Cnidarian	Unidentified Gorgonian	F	Pettibone 1969a
<i>Australaugenira pottsii</i>	(Potts)	Cnidarian	Unidentified Gorgonian	O	Pettibone 1969a, 1969d
<i>Australaugenira rutilans</i>	(Grube)	Cnidarian	<i>Xenia</i> sp.	F	Okuda 1950, Pettibone 1969a
<i>Bathynoe cascadiensis</i>	Ruff	Asteroid	<i>Astrocles actinodetus</i>	O	Ruff 1991
“		Asteroid	<i>Astrolirus panamensis</i>	O	Ruff 1991
<i>Bathynoe tuberculata</i>	(Treadwell)	Asteroid	<i>Brisinga alberti</i>	O	Hanley 1989, Ruff 1991
<i>Bayerpolynoe floridensis</i>	Pettibone	Cnidarian	<i>Antipathes columnaris</i>	O	Pettibone 1991b
<i>Benhamipolynoe</i>	(Benham)	Cnidarian	<i>Paranthipathes tenuispina</i>	O	Pettibone 1970, 1989a
<i>anthipathicola</i>					
“		Cnidarian	<i>Antipathes columnaris</i>	O	Pettibone 1970, 1989a
“		Polychaete	Unidentified Eunicid	O	Pettibone 1970
<i>Benhamipolynoe cairnsi</i>	Pettibone	Cnidarian	<i>Conopora adeta</i>	O	Pettibone 1989a, Hanley & Burke 1991b
<i>Branchipolynoe seepensis</i>	Pettibone	Bivalve	Unidentified Mytilid	O	Pettibone 1986a
<i>Branchipolynoe</i>	Pettibone	Bivalve	<i>Bathymodiolus</i>	O	Pettibone 1984a
<i>symmitylida</i>			<i>thermophilus</i>		
<i>Branchipolynoe pettiboneae</i>	Miura & Hashimoto	Bivalve	<i>Adula</i> sp.	O	Miura & Hashimoto 1991
“		Bivalve	<i>Bathymodiolus</i> sp.	O	Miura & Hashimoto 1991
<i>Brychionoe karenae</i>	Hanley & Burke	Cnidarian	<i>Leiopathes</i> sp.	O	Hanley & Burke 1991a
<i>Capitulatinoe cupisetis</i>	Hanley & Burke	Asteroid	<i>Astropecten granulatus</i>	O	Hanley & Burke 1989
<i>Disconatis accolus</i>	(Estcourt)	Polychaete	<i>Abarenicola affinis</i>	O	Hanley & Burke 1988
<i>Disconatis contubernalis</i>	Hanley & Burke	Polychaete	Unidentified Maldanid	O	Hanley & Burke 1988
<i>Enipo gracilis</i>	Verrill	Polychaete	<i>Nicomache lumbricalis</i>	F	Berkeley & Berkeley 1942, Pettibone 1953, 1954
<i>Eunoe bathydomus</i>	Ditlevsen	Holothuroid	<i>Bathyploetes natans</i>	O	Wesenberg-Lund 1941
<i>Eunoe depressa</i>	Moore	Decapod	Unidentified Pagurid	F	Moore 1905, 1908
“		Decapod	<i>Paralithodes kamtchatica</i>	F	Hartman 1948
<i>Eunoe laetmogonensis</i>	Kirkegaard & Billet	Holothuroid	<i>Laetmogone violacea</i>	O	Kirkegaard & Billett 1980
<i>Gastrolepidia clavigera</i>	Schmarda	Holothuroid	<i>Actinopyga echinites</i>	O	T.A. Britayev personal observations
“		Holothuroid	<i>Actinopyga mauritana</i>	O	J.R. Hanley personal communication
“		Holothuroid	<i>Actinopyga</i> sp.	O	Potts 1910
“		Holothuroid	<i>Bohadschia argus</i>	O	Gibbs 1969, Hanley 1989
“		Holothuroid	<i>Bohadschia graffei</i>	O	Gibbs 1969, T.A. Britayev personal observations
“		Holothuroid	<i>Holothuria atra</i>	O	Day 1967, Gibbs 1969, Hanley 1989
“		Holothuroid	<i>Holothuria edulis</i>	O	J.R. Hanley personal communication
“		Holothuroid	<i>Holothuria gyrifer</i>	O	Hartman 1954
“		Holothuroid	<i>Holothuria leucospilota</i>	O	T.A. Britayev personal observations
“		Holothuroid	<i>Holothuria maculata</i>	O	Potts 1910
“		Holothuroid	<i>Holothuria scabra</i>	O	J.R. Hanley personal communication
“		Holothuroid	<i>Microthele axiologa</i>	O	J.R. Hanley personal communication
“		Holothuroid	<i>Microthele nobilis</i>	O	J.R. Hanley personal communication

“		Holothuroid	<i>Stichopus chloronotus</i>	O	Gibbs 1971, T.A. Britayev personal observations
“		Holothuroid	<i>Stichopus hermeni</i>	O	Hanley 1989
“		Holothuroid	<i>Stichopus horrens</i>	O	Hartman 1954
“		Holothuroid	<i>Stichopus mollis</i>	O	Hanley 1993
“		Holothuroid	<i>Stichopus variegatus</i>	O	Hanley 1989
“		Holothuroid	<i>Thelenota ananas</i>	O	Gibbs 1969
“		Holothuroid	<i>Thelenota anax</i>	O	J.R. Hanley personal communication
<i>Gattyana cirrosa</i>	(Pallas)	Polychaete	<i>Amphitrite edwardsi</i>	F	Bellan 1959
“		Polychaete	<i>Amphitrite johnstoni</i>	F	McIntosh 1900, Orton & Smith 1936, Pettibone 1955, 1963, Bellan 1959
“		Polychaete	<i>Arenicola</i> sp.	F	McIntosh 1900, Newell 1954, Pettibone 1955, 1963
“		Polychaete	<i>Chaetopterus sarsii</i>	F	Storm 1881
“		Polychaete	<i>Chaetopterus</i>	F	Euders 1905, Paris 1955
“		Polychaete	<i>pergamentaceus</i>		
“		Polychaete	<i>Chaetopterus variopedatus</i>	F	Southern 1914, Southward 1956, Bellan 1959, Mettam 1980
<i>Gattyana aff. cirrosa</i>		Polychaete	<i>Chaetopterus</i> sp. n. Peters.	?	Petersen & Britayev 1997
<i>Gattyana mossambica</i>	Day	Polychaete	<i>Eunice tubifex</i>	F	Day 1960
<i>Gaudichaudius cimex</i>	(Quatrefages)	Decapod	<i>Diogenes custos</i>	O	Pettibone 1986b, Achari 1977
“		Decapod	<i>Diogenes diogenes</i>	O	Pettibone 1986b, Achari 1977
<i>Gorgoniapolynoe bayeri</i>	Pettibone	Cnidarian	<i>Narella clavata</i>	O	Pettibone 1991a
<i>Gorgoniapolynoe caeciliae</i>	(Fauvel)	Cnidarian	<i>Acanthogorgia aspera</i>	O	Pettibone 1991a
“		Cnidarian	<i>Candidella imbricata</i>	O	Pettibone 1991a
“		Cnidarian	<i>Corallium jonhsoni</i>	O	Fauvel 1913
“		Cnidarian	<i>Corallium niobe</i>	O	Hartmann-Schröder 1985, Pettibone 1991a
“		Cnidarian	<i>Corallium tricolor</i>	O	Hartmann-Schröder 1985
“		Cnidarian	<i>Pleurocorallium johnstoni</i>	O	Fauvel 1913, Hartmann-Schröder 1985, Pettibone 1991a
<i>Gorgoniapolynoe cairnsi</i>	Pettibone	Cnidarian	<i>Allopora eguchii</i>	O	Pettibone 1991a
<i>Gorgoniapolynoe corralophyla</i>	(Day)	Cnidarian	<i>Allopora bithalamus</i>	O	Day 1967
“		Cnidarian	<i>Stylaster</i> sp.	O	Stock 1986
“		Cnidarian	<i>Conopora</i> sp.	O	Stock 1986
“		Cnidarian	<i>Cryptohelia</i> sp.	O	Stock 1986
<i>Gorgoniapolynoe galapagensis</i>	Pettibone	Cnidarian	<i>Narella ambigua</i>	O	Pettibone 1991a
<i>Gorgoniapolynoe guadalupensis</i>	Pettibone	Cnidarian	<i>Corallium imperiale</i>	O	Britayev 1981, Pettibone 1991a
<i>Gorgoniapolynoe muzikae</i>	Pettibone	Cnidarian	<i>Acanthogorgia</i> sp.	O	Pettibone 1991a
“		Cnidarian	<i>Candidella helminthophora</i>	O	Pettibone 1991a
“		Cnidarian	<i>Corallium</i> sp.	O	Pettibone 1991a
<i>Gorgoniapolynoe uschacovi</i>	Britayev	Cnidarian	<i>Allophora</i> sp. 1	O	Britayev 1981
“		Cnidarian	<i>Callogorgia</i> sp.	O	Britayev 1981, Pettibone 1991a
<i>Grubeopolynoe semenovi</i>	(Annenkova)	Polychaete	Unidentified Ampharetid	F	Pettibone 1969c, Uschakov 1982
<i>Grubeopolynoe tuta</i>	(Grube)	Polychaete	<i>Amphitrite robusta</i>	F	Pettibone 1969c
“		Polychaete	<i>Thelepus crispus</i>	F	Gravier 1905a, 1905b, Pettibone 1969c

<i>Halosydna brevisetosa</i>	Kinberg	Decapod	<i>Paguristes bakeri</i>	F	Clark 1956
“		Nudibranch	<i>Melibe leonina</i>	F	Ajeska & Nibakken 1976
“		Polychaete	<i>Amphitrite robusta</i>	F	Hickok & Davenport 1951
“		Polychaete	<i>Pista pacifica</i>	F	Clark 1956
“		Polychaete	<i>Platinereis agassizi</i>	F	Clark 1956
“		Polychaete	<i>Thelepus crispus</i>	F	Pettibone 1953
<i>Halosydna johnsoni</i>	(Darboux)	Polychaete	<i>Pista fratrella</i>	F	McGinitie & McGinitie 1949
<i>Harmothoinae</i> sp.		Polychaete	<i>Polyodontes lupinus</i>	O	Fox & Rupert 1985, Pettibone 1989b
<i>Harmothoe acanellae</i>	(Verrill)	Cnidarian	<i>Acanella orbuscula</i>	F	Verrill 1881, Ditlevsen 1917
“		Cnidarian	<i>Acanthogorgia armata</i>	F	Verrill 1881
“		Cnidarian	<i>Anthomastus grandifloris</i>	F	Ditlevsen 1917
“		Cnidarian	<i>Pennatula grandis</i>	F	Pettibone 1963
<i>Harmothoe areolata</i>	Grube	Polychaete	<i>Eupolymnia nebulosa</i>	O	McIntosh 1900
“		Polychaete	<i>Chaetopterus</i> sp.	O	McIntosh 1900
<i>Harmothoe brevipalpa</i>	Bergstrom	Polychaete	<i>Phyllochaetopterus</i> sp.	F	Cañete at al.1993
“		Polychaete	<i>Pectinaria chilensis</i>	F	Cañete at al. 1993
<i>Harmothoe coeliaca</i>	Saint-Joseph	Decapod	<i>Eupagurus bernhardus</i>	O	Dales 1957
<i>Harmothoe commensalis</i>	Rozbaczyllo & Cañete	Bivalve	<i>Gari solida</i>	O	Rozbaczyllo & Cañete 1993
“		Bivalve	<i>Semele solida</i>	O	Rozbaczyllo & Cañete 1993
<i>Harmothoe hyalonemae</i>	Martin, Rosell & Uriz	Sponge	<i>Hyalonema thomsoni</i>	O	Martin et al. 1992
“		Sponge	<i>Hyalonema lusitanicum</i>	O	Martin et al. 1992
“		Sponge	<i>Hyalonema toxeras</i>	O	Martin et al. 1992
“		Sponge	<i>Hyalonema infundibulum</i>	O	Martin et al. 1992
<i>Harmothoe imbricata</i>	Linnaeus	Asteroid	<i>Asterias amurensis</i>	F	Okuda 1936b
“		Decapod	<i>Pagurus ochotoensis</i>	F	Pettibone 1963
“		Polychaete	<i>Amphitrite robusta</i>	F	Berkeley & Berkeley 1948
“		Polychaete	<i>Chaetopterus cautus</i>	F	Britayev 1993
“		Polychaete	<i>Chaetopterus</i> sp.	F	McIntosh 1900, Fauvel 1923
“		Polychaete	<i>Diopatra ornata</i>	F	Pettibone 1953
“		Polychaete	<i>Eupolymnia nebulosa</i>	F	McIntosh 1900
“		Polychaete	<i>Polycirrus</i> sp.	F	McIntosh 1900
“		Polychaete	<i>Thelepus crispus</i>	F	McIntosh 1900
<i>Harmothoe impar</i>	(Johnson)	Holothuroid	<i>Cucumaria planci</i>	F	Fauvel 1923, Barel & Kramers 1977
<i>Harmothoe ljunghmani</i>	(Malmgren)	Polychaete	<i>Lanice conchilega</i>	F	Fauvel 1923
<i>Harmothoe longisetis</i>	(Grube)	Polychaete	<i>Amphitrite edwardsi</i>	F	Fauvel 1923
“		Polychaete	<i>Arenicola marina</i>	F	Fauvel 1923
“		Polychaete	<i>Chaetopterus insignis</i>	F	Hornell 1891
“		Polychaete	<i>Chaetopterus</i> <i>pergamentaceus</i>	F	Euders 1905, Fauvel 1923, Paris 1955
“		Polychaete	<i>Chaetopterus variopedatus</i>	F	Fauvel 1923, Paris 1955
<i>Harmothoe melanicornis</i>	Britayev	Cnidarian	<i>Allophora</i> sp. 2	F	Britayev 1981
<i>Harmothoe spinifera</i>	(Ehlers)	Polychaete	<i>Amphitrite gracilis</i>	F	Beauchamp & Zschs 1913, Davenport 1953b
“		Polychaete	<i>Polycirrus caliendrum</i>	F	Davenport 1953b
<i>Harmothoe spongicola</i>	Hanley & Burke	Sponge	<i>Aulochone clathroclada</i>	O	Hanley & Burke 1991b
<i>Harmothoe tenebricosa</i>	Moore	Asteroid	<i>Heterozonias alternatus</i>	O	Pettibone 1969b

“		Asteroid	<i>Hoppasteria californica</i>	O	Pettibone 1969b
“		Asteroid	<i>Solaster borealis</i>	O	Pettibone 1969b
<i>Harmothoe vinogradovae</i>	Averincev	Cnidarian	Unidentified Hydrocoral	F	Britayev 1981
<i>Harmothoe</i> sp.		Polychaete	<i>Amphitrite gracilis</i>	F	Clark 1956
“		Polychaete	<i>Nereis</i> spp.	F	Clark 1956
“		Polychaete	<i>Polycirrus aurantiacus</i>	F	Clark 1956
“		Polychaete	<i>Eupolymnia nebulosa</i>	F	Clark 1956
<i>Hartmania moorei</i>	Pettibone	Polychaete	<i>Nereis virens</i>	F	Pettibone 1955, 1963
“		Polychaete	<i>Praxilella gracilis</i>	F	Pettibone 1963
<i>Hemilepidia verslusii</i>	Horst	Cnidarian	<i>Touarella hilgendorfi</i>	F	Horst 1915, Britayev 1981
<i>Hermadion fauveli</i>	Gravier	Sponge	<i>Sarcostegia oculata</i>	F	Gravier 1918, Paris 1955, Clark 1956, Barel & Kramers 1977
<i>Hermadion hyalinus</i>	Sars	Echinoid	<i>Echinus acutus</i>	O	Barel & Kramers 1977
<i>Hermenia verruculosa</i>	Grube	Ophiuroid	<i>Ophiocoma pusilla</i>	F	Devaney 1974, Pettibone 1975
<i>Hesperonoe adventor</i>	(Skolgsberg)	Echinoid	<i>Urechis caupo</i>	F	Dales 1957
<i>Hesperonoe complanata</i>	(Johnson)	Decapod	<i>Callianassa californiensis</i>	F	Clark 1956
“		Decapod	<i>Callianassa gigas</i>	F	Clark 1956
<i>Hesperonoe hwanghaiensis</i>	Uschacov & Wu	Decapod	<i>Callianassa</i> sp.	F	Uschacov & Wu 1959, Uschacov 1982
“		Decapod	<i>Upogebia</i> sp.	F	Uschacov & Wu 1959, Uschacov 1982
<i>Hesperonoe</i> sp.		Decapod	<i>Upogebia</i> sp.	F	Clark 1956
<i>Hololepidella alba</i>	Hartman-Schröder	Asteroid	<i>Acanthaster planci</i>	O	Hartmann-Schröder 1981
<i>Hololepidella comatula</i>	Uchida	Crinoid	<i>Comanthus parvicirrus</i>	O	Uchida 1975
“		Crinoid	<i>Comanthina schlegeli</i>	O	Uchida 1975
“		Crinoid	<i>Lamprometra parmata</i>	O	Uchida 1975
<i>Hololepidella commensalis</i>	Willey	Ophiuroid	<i>Macrophiotrix koehleri</i>	O	Willey 1905, Gibbs 1969
“		Ophiuroid	<i>Ophiarthrum pictum</i>	O	Gibbs 1969
“		Echinoid	<i>Clypeaster humilis</i>	O	Pettibone 1969c
“		Echinoid	<i>Peronella lesueuri</i>	O	Augener 1922, Gibbs 1969
<i>Hololepidella lobata</i>	Hartman-Schröder	Asteroid	<i>Protoreaster</i> sp.	O	Hartmann-Schröder 1984
<i>Hololepidella nigropunctata</i>	(Horst)	Asteroid	<i>Acanthaster planci</i>	O	Devaney 1967, Uchida 1975
“		Asteroid	<i>Linckia multiflora</i>	O	Pettibone 1993
“		Asteroid	<i>Mithrodia</i> sp.	O	Pettibone 1963
“		Asteroid	<i>Pentagonaster regulus</i>	O	Hendler & Meyer 1982
“		Cnidarian	<i>Fungia scutaria</i>	O	Pettibone 1993
“		Crinoid	<i>Tropiometra afra</i>	O	Hanley 1992
“		Echinoid	<i>Diadema savigny</i>	O	Hendler & Meyer 1982
“		Nudibranch	<i>Phyllidia varicosa</i>	O	Hanley 1992
“		Ophiuroid	<i>Comanthus annulatus</i>	O	Gibbs 1969
“		Ophiuroid	<i>Macrophiotrix hisurta</i>	O	MacNae & Kalk 1962, Hendler & Meyer 1982
“		Ophiuroid	<i>Macrophiotrix belli</i>	O	Hendler & Meyer 1982
“		Echinoid	Unidentified	O	Pettibone 1993
“		Ophiuroid	<i>Ophiarthrum elegans</i>	O	Gibbs 1969
“		Ophiuroid	<i>Ophiocoma anaglyptica</i>	O	Devaney 1967
“		Ophiuroid	<i>Ophiocoma brevipes</i>	O	Devaney 1967, Gibbs 1969
“		Ophiuroid	<i>Ophiocoma dentata</i>	O	Devaney 1967

“		Ophiuroid	<i>Ophiocoma doederleini</i>	O	Pettibone 1993
“		Ophiuroid	<i>Ophiocoma erinaceus</i>	O	Devaney 1967
“		Ophiuroid	<i>Ophiocoma</i> sp.	O	Hanley & Burke 1991b
“		Sponge	<i>Latrunculia magnifica</i>	O	Pettibone 1993
<i>Hololepidella obtusa</i>	Hartmann-Schröder	Crinoid	<i>Echinometra</i> sp.	O	Hartmann-Schröder 1984
<i>Hololepidella ophiuricola</i>	Gibbs	Ophiuroid	<i>Macrophiothrix koehleri</i>	O	Gibbs 1969, 1971, Pettibone 1993
“		Ophiuroid	<i>Ophiarthrum pictum</i>	O	Gibbs 1969, 1971
<i>Hololepidella</i> sp.	Day	Ophiuroid	<i>Macrophiotrix hirsuta</i>	O	Pettibone 1993
<i>Hyperhalosydna striata</i>	(Kinberg)	Polychaete	<i>Eunice</i> ssp.	F	Hanley & Burke 1991b
<i>Intoshella euplectellae</i>	McIntosh	Sponge	<i>Euplectella aspergillum</i>	O	Uschacov 1982, Pettibone 1996
<i>Intoshella holothuricola</i>	(Izuka)	Holothuroid	Unidentified	O	Izuka 1912, Okuda 1936a, Gallardo 1967, Uschacov 1982
<i>Lagisca irritans</i>	Marenzeller	Cnidarian	<i>Errina macrogasta</i>	O	Marenzeller 1904, Zibrovius 1981
“		Cnidarian	<i>Stenobelia robusta</i>	O	Marenzeller 1904, Zibrovius 1981
<i>Lagisca zibrowii</i>	Hartmann-Schröder	Cnidarian	<i>Pseudosolanderia</i> sp.	O	Hartmann-Schröder 1992
<i>Lepidastenia alba</i>	Hartman	Polychaete	<i>Phyllochaetopterus verrilli</i>	O	Hartman 1966
“		Polychaete	<i>Phyllochaetopterus major</i>	O	Rullier 1972
<i>Lepidastenia accolus</i>	Estcourt	Polychaete	Unidentified Arenicolid	O	Estcourt 1967
<i>Lepidasthenia argus</i>	Hodgson	Polychaete	<i>Amphitrite edwardsi</i>	F	Clark 1956, Davenport 1953a, b, Paris 1955
<i>Lepidasthenia digueti</i>	Gravier	Balanoglossid	<i>Balanoglossus gigas</i>	O	Gravier 1905a
<i>Lepidasthenia berkeleyae</i>	Pettibone	Polychaete	<i>Praxilella affinis</i>	F	Clark 1956
<i>Lepidastenia commensalis</i>	Webster	Polychaete	<i>Amphitrite ornata</i>	O	Gravier 1905b, Pettibone 1963, Gadiner 1976
“		Polychaete	<i>Diopatra cuprea</i>	O	Pettibone 1963
“		Polychaete	<i>Thelepus setosus</i>	O	Pettibone 1963
“		Sponge	<i>Ircinia campana</i>	?	Dauer 1974
<i>Lepidasthenia elegans</i>	(Grube)	Polychaete	Unidentified Terebellid	O	Day 1967
“		Polychaete	<i>Terebellides</i> sp.	O	Gibbs 1969
“		Polychaete	<i>Mesochaetopterus sagittarius</i>	O	Gibbs 1971
“		Sponge	Unidentified	O	Rullier 1974
<i>Lepidastenia gigas</i>	(Johnson)	Polychaete	<i>Amphitrites</i> sp.	O	Gravier 1905b, Essenberg 1918
<i>Lepidasthenia guadalcanalis</i>	Gibbs	Balanoglossid	<i>Balanoglossus carnosus</i> ?	O	Gibbs 1971
<i>Lepidasthenia longissima</i>	(Izuka)	Polychaete	<i>Thelepus setosus</i>	F	Okuda 1936b, Clark 1956
<i>Lepidasthenia ocellata</i>	(McIntosh)	Polychaete	<i>Spiochaetopterus chaellengeri</i>	F	Okuda 1936b, Clark 1956
<i>Lepidasthenia ohshimai</i>	Okuda	Holothuroid	<i>Protankyra bidentata</i>	F	Okuda 1936a, b, Clark 1956
<i>Lepidasthenia maculata</i>		Polychaete	<i>Chaetopterus</i> sp.	O	Gibbs 1969
“		Polychaete	<i>Phyllochaetopterus herdmani</i>	O	Gibbs 1971
“		Polychaete	<i>Phyllochaetopterus socialis</i>	F	Fauvel 1913
“		Polychaete	<i>Phyllochaetopterus</i> sp.	O	Gibbs 1969
“		Polychaete	<i>Dasybranchus caducus</i>	O	Gibbs 1969
<i>Lepidasthenia microlepis</i>	Potts	Sipunculid	<i>Siphonostoma vastus</i>	O	Gibbs 1969, 1971
“		Sipunculid	<i>Paraspidosiphon cumingi</i>	O	Gibbs 1969, 1971
“		Sipunculid	Unidentified	O	Hanley & Burke 1991b
<i>Lepidasthenia mossambica</i>	Day	Balanoglossid	<i>Balanoglossus carnosus</i>	O	Day 1962, Gibbs 1969

<i>Lepidasthenia stylolepis</i>	Willey	Sipunculid	<i>Siphonostoma vastus</i>	O	Gibbs 1969, 1971
<i>Lepidasthenia varia</i>	Treadwell	Polychaete	<i>Notomastus lobatus</i>	O	Gardiner 1976
<i>Lepidastheniella comma</i>	(Thomson)	Polychaete	Unidentified Terebellid	O	Pettibone 1973
<i>Lepidonotopodium fimbriatum</i>	Pettibone	Polychaete	<i>Alvinella pompejana</i>	F	Pettibone 1984b
“		Bivalve	<i>Calymene magnifica</i>	F	Pettibone 1984b
“		Vetimentiferan	<i>Riftia pachyptila</i>	F	Pettibone 1984b
<i>Lepidonotopodium riftense</i>	Pettibone	Vetimentiferan	<i>Riftia pachyptila</i>	F	Pettibone 1984b
“		Polychaete	<i>Alvinella pompejana</i>	F	Pettibone 1984b
“		Bivalve	<i>Calymene magnifica</i>	F	Pettibone 1984b
“		Bivalve	Unidentified Mytilid (deep-sea)	F	Pettibone 1984b
<i>Lepidonotopodium williamsae</i>	Pettibone	Bivalve	<i>Calymene magnifica</i>	F	Pettibone 1984b
“		Bivalve	Unidentified Mytilid (deep-sea)	F	Pettibone 1984b
“		Polychaete	<i>Alvinella pompejana</i>	F	Pettibone 1984b
“		Vetimentiferan	<i>Riftia pachyptila</i>	F	Pettibone 1984b
<i>Lepidonopsis humilis</i>	(Augener)	Echinoid	<i>Mellita quinquesperforata</i>	F	Pettibone 1993
“		Ophiuroid	<i>Ophiotrix lineata</i>	F	Pettibone 1993
“		Ophiuroid	<i>Micropholis gracillima</i>	F	Gardiner 1976
<i>Lepidonotus elongatus</i>	Marenzeller	Polychaete	<i>Thelepus setosus</i>	F	Okuda 1936b, Clark 1956
<i>Lepidonotus glaucus</i>	(Peters)	Polychaete	<i>Eunice sp.1</i>	F	Hanley & Burke 1990
“		Polychaete	<i>Eunice sp.2</i>	F	Hanley & Burke 1990
“		Polychaete	<i>Eunice sp.3</i>	F	Hanley & Burke 1990
“		Polychaete	<i>Eunice sp.4</i>	F	Hanley & Burke 1990
<i>Lepidonopsis humilis</i>	(Augener)	Echinoid	<i>Mellita quinquesperforata</i>	F	Pettibone 1993
“		Ophiuroid	<i>Ophiotrix lineata</i>	F	Pettibone 1993
“		Ophiuroid	<i>Micropholis gracillima</i>	F	Pettibone 1993
<i>Lepidonotus melanogrammus</i>	Haswell	Ophiuroid	Unidentified	F	Hanley & Burke 1990
<i>Lepidonotus sublevis</i>	Verrill	Decapod	<i>Pagurus pollicaris</i>	F	Pettibone 1963
“		Decapod	<i>Pagurus pollicaris</i>	F	Gardiner 1976
“		Decapod	<i>Pagurus impressus</i>	F	Gardiner 1976
“		Decapod	<i>Clibanarius vittatus</i>	F	Gardiner 1976
<i>Lepidonotus sp.</i>		Holothuroid	<i>Labidoplax digitata</i>	F	Barel & Kramers 1977
<i>Lepidonotus variabilis</i>	Webster	Sponge	<i>Ircinia campana</i>	F	Dauer 1974
“		Sponge	Unidentified	F	Rullier 1974
<i>Malmgreniella andreapolis</i>	(McIntosh)	Holothuroid	<i>Leptosynapta bergenensis</i>	F	Pettibone 1993
“		Holothuroid	<i>Labidoplax digitata</i>	F	Pettibone 1993
“		Holothuroid	<i>Leptosynapta galliennii</i>	F	Orton 1923, Spooner et al. 1957
“		Holothuroid	Unidentified Synaptid	F	Cazaux 1968
“		Ophiuroid	<i>Acrocnida brachiata</i>	F	Orton 1923, Spooner et al. 1957, Pettibone 1953
<i>Malmgreniella arenicola</i>	(Saint-Joseph)	Polychaete	<i>Arenicola marina</i>	F	Saint-Joseph 1888, Spooner et al. 1957, Pettibone 1993
“		Polychaete	<i>Arenicola sp.</i>	F	Spooner et al. 1957, Pettibone 1993

“		Polychaete	<i>Notomastus latericeus</i>	F	Spooner et al. 1957, Pettibone 1993
“		Polychaete	<i>Amphitrite johnstoni</i>	F	Spooner et al. 1957, Pettibone 1993
“		Polychaete	<i>Loimia medusa</i>	F	Spooner et al. 1957, Pettibone 1993
“		Polychaete	<i>Lanice conchilega</i>	F	Hamond 1966, Pettibone 1993
“		Sipunculid	<i>Golfingia elongata</i>	F	Spooner et al. 1957, Pettibone 1993
“		Sipunculid	<i>Golfingia vulgaris</i>	F	Spooner et al. 1957, Pettibone 1993
<i>Malmgreniella baschi</i>	Pettibone	Ophiuroid	<i>Ophiopsila californica</i>	F	Pettibone 1953
“		Polychaete	<i>Chaetopterus variopedatus</i>	F	Ruff 1995
<i>Malmgreniella castanea</i>	(McIntosh)	Echinoid	<i>Spatangus purpureus</i>	F	Clark 1956, Barel & Kramers 1977, Pettibone 1993
“		Echinoid	<i>Spatangus raschi</i>	F	Barel & Kramers 1977
“		Asteroid	<i>Astropecten irregularis</i>	F	Barel & Kramers 1977
<i>Malmgreniella capensis</i>	(McIntosh)	Echinoid	<i>Spatangus capensis</i>	F	Pettibone 1993
<i>Malmgreniella dicirra</i>	Hartman	Cnidarian	<i>Allopora eguchii</i>	O	Pettibone 1993
“		Cnidarian	<i>Caliptopora reticulata</i>	O	Pettibone 1993
“		Cnidarian	<i>Conopora pauciseptata</i>	O	Pettibone 1993
“		Cnidarian	<i>Lepidopora</i> sp.	O	Pettibone 1993
“		Cnidarian	<i>Stylaster densiculis</i>	O	Pettibone 1993
<i>Malmgreniella galataensis</i>	Pettibone	Ophiuroid	<i>Amphiura</i> cf. <i>fibulata</i>	O	Pettibone 1993
“		Ophiuroid	<i>Ophiophragmus septus</i>	O	Pettibone 1993
<i>Malmgreniella hendleri</i>	Pettibone	Ophiuroid	<i>Amphiura</i> cf. <i>fibulata</i>	O	Pettibone 1993
“		Ophiuroid	<i>Ophionereis limicola</i>	O	Pettibone 1993
<i>Malmgreniella inhacaensis</i>	Pettibone	Balanoglossid	<i>Balanoglossus</i> sp.	O	Day 1962, Pettibone 1993
“		Balanoglossid	<i>Ptychodera</i> sp.	O	Pettibone 1993
<i>Malmgreniella lunulata</i>	(Delle Chiaje)	Balanoglossid	Unidentified Balanoglossids	O	Pettibone 1993
<i>Malmgreniella</i> cf. “ <i>lunulata</i> ”		Polychaete	<i>Mesochaetopterus rickettsi</i>	?	Petersen & Britayev 1997
<i>Malmgreniella maccrarya</i>	Pettibone	Ophiuroid	Unidentified	F	Pettibone 1993
“		Ophiuroid	<i>Amphiopholis gracillima</i>	F	Pettibone 1993
“		Ophiuroid	<i>Amphioplus sepultus</i>	F	Pettibone 1993
<i>Malmgreniella macginitiei</i>	Pettibone	Decapod	<i>Calianassa californiensis</i>	O	Berkeley & Berkeley 1941, Pettibone 1993, Ruff 1995
“		Polychaete	<i>Axiotella rubrocincta</i>	O	Kudenov 1975, Pettibone 1993, Ruff 1995
“		Ophiuroid	<i>Amphiodia urtica</i>	O	Pettibone 1993, Ruff 1995
<i>Malmgreniella marphysae</i>	(Mcintosh)	Polychaete	<i>Marphysa sanguinea</i>	O	Pettibone 1993
“		Polychaete	<i>Lagis koreni</i>	O	Pettibone 1993
<i>Malmgreniella murrayensis</i>	Pettibone	Sponge	Unidentified	O	Pettibone 1993
<i>Malmgreniella nigralba</i>	(Berkeley)	Holothuroid	<i>Leptosynapta clarki</i>	O	Berkeley 1924, Pettibone 1953, 1993, Ruff 1995
<i>Malmgreniella panamensis</i>	Pettibone	Ophiuroid	<i>Ophiopsila</i> cf. <i>polysticta</i>	O	Pettibone 1993
<i>Malmgreniella pettiti</i>	Pettibone	Cnidarian	Unidentified Alcyonarian	O	Pettibone 1993
<i>Malmgreniella pierceae</i>	Pettibone	Ophiuroid	<i>Amphiura</i> cf. <i>fibulata</i>	F	Pettibone 1993
<i>Malmgreniella puntotorensis</i>	Pettibone	Ophiuroid	<i>Amphiodia trychna</i>	O	Pettibone 1993
“		Ophiuroid	<i>Ophionephthys limicola</i>	O	Pettibone 1993
“		Ophiuroid	<i>Ophiophragmus cubanus</i>	O	Pettibone 1993
“		Ophiuroid	<i>Ophiophragmus pulcher</i>	O	Pettibone 1993
“		Ophiuroid	<i>Ophiophragmus septus</i>	O	Pettibone 1993
“		Ophiuroid	Unidentified	O	Pettibone 1993

<i>Malmgreniella scriptoria</i>	(Moore)	Echinoid	<i>Briaster latifrons</i>	F	Moore 1910, Pettibone 1953, 1993, Ruff 1995
<i>Malmgreniella taylori</i>	Pettibone	Ophiuroid	<i>Amphiodia atra</i>	F	Pettibone 1993
"		Ophiuroid	<i>Amphiopholis gracillima</i>	F	Pettibone 1993
<i>Malmgreniella variegata</i>	(Treadwell)	Ophiuroid	<i>Ophionereis reticulata</i>	F	Millot 1953, Pettibone 1993
"		Ophiuroid	<i>Ophionereis annulata</i>	F	Pettibone 1993
<i>Malmgreniella</i> sp.		Holothuroid	Unidentified synaptid	O	D. Martin personal observations
<i>Minusculisquama hughesi</i>	Pettibone	Polychaete	Unidentified Maldanid	F	Pettibone 1983
<i>Neoholepidella murrayi</i>	Pettibone	Sponge	Calcareous sponge	O	Pettibone 1969c
<i>Ophthalmonoe pettiboneae</i>	Petersen & Britayev	Polychaete	<i>Chaetopterus appendiculatus</i>	O	Petersen & Britayev 1997
<i>Parabathynoe brisinga</i>	Pettibone	Asteroid	<i>Brisinga</i> sp.	O	Pettibone 1990
<i>Paractonoella aphthalma</i>	Gallardo	Ophiuroid	Unidentified	F?	Gallardo 1967, Uschacov 1982, Pettibone 1996
<i>Paradyte crinoidicola</i>	(Potts)	Asteroid	<i>Astropecten</i> sp.	O	Hanley 1984, 1991
"		Crinoid	<i>Capillaster multirradiatus</i>	O	Thesunov et al. 1989, Hanley 1984, 1991
"		Crinoid	<i>Colobometra persispinosa</i>	O	Thesunov et al. 1989
"		Crinoid	<i>Comantheria rotula</i>	O	Hanley 1984, Hanley & Burke 1991b
"		Crinoid	<i>Comanthina belli</i>	O	Hanley 1984, Hanley & Burke 1991b
"		Crinoid	<i>Comanthina schelegi</i>	O	Hanley 1984, Hanley & Burke 1991b
"		Crinoid	<i>Comanthus annulatus</i>	O	Thesunov et al. 1989
"		Crinoid	<i>Comanthus bennetti</i>	O	Hanley 1984, Hanley & Burke 1991b
"		Crinoid	<i>Comanthus parvicirrus</i>	O	Hanley 1984, Hanley & Burke 1991b
"		Crinoid	<i>Comantula purpurea</i>	O	Hanley 1984, Hanley & Burke 1991b
"		Crinoid	<i>Comatella stelligera</i>	O	Hanley 1984, Hanley & Burke 1991b
"		Crinoid	<i>Himenometra robustispina</i>	O	Hanley 1984, Hanley & Burke 1991b
"		Crinoid	<i>Lampometra klunzingeri</i>	O	Hanley 1984, Hanley & Burke 1991b
"		Crinoid	<i>Lampometra palmata</i>	O	Hanley 1984, Hanley & Burke 1991b
"		Crinoid	<i>Oligometra carpenteri</i>	O	Hanley 1984, Hanley & Burke 1991b
"		Crinoid	<i>Oligometra serripinna</i>	O	Hanley 1984, 1992, Hanley & Burke 1991b
"		Crinoid	<i>Petasometra helianthoides</i>	O	Hanley 1984, Hanley & Burke 1991b
"		Crinoid	<i>Stephanometra indica</i>	O	Hanley 1984, Hanley & Burke 1991b
"		Crinoid	<i>Tropiometra carinata</i>	O	Day 1962, Pettibone 1969a, Hanley 1984, Hanley & Burke 1991b
"		Crinoid	<i>Zygometa comata</i>	O	Hanley 1984, Hanley & Burke 1991b
"		Crinoid	<i>Zygometa elegans</i>	O	T.A. Britayev personal observstions
"		Crinoid	Unidentified	O	Hanley 1992
<i>Paradite laevis</i>	(Day)	Cnidarian	<i>Dendronephthya</i> sp.	F	Okuda 1950
<i>Paradite tentaculata</i>	(Horst)	Cnidarian	<i>Dendronephthya</i> sp.	O	Hanley 1992
"		Cnidarian	<i>Nepthea</i> sp.	O	Pettibone 1969a, Hanley 1992
<i>Parahalosidnopsis tubicola</i>	(Day)	Polychaete	<i>Loimia medusa</i>	O	Day 1973, Pettibone 1977, Gaikwad 1993
<i>Phyllosheila wigleyi</i>	McIntosh	Asteroid	<i>Brisinga</i> sp.	O	Pettibone 1961
<i>Polyeunoa laevis</i>	McIntosh	Cnidarian	<i>Thouarella variabilis</i>	F	Pettibone 1969c
<i>Polyeunoa maculata</i>	(Day)	Polychaete	<i>Mesochaetopterus japonicus</i>	O	Day 1973, Hartmann-Schröder 1981, Gaikwad 1993
<i>Polynoe antarctica</i>	Kinberg	Polychaete	Unidentified terebellid	F	Uschakov 1962, Hartmann-Schröder 1989
"		Cnidarian	<i>Thuiaria</i> sp.	F	Hartmann-Schröder 1989
<i>Polynoe arenicolae</i>	Benham	Polychaete	<i>Arenicola</i> sp.	O	Benham 1910
<i>Polynoe pentactes</i>	Benham	Holothuroid	<i>Cucumaria</i> sp.	O	Benham 1910

<i>Polynoe scolopendrina</i>	Savigny	Polychaete	<i>Eupolymnia nebulosa</i>	F	Davenport 1953b, Paris 1955 , D. Martin personal observations
“		Polychaete	<i>Lanice conchilega</i>	F	Davenport 1953b
“		Polychaete	<i>Lysidice ninetta</i>	F	McIntosh 1900, Davenport 1953b, Paris 1955
<i>Polynoe thouarellicola</i>	Hartmann-Schröder	Cnidarian	<i>Thouarella</i> sp.	O	Hartmann-Schröder 1989
“		Cnidarian	<i>Acanthogorgiidae</i> sp.	O	Hartmann-Schröder 1989
<i>Pottsiscalisetosus praelongus</i>	(Marenzeller)	Asteroid	Unidentified	F	Pettibone 1969a
<i>Subadyte pellucida</i>	(Ehlers)	Ophiuroid	<i>Ophiothrix fragilis</i>	F	Barel & Kramers 1977, Ockelmann personal communication
“		Ophiuroid	<i>Ophiothrix echinata</i>	F	Devaney 1967
“		Ophiuroid	<i>Ophiothrix alopecurus</i>	F	Devaney 1967
“		Ophiuroid	<i>Ophiothrix quinquemaculata</i>	F	Bellan 1964, Guille 1965
“		Asteroid	<i>Solaster papposus</i>	F	Okuda 1950, Barel & Kramers 1977
“		Asteroid	<i>Astropecten irregularis</i>	F	Okuda 1950, Barel & Kramers 1977
“		Crinoid	<i>Antedon mediterranea</i>	F	Barel & Kramers 1977
“		Echinoid	<i>Paracentrotus lividus</i>	F	Barel & Kramers 1977
<i>Subadyte papillifera</i>	(Horst)	Cnidarian	Unidentified Coral	O	Pettibone 1969a
<i>Telolepidasthenia lobetobiensis</i>	Augener & Pettibone	Polychaete	Unidentified chaetopterid (tube)	O	Pettibone 1970
“		Polychaete	<i>Phyllochaetopterus</i> sp.	O	Pettibone 1970
<i>Tottonpolynoe symantipatharia</i>	Pettibone	Cnidarian	<i>Parantipathes</i> sp.	O	Pettibone 1991b
“		Cnidarian	<i>Sclerisis macquarina</i>	O	Pettibone 1991b
<i>Unkopolynoe corallicola</i>	Hartmann-Schröder	Cnidarian	Unidentified Alcyonarian	O	Hartmann-Schröder 1960
<i>Wilsoniella furcosestosa</i>	(Loshamn)	Polychaete	<i>Amphitrite edwardsi</i>	F	Spooner et al. 1957, Pettibone 1993
SABELLARIDAE					
<i>Phalacrostemma cidariophilum</i>	Marenzeller	Echinoid	<i>Cidaris cidaris</i>	O	Barel & Kramers 1977
SABELLIDAE					
<i>Potamilla symbiotica</i>	Uschacov	Sponge	<i>Cryptospongia enigmatica</i>	O	Uschacov 1950
SERPULIDAE					
<i>Floriprotis sabiuraensis</i>	Uchida	Cnidarian	<i>Favites abdita</i>	O	Uchida 1978
“		Cnidarian	<i>Favia speciosa</i>	O	Bailey-Brock 1985
“		Cnidarian	<i>Goniastrea pectinata</i>	O	Bailey-Brock 1985
“		Cnidarian	<i>Hydnophora</i> sp.	O	ten Hove 1989
“		Cnidarian	<i>Platygyra</i> sp.	O	ten Hove 1989
<i>Hydroides spongicola</i>	Benedict	Sponge	<i>Neofibularia nolitangere</i>	O	ten Hove 1989
“		Sponge	<i>Mycale microsigmatosa</i>	O	ten Hove 1989
<i>Pseudovermilia madracicola</i>	ten Hove	Cnidarian	<i>Madracis pharensis</i>	O	ten Hove 1989
“		Cnidarian	<i>Madracis decactis</i>	O	ten Hove 1989
<i>Serpula</i> sp. 2	ten Hove	Cnidarian	<i>Echinopora gemmacea</i>	O	ten Hove 1994
<i>Spirobranchus gardineri</i>	Pixell	Cnidarian	<i>Gardenosieris planulata</i>		ten Hove 1994
“		Cnidarian	<i>Porites lutea</i>		ten Hove 1994
“		Cnidarian	<i>Pavona varians</i>		ten Hove 1994

<i>Spirobranchus giganteus/corniculatus</i>	(Pallas)	Cnidarian	<i>Agaricia</i> spp.	O	Hunte et al. 1990
“		Cnidarian	<i>Acropora</i> sp.	O	ten Hove 1994
“		Cnidarian	<i>Diploria labyrinthiformes</i>	O	Hunte et al. 1990
“		Cnidarian	<i>Diploria strigosa</i>	O	Hunte et al. 1990
“		Cnidarian	<i>Gardenoseris planulata</i>	O	ten Hove 1994
“		Cnidarian	<i>Hydnophora microconos</i>	O	ten Hove 1994
“		Cnidarian	<i>Madracis</i> spp.	O	Hunte et al. 1990
“		Cnidarian	<i>Millepora alcicornis</i>	O	Pallas 1766 in ten Hove 1989
“		Cnidarian	<i>Millepora complanata</i>	O	Hunte et al. 1990; Marsden1992
“		Cnidarian	<i>Millepora</i> sp.	O	ten Hove 1994
“		Cnidarian	<i>Montastrea annularis</i>	O	Hunte et al. 1990
“		Cnidarian	<i>Montastrea cavernos</i>	O	Hunte et al. 1990
“		Cnidarian	<i>Montipora</i> sp.	O	ten Hove 1994
“		Cnidarian	<i>Pavona maldivensis</i>	O	ten Hove 1994
“		Cnidarian	<i>Porites astreoides</i>	O	Hunte et al. 1990
“		Cnidarian	<i>Porites lutea</i>	O	ten Hove 1994
“		Cnidarian	<i>Porites porites</i>	O	DeVantier et al. 1985
“		Cnidarian	<i>Porites</i> sp.	O	Bailey-Brock 1985, Hunte et al. 1990
“		Cnidarian	<i>Siderastrea siderea</i>	O	Hunte et al. 1990
“		Cnidarian	<i>Stylophora</i> sp.	O	ten Hove 1994
<i>Spirobranchus</i> cf. <i>nigranucha</i>	(Fischli)	Cnidarian	<i>Porites</i> sp.	O	ten Hove 1989
<i>Spirobranchus polycerus</i>	(Schmarda)	Cnidarian	<i>Millepora complanata</i>	O	Marsden 1992
“		Cnidarian	<i>Porites asteroides</i>	O	Marsden 1992
<i>Spirobranchus tetraceros</i>		Cnidarian	<i>Millepora tuberosa</i>	F	ten Hove 1970, 1994
“		Cnidarian	<i>Pavona maldivensis</i>	F	ten Hove 1970, 1994
SPHAERODORIDAE					
<i>Sphaerodorum ophiurophoretos</i>	Martin & Alvà	Ophiuroid	<i>Amphipholis squamata</i>	O	Martin & Alvà 1989, Alvà & Jangoux 1990
<i>Sphaerodorum flavus</i>	Oersted	Ophiuroid	<i>Amphiura chiajei</i>	O	Ockelman personal communication
“		Ophiuroid	<i>Amphiura filiformis</i>	O	Ockelman personal communication
<i>Sphaerodoridium guilbaulti</i>	Rullier	Cnidarian	<i>Paragorgia arborea</i>	O	Rullier 1974
<i>Commensodorum commensalis</i>	(Lutzen)	Polychaete	<i>Terebellides stroemi</i>	O	Lützen 1961
SPINTHERIDAE					
<i>Spinther arcticus</i>	(Sars)	Sponge	<i>Halichondria</i> sp.	O	George & Hartmann-Schröder 1985
“		Sponge	<i>Tedania</i> sp.	O	George & Hartmann-Schröder 1985
“		Sponge	Unidentified	O	Sardá 1984, George & Hartmann-Schröder 1985
“		Cnidarian	Unidentified Hydroids	O	George & Hartmann-Schröder 1985
<i>Spinther citrinus</i>	(Stimpson)	Sponge	Unidentified	O	Hartman 1942, Pettibone 1963
<i>Spinther ericinus</i>	Yamamoto & Imajima	Sponge	Unidentified	O	Yamamoto & Imajima 1988
<i>Spinther oniscoides</i>	Johnston	Sponge	<i>Stylostichon plumosum</i>	O	Campoy 1982
“		Sponge	<i>Desmacidon</i> sp.	O	George & Hartmann-Schröder 1985
SPIONIDAE					
<i>Polydora carunculata</i>	Radshevsky	Sponge	<i>Halichondria panicea</i>	F	Radashevsky 1993

“		Sponge	<i>Dysidea fragilis</i>	F	Radashevsky 1993
<i>Polydora colonia</i>	Moore	Sponge	<i>Tedania ignis</i>	?	Blake 1971, Dauer 1974
<i>Polydora spongiicola</i>	Berkeley & Berkeley	Sponge	<i>Adocia cinerea</i>	O	Buzhinskaja 1971, Radashevsky 1988
“		Sponge	<i>Halichondria panicea</i>	O	Radashevsky 1993
“		Sponge	<i>Ophlitaspongia pennata</i>	O	Radashevsky 1993
“		Sponge	<i>Myxilla incrusatans</i>	O	Radashevsky 1993
“		Sponge	<i>Lyssodendoryx firma</i>	O	Berkeley & Berkeley 1950
<i>Polydorella prolifera</i>	Augener	Sponge	Unidentified	O	Augener 1914, Blake & Kudenov 1978
<i>Polydorella smurovi</i>	Tzetlin & Britayev	Sponge	Unidentified	O	Tzetlin & Britayev 1985
<i>Polydorella stolonifera</i>	Blake & Kudenov	Sponge	Unidentified	O	Blake & Kudenov 1978
<i>Polydorella dawydoffi</i>	Radashevsky	Sponge	<i>Petrosia</i> sp.	O	Radashevsky 1996
“		Sponge	<i>Rhaphidiophlus erectus</i>	O	Radashevsky 1996
“		Sponge	<i>Amphimedon</i> sp.	O	Radashevsky 1996
“		Sponge	<i>Callispongia</i> sp.	O	Radashevsky 1996
“		Sponge	<i>Haliclona</i> sp.	O	Radashevsky 1996
“		Sponge	<i>Mycale</i> sp.	O	Radashevsky 1996
“		Sponge	<i>Niphates</i> sp.	O	Radashevsky 1996
“		Sponge	<i>Suberites</i> sp.	O	Radashevsky 1996
“		Sponge	<i>Xestospongia testudinaria</i>	O	Radashevsky 1996
“		Sponge	<i>Polymastia</i> sp.	O	Radashevsky 1996
SPIRORBIDAE					
<i>Circeis armoricana</i>	(Saint-Joseph)	Decapod	<i>Pagurus middendorfi</i>	F	Rzhavski & Britayev 1988
“		Decapod	<i>Pagurus hirsutiusculus</i>	F	Rzhavski & Britayev 1988
<i>Circeis paguri</i>	Knight-Jones & Knight-Jones	Decapod	<i>Eupagurus bernhardus</i>	O	Al-Ogyli & Knight-Jones 1981
SYLLIDAE					
<i>Amblyosyllis cincinnata</i>	(Verrill)	Sponge	<i>Haliclona oculata</i>	O	Riser 1982
“		Sponge	<i>Halichondria panicea</i>	O	Riser 1982
“		Sponge	<i>Isodyctia deichmanae</i>	O	Riser 1982
<i>Autolytus cornutus</i>	Agassiz	Cnidarian	Unidentified hydroid	?	Pettobone 1963
<i>Bollandia antipathicola</i>	Glasby	Cnidarian	<i>Antipathes</i> sp.	O	Glasby 1994
<i>Branchiosyllis exilis</i>	(Gravier)	Ophiuroid	<i>Ophiocoma echinata</i>	?	Hendler & Meyer 1982
“		Ophiuroid	Unidentified	?	Hartmann-Schröder 1978
<i>Brania pusilla</i>	(Dujardin)	Cnidarian	Unidentified Coral	?	Gardiner 1976
<i>Exogone</i> sp.		Holothuroid	<i>Cucumaria planci</i>	F	Barel & Kramers 1977
<i>Haplosyllides floridana</i>	Augener	Ophiuroid	<i>Ophiocoma pusilla</i>	O	Hartmann-Schröder 1978
“		Sponge	<i>Xestospongia muta</i>	O	San Martín et al. 1997
“		Sponge	Unidentified	O	Fauvel 1923
“		Cnidarian	Unidentified Coral	O	Hartman 1954, Rullier & Amoureux 1979
<i>Haplosyllis agelas</i>	Uebelacker	Sponge	<i>Agelas dispar</i>	O	Uebelacker 1982
<i>Haplosyllis anthogorgicola</i>	Utinomi	Cnidarian	<i>Anthogorgia bocki</i>	O	Utinomi 1956, Imajima & Hartman 1964
<i>Haplosyllis bisetosa</i>	Hartmann-Schröder	Cnidarian	Unidentified Alcyonarian	O	Hartmann-Schröder 1960
<i>Haplosyllis chamaeleon</i>	Laubier	Cnidarian	<i>Paramunicea clavata</i>	O	Laubier 1960, López et al. 1996
<i>Haplosyllis xeniacola</i>	Hartmann-Schröder	Cnidarian	<i>Xenia viridis</i>	O	Hartmann-Schröder 1993
<i>Pionosyllis magnifica</i>	Uschakov	Decapod	<i>Paralithodes kamtchatica</i>	F	T.A. Britayev personal observations

“		Decapod	Unidentified Pagurid	F	T.A. Britayev personal observations
<i>Proceraea cornuta</i>	(Agassiz)	Cnidarian	Unidentified Coral	F	Gardiner 1976
<i>Syllis armillaris</i>	(Müller)	Decapod	Unidentified Pagurid	F	T.A. Britayev personal observations
<i>Trypanosyllis asterobia</i>	Okada	Asteroid	<i>Louidia quinaria</i>	O	Imajima 1966
<i>Syllis cornuta</i>	Rathke	Decapod	Unidentified Pagurid	F	Fauvel 1923, T.A. Britayev personal observations
“		-	Unidentified inkeepers	F	Fauvel 1923
<i>Syllis gracilis</i>	Grube	Bryozoan	<i>Pentapora</i> sp.	F	López et al. 1996
“		Cnidarian	<i>Elisella parplexauroides</i>	F	López et al. 1996
“		Cnidarian	Unidentified Hydroids	F	López et al. 1996
“		Cnidarian	<i>Paramunicea clavata</i>	F	Alós 1988, López et al. 1996
“		Sponge	Unidentified	F	Amoureux et al. 1980, Campoy 1982
<i>Syllis onkylochaeta</i>	Hartmann-Schröder	Cnidarian	<i>Xenia</i> sp.	O	Hartmann-Schröder 1991
<i>Syllis sclerolaema</i>	Hartmann-Schröder	Sponge	Unidentified	F	Ushakov 1955

Table 10.- Summary of known data on infestations by boring polychaetes. Numbers between brackets indicate the amount of hosts examined.

PARASITIC BORERS	SHELL	INTENSITY	PREVALENCE
<i>Boccardia acus</i>		several	-
<i>Boccardiella hamata</i>		10 ind. / host shell	-
<i>Caobangiabrandti</i>		28 ind. / host shell	-
<i>Polydora alborectalis</i>		1500 ind. / host valve	-
<i>Polydora bidentata</i>		some ten ind. / host shell	-
<i>Polydora brevipalpa</i>		some ten ind. / host shell	-
<i>Polydora carunculata</i>		1 - 2 ind. / host shell	-
<i>Polydora concharum</i>		dense aggregates	-
<i>Polydora ciliata</i>		1 - >4 ind. / host shell	-
<i>Polydora glycymerica</i>		8 ind. / host shell	-
<i>Polydora trilobata</i>		several hundreds / host shell	-
<i>Polydora vulgaris</i>		-	4.68% - 41.2%
<i>Pseudopotamilla reniformis</i>		30 ind. / host shell	-
PARASITIC BORERS OF ORGANISMS OTHER THAN MOLLUSCS			
<i>Polydora armata</i>		6 - 50 ind. per cm ³	-
<i>Polydora hoplura</i>		1 ind. per cm ²	-
<i>Polydora wobberi</i>		10-16 ind. / host colony	-
COMMENSAL BORERS			
<i>Polydora commensalis</i>		1-10-70 ind. / host	36.6% (508)- 70.9% (158)
<i>Polydora glycymerica</i>		8 ind. / host	-
<i>Polydora rogeri</i>		10 - 18 ind. / host cm ³	100% (3)

Table 2.- List of commensal polychaetes with known infestation intensities of 1 symbiont per host.

SPECIES	SPECIES	SPECIES
<i>Arcteobia anticostiensis</i>	<i>Harmothoe impar</i>	<i>Microphthalmus szcelkowii</i>
<i>Arctonoe vittata</i>	<i>Harmothoe spinifera</i>	<i>Neohololepidella murrayi</i>
<i>Arctonoe pulchra</i>	<i>Hesionella maccullochia</i>	<i>Nereis fucata</i>
<i>Bathynoe tuberculata</i>	<i>Hipponoe gaudichaudi</i>	<i>Parahalosydropsis tubicola</i>
<i>Benhamipolynoe cairnsi</i>	<i>Hololepidella nigropunctata</i>	<i>Parasyllidea humesi</i>
<i>Bhawania goodei</i>	<i>Hololepidella ophiuricola</i>	<i>Perinereis cultrifera</i>
<i>Bhawania pottsiana</i>	<i>Lepidasthenia digueti</i>	<i>Petrecca thysira</i>
<i>Cheilonereis cyclurus</i>	<i>Lepidonotus glaucus</i>	<i>Pholadiphila turnerae</i>
<i>Disconatis contubernalis</i>	<i>Lepidonotus melanogrammus</i>	<i>Pilargis berkeleyae</i>
<i>Eunice moraovi</i>	<i>Lumbrineris flabellicola</i>	<i>Polyeunoa laevis</i>
<i>Gattyana cirrosa</i>	<i>Malmgreniella andreapolis</i>	<i>Sphaerodoridium</i>
		<i>commensalis</i>
<i>Gorgoniapolynoe bayeri</i>	<i>Malmgreniella macginitiei</i>	<i>Tottonpolynoe</i>
		<i>symantipatharia</i>
<i>Halosydna brevisetosa</i>	<i>Microphthalmus aberrans</i>	
<i>Harmothoe brevipalpa</i>	<i>Microphthalmus hamosus</i>	

Table 3.- Commensal polychaetes with known infestation intensities higher than one symbiont per host.

(*) indicate that the number of adult worms is one per host, the others being juveniles accompanying the adult; (**) indicate species that are only known from the types. Numbers between brackets indicate unusual maxima.

SPECIES	INTENSITY	SPECIES	INTENSITY
<i>Acholoe astericola</i>	1-6 symb. / host (*)	<i>Harmothoe melanicornis</i>	0.2-0.4 symb. / host cm
<i>Adyte assimilis</i>	1-5 symb. / host (*)	<i>Harmothoe spongicola</i>	1 symb.(**)
<i>Amblosyllis cincinnata</i>	1-35 symb. / host	<i>Histriobdella homari</i>	648 symb. / host
<i>Arctonoe vittata</i>	1-4 symb. / host (*)	<i>Hydroides spongicola</i>	several
<i>Arctonoe pulchra</i>	1-7 symb. / host (*)	<i>Iphitime cuenoti</i>	1-6(128) symb. / host
<i>Branchiosyllis exilis</i>	1-3 symb. / host (*)	<i>Iphitime hartmanae</i>	1-8 symb. / host
<i>Branchipolynoe pettiboneae</i>	4 symb.(**)	<i>Iphitime holobranchiata</i>	1-39 symb. / host
<i>Branchipolynoe seepensis</i>	6 symb.(**)	<i>Mytilidiphila enseiensis</i>	1-21 symb. / host
<i>Branchipolynoe symmytilida</i>	1-3 symb. / host	<i>Nereis grayi</i>	2 symb.(**)
<i>Brychionoe karenae</i>	1-18 symb. / host	<i>Ophryotrocha geryoncola</i>	1-12 symb. / host
<i>Capitella capitata</i>	few (71) symb. / host	<i>Ophryotrocha mediterranea</i>	1-20 symb. / host
<i>Disconatis accolus</i>	1 symb.(**)	<i>Ophyodromus pugettiensis</i>	1-20 symb. / host
<i>Flabelligera affinis</i>	1-7 symb. / host	<i>Phalacrostemma cidariophilum</i>	2-3 symb. / host
<i>Gaudichaudius cimex</i>	1-3 symb. / host	<i>Polydorella dawidoffi</i>	130 symb / host cm ²
<i>Gorgoniapolynoe guadalupensis</i>	0.2-0.4 symb. / host cm	<i>Polydorella smurovi</i>	5-10 symb / host cm ²
<i>Gorgoniapolynoe uschacovi</i>	0.2-0.4 symb. / host cm	<i>Sabellaria alcocki</i>	several symb. / host
<i>Haplosyllides floridana</i>	hundreds of thousands	<i>Spirobranchus giganteus</i>	0.2-12 symb / host cm ²
<i>Haplosyllis agelas</i>	1-4 symb. / host	<i>Stratiodrilus platensis</i>	0-30 symb / host
<i>Haplosyllis chamaeleon</i>	> 1 symb. / host	<i>Vermiliopsis</i> sp.	several ten

Table 4.- Commensal polychaetes with known prevalence. HOST: number of hosts examined.

SPECIES		PREVALENCE	HOSTS
<i>Acholoe astericola</i>		75% - 100%	-
<i>Adyte assimilis</i>		10% - 80%	-
<i>Ancistrosyllis cf groenlandica</i>		50%	-
<i>Antonbruunia viridis</i>		80%	>100
<i>Arctonoe vitatta</i>	<i>Asterias amurensis</i>	0% - 79.1%	-
	<i>Asterias rathbunae</i>	5% - 59%	-
	<i>Acmaea pallida</i>	90% - 94%	-
<i>Arctonoe pulchra</i>	<i>Stichopus parvimensis</i>	60% - 100%	-
	<i>Megatura crenulata</i>	25% - 28%	-
<i>Asterophilia carlae</i>		3.3% - 13%	-
<i>Benhamipolynoe cairnsi</i>		100%	10
<i>Benthoscolex cubanus</i>		65.5% - 100%	-
<i>Branchiosyllis exilis</i>		49.5% (29% - 100%)	142 (1 - 960)
<i>Capitella capitata</i>		100% (males) - 0% (females)	-
<i>Flabelliderma commensalis</i>		6% - 50%	30 - 20
<i>Gastrolepidia clavigera</i>		32% - 80%	-
<i>Gyptis ophiocomae</i>		10%	400
<i>Harmothoe brevipalpa</i>	<i>Pectinaria</i>	60%	68
	<i>Phyllochaetoperus</i>	100%	108
<i>Harmothoe commensalis</i>		22% - 78%	-
<i>Harmothoe hyalonemae</i>		88.3%	171
<i>Hipponoe gaudichaudi</i>		1.2% - 1.5%	247-587
<i>Histriobdella homari</i>		100%	-
<i>Hololepidella nigropunctata</i>		20% - 60%	-
<i>Iphitime cuenoti</i>	<i>Liocarcinus puber</i>	70%	181
	<i>Liocarcinus corrugatus</i>	100%	123
	<i>Liocarcinus depuratus</i>	5.5% - 35%	1964 - 741
	Other hosts	<15%	-
<i>Iphitime sartoral</i>	<i>Libinia spinosa</i>	0.25%	-
	<i>Portunus spinicarpus</i>	0.03%	-
<i>Iphitime paguri</i>		2.6% - 155%	155 - ?
<i>Lumbrineris flabellicola</i>		80% (worms) - 100% (signals)	20
<i>Mytilidiphila enseiensis</i>		100%	-
<i>Nereis fucata</i>		50% - 90%	-
<i>Ophryotrocha geryonicola</i>	<i>Cancer borealis</i>	0.5%	197
	<i>Geryon tridens</i>	33%	65
	<i>Geryon quinquedens</i>	8.8% (males) - 44.4% (females)	277
<i>Ophryotrocha mediterranea</i>		20% (males) - 0% (females)	1072
<i>Ophyodromus pugettensis</i>		50%	200
<i>Petrecca thyasira</i>		50%	10
<i>Pilargis berkeleyae</i>		21.7%	-
<i>Sphaerodoridium commensalis</i>		3.5%	1065
<i>Sphaerodorum ophiurophoretos</i>		6.6% - 11.9%	30 - 256

Table 5.- Commensal polychaetes with reported host-recognition behavior. HOSTS: AST: asteroid, HOL: holothuroid, OPH: Ophiuroid, GAS: gastropod, POP: polyplacophor.

SYMBIONT	HOST	SPECIES	SOURCE OF INFORMATION
Polynoidae			
<i>Arctonoe pulchra</i>	HOL	<i>Stichopus californicus</i>	Davenport 1950, Davenport & Hickok 1951, Dimock & Davenport 1971
“	HOL	<i>Stichopus parvimensis</i>	“
“	GAS	<i>Megathura crenulata</i>	“
“	AST	<i>Dermasterias imbricata</i>	“
“	AST	<i>Luidia foliolata</i>	“
<i>Arctonoe fragilis</i>	GAS	<i>Diodora aspera</i>	Davenport 1950
<i>Arctonoe vittata</i>	AST	<i>Evasterias trochelii</i>	Gerber & Stout 1968, Palmer 1968
“	POP	<i>Cryptochiton stelleri</i>	“
“	GAS	<i>Acmaea pallida</i>	Britayev et al. 1977
“	AST	<i>Asterias amurensis</i>	“
“	AST	<i>Aphelasterias japonica</i>	Britayev 1978(abstract)
<i>Acholoe astericola</i>	AST	<i>Astropecten irregularis</i>	Davenport 1953a
<i>Gattiana cirrosa</i>	POL	<i>Amphitrite johnstoni</i>	“
<i>Lepidasthenia argus</i>	POL	<i>Amphitrite edwardsii</i>	Davenport 1953b
<i>Halosydna brevisetosa</i>	POL	<i>Amphitrite robusta</i>	Davenport & Hickok 1951
<i>Polynoe scolopendrina</i>	POL	<i>Eupolymnia nebulosa</i>	Davenport 1953b
<i>Harmothoe spinifer</i>	POL	<i>Amphitrite gracilis</i>	“
<i>Malmgreniella andreapolis</i>	OPH	<i>Acrocorda brachiata</i>	“
(as <i>Harmothoe lunulata</i> part.)	HOL	<i>Leptosynapta inhaerens</i>	“
<i>Malmgreniella arenicola</i>	POL	<i>Amphitrite johnsoni</i>	“
<i>Hololepidella nigropunctata</i>	OPH	<i>Ophiocoma brevipes</i>	Devaney 1967
“	OPH	<i>Ophiocoma dentata</i>	“
<i>Lepidasthenia tubicola</i>	POL	<i>Loimia medusa</i>	Gaikwad 1993
Hesionidae			
<i>Podarke puggetensis</i>	AST	<i>Patiria miniata</i>	Davenport et al. 1960
“	AST	<i>Luidia foliolata</i>	“

Table 6.- List of parasitic polychaete species (boring species excluded). TYPE: Type of relationship (O, obligatory; F, facultative; P, permanent; T,temporal).

PARASITIC SPECIES	AUTHORITY	HOST GROUP	SPECIES	TYPE	SOURCE
ALCIOPIDAE					
<i>Alciopina parasitica</i>	Claparède & Panceri	Ctenophor	<i>Cydidpe densa</i>	T	Fauvel 1923, Day 1967
OENONIDAE					
<i>Arabella endonata</i>	Emerson	Polychaete	<i>Diopatra ornata</i>	P	Emerson 1974
<i>Arabella iricolor</i>	(Montagu)	Polychaete	<i>Diopatra ornata</i>	T	Hartman 1968
<i>Drilognathus capensis</i>	Day	Polychaete	<i>Onuphis holobranchiata</i>	P	Day 1967
<i>Drilonereis benedicti</i>	Pettibone	Polychaete	<i>Onuphis magna</i>	P	Pettibone 1957
<i>Drilonereis caulleryi</i>	Pettibone	Polychaete	<i>Onuphis (Nothria) conchylega</i>	P	Pettibone 1957
<i>Drilonereis forcipes</i>	(Hartman)	Polychaete	<i>Eunice</i> sp.	P	Pettibone 1957
“		Polychaete	<i>Eunice antennata</i>	P	Pettibone 1957
<i>Drilonereis parasiticus</i>	(Caullery)	Polychaete	Terebellidae p.i.	P	Pettibone 1957
<i>Drilonereis</i> sp.	Pérès	Polychaete	<i>Protula tubularia</i>	P	Pérès 1949
<i>Haematocleptes laenae</i>	Hartman & Fauchald	Polychaete	<i>Leaena minima</i>	P	Hartman & Fauchald 1971
<i>Haematocleptes terebellides</i>	Wiren	Polychaete	<i>Terebellides stroemi</i>	P	Wiren 1886, Pettibone 1957, George & Hartmann-Schröder 1985
<i>Labrorostratus luteus</i>	Uebelacker	Polychaete	<i>Haplosyllis spongicola</i>	P	Uebelacker 1978
<i>Labrorostratus parasiticus</i>	Saint Joseph	Polychaete	<i>Eusyllis monilicornis</i>	T	Pettibone 1957
“		Polychaete	<i>Grubeosyllis clavata</i>	T	Pettibone 1957
“		Polychaete	<i>Odontosyllis ctenostoma</i>	T	Pettibone 1957
“		Polychaete	<i>Pionosyllis lamelligera</i>	T	Pettibone 1957
“		Polychaete	<i>Sphaerosyllis pirifera</i>	T	Wu et al. 1982
“		Polychaete	<i>Syllis prolifera</i>	T	Pettibone 1957
<i>Labrorostratus prolificus</i>	Amaral	Polychaete	<i>Perinereis cultrifera</i>	T	Amaral 1977
<i>Labrorostratus</i> sp.	San Martín & Sardá	Polychaete	<i>Syllis columbretensis</i>	P	San Martín & Sardá 1986
“		Polychaete	<i>Grubeosyllis clavata</i>	P	San Martín & Sardá 1986
“		Polychaete	<i>Sphaerosyllis hystrix</i>	P	San Martín & Sardá 1986
<i>Notocirrus spiniferus</i>	(Moore)	Polychaete	<i>Diopatra cuprea</i>	T	Allen 1952, Pettibone 1957
<i>Notocirrus</i> sp. (Juvenil)		Polychaete	<i>Marphysa sanguinea</i>	T	Koch 1846, Pettibone 1957
<i>Oligognathus bonelliae</i>	Spengel	Echiuroid	<i>Bonelia viridis</i>	P	Pettibone 1957
<i>Oligognathus parasiticus</i>	Cerruti	Polychaete	<i>Microspio mecznikovianus</i>	P	Pettibone 1957
<i>Pholadiphilia turnerae</i>	Dean	Bivalve	<i>Xyloredo ingolfia</i>	P	Dean 1992
“		Bivalve	Xilophangidae p.i.	P	Dean 1992
CALAMYZIDAE					

<i>Calamyzas amphictenicola</i>	Arwidson	Polychaete	<i>Amphicteis gunneri</i>	P	Ardwisson 1933, Hartmann-Schröder 1971
<i>Asetocalamyzas laoncola</i>	Tzetlin	Polychaete	<i>Laonome cirrata</i>	P	Tzetlin 1985
CAPITELLIDAE					
<i>Capitomastus minimus</i>	Langerhans	Cephalopod	<i>Loligo vulgaris</i>	T	Clark 1956
<i>Capitella ovinicola</i>	Hartman	Cephalopod	<i>Loligo opalescens</i>	T	Clark 1956
DORVILLEIDAE					
<i>Dorvillea sociabilis</i>	(Webster)	Sponge	<i>Ircinia campana</i>	?	Dean 1973
<i>Ophryotrocha puerilis</i>	Claparède & Mecznikov	Holothuroid	<i>Ocnus planci</i>	T	Paris 1955, Clark 1956, Jangoux 1987
ICHTHYOTOMIDAE					
<i>Ichthyotomus sanguinarius</i>	Eisig	Fish	<i>Myrus vulgaris</i>	P	Paris 1955, Fauchald & Jumars 1977
“		Fish	<i>Conger vulgaris</i>	P	Paris 1955, Fauchald & Jumars 1977
“		Fish	<i>Sphagebranchus inberbis</i>	P	Clark 1956
IPHITIMIDAE					
<i>Veneriserva pygoclava</i>	Rossi	Polychaete	<i>Aphrodita longipalpa</i>	P	Rossi 1984
LUMBRINERIDAE					
<i>Ophiuricola cynipis</i>	Ludwig	Ophiuroid	<i>Ophiura irrorata</i>	P	Ludwig 1905, Clark 1956, Alvà & Jangoux 1989
“		Ophiuroid	<i>Ophioglypha tumulosa</i>	P	Jangoux 1987
SPHAERODORIDAE					
<i>Sphaerodorum flavus</i>	Oersted	Ophiuroid	<i>Ophiura</i> sp.	F	Ockelman personal communication
“		Ophiuroid	<i>Amphiura filiformis</i>	F	Ockelman personal communication
“		Ophiuroid	<i>Amphiura chiajei</i>	F	Ockelman personal communication
SYLLIDAE					
<i>Branchiosyllis exilis</i> (Juvenil)	(Gravier)	Sponge	<i>Speciospongia vesperia</i>	F	Clark 1956
<i>Branchiosyllis oculata</i>	Elhers	Sponge	<i>Aplysilla longispina</i>	O	Pawlik 1983
“		Sponge	<i>Aplysina fistularis</i>	O	Pawlik 1983
“		Sponge	<i>Chondrilla nucula</i>	O	Pawlik 1983
“		Sponge	<i>Cinachyra alloclada</i>	O	Pawlik 1983
“		Sponge	<i>Ircinia felix</i>	O	Pawlik 1983
“		Sponge	<i>Pseudoceratina crassa</i>	O	Pawlik 1983
“		Sponge	<i>Speciospongia othella</i>	O	Pawlik 1983
“		Sponge	<i>Speciospongia vesperia</i>	O	Dauer 1974
“		Sponge	<i>Tedania ignis</i>	O	Pawlik 1983
“		Sponge	<i>Tethya actinia</i>	O	Pawlik 1983
<i>Haplosyllis spongicola</i>	(Grube)	Sponge	<i>Aaptos</i> cf <i>aaptos</i>	O	T.A. Britayev personal observations
“		Sponge	<i>Adocia neens</i>	O	Dauer 1974
“		Sponge	<i>Aplysina cauliformis</i>	O	Tsurumi & Reiswig 1997
“		Sponge	<i>Clatrina coriacea</i>	O	Clark 1956
“		Sponge	<i>Gellioides digitalis</i>	O	Uebelacker 1978
“		Sponge	<i>Geodia gibberos</i>	O	Dauer 1974
“		Sponge	<i>Halichondria</i> sp.	O	Spooner et al. 1957

“		Sponge	<i>Halichondria agglomerans</i>	O	Uriz 1978
“		Sponge	<i>Haliclona</i> sp.	O	T.A. Britayev personal observations
“		Sponge	<i>Ircinia campana</i>	O	Dauer 1974
“		Sponge	<i>Ircinia fasciculata</i>	O	Alós et al. 1982
“		Sponge	<i>Ircinia ramosa</i>	O	Dauer 1974
“		Sponge	<i>Petrosia ficiformis</i>	O	Alós et al. 1982
“		Sponge	<i>Phoriospongia</i> (<i>Chondropsis</i>) sp.	O	Magnino & Gaino in press
“		Sponge	<i>Reniera rosea</i>	O	Clark 1956
“		Sponge	<i>Rhizaxinella pyrifera</i>	O	Uriz 1983
“		Sponge	<i>Speciospongia vesparia</i>	O	Dauer 1974
“		Sponge	<i>Theonella swinhoei</i>	O	Magnino & Gaino in press
“		Sponge	<i>Verongula reisi</i>	O	Reiswig 1973
“		Sponge	<i>Xytopsene sigmatum</i>	O	Dauer 1974
“		Sponge	Young specimen	O	Bacescu 1971
“		Sponge	Unidentified	O	Lee & Rho 1994
“		Polychaete	<i>Eunice</i> sp.	T	Treadwell 1909, Potts 1912
<i>Myrianida piningera</i>	(Montagu)	Tunicate	<i>Phallusia mammilata</i>	T	Spooner et al. 1957
“		Tunicate	<i>Ascidella aspersa</i>	T	Spooner et al. 1957
<i>Parasitosyllis claparede</i>	Potts	Nemertini	Unidentified	P	Potts 1912
“		Polychaete	Unidentified	P	Potts 1912
<i>Procerastea fasciata</i>	Hartmann-Schröder	Cnidarian	<i>Eudendrium carneum</i>	F	Cruz-Rivera personal communication
<i>Procerastea halleniana</i>	Malaquin	Cnidarian	<i>Syncoryne eximia</i>	F	Allen 1915, 1921, Spooner et al. 1957, Alós 1989
“		Cnidarian	<i>Tubularia indivisa</i>	F	Caullery 1925, Spooner et al. 1957
<i>Procerastea hydrozoicola</i>	Hartmann-Schröder	Cnidarian	<i>Pseudosolanderia</i> sp.	O	Hartmann-Schröder 1992
<i>Procerastea parasimpliseta</i>	Hartmann-Schröder	Cnidarian	<i>Pseudosolanderia</i> sp.	O	Hartmann-Schröder 1992
<i>Proceraea</i> sp.	Britayev, San Martín & Sheiko	Cnidarian	<i>Abietinaria turgida</i>	O	Britayev et al. unpubl.
“		Cnidarian	<i>Orthopixis integra</i>	O	T.A. Britayev personal observations
<i>Typosyllis extenuata</i>		Sponge	<i>Speciospongia vesperia</i>	F	Pearse 1932, Dauer 1974

Table 7.- Parasitic polychaetes with known infestation intensities. The asterisk indicates the mentioning of male and female individuals living near together on the same host.

SPECIES	INTENSITY
<i>Arabella endonata</i>	> 4 parasites / host
<i>Asetocalamyzas laoncola</i>	1 parasites / host
<i>Branchiosyllis oculata</i>	4-34 parasites / host
<i>Calamyzas amphictenicola</i>	>2* parasites / host
<i>Drilognathus capensis</i>	1 parasites / host
<i>Drilonereis benedicti</i>	1 parasites / host
<i>Drilonereis caulleryi</i>	1 parasites / host
<i>Drilonereis forcipes</i>	1 parasites / host
<i>Drilonereis parasiticus</i>	1 parasites / host
<i>Drilonereis sp.</i>	1 parasites / host
<i>Haematocleptes laenae</i>	1 parasites / host
<i>Haplosyllis spongicola</i>	
Young sponge	21000 parasites / host
<i>Verongula reisiwigi</i>	50-100 parasites / host cm ³
<i>Theonella swinhoei</i>	68 parasites / host cm ³
<i>Phorospongia sp.</i>	56-240 parasites / host cm ³
<i>Haplosyllis spongicola</i> (as <i>H. cephalata</i>)	2 parasites / host
<i>Ichthyotomus sanguinarius</i>	1-2 * parasites / host
<i>Labrorostratus luteus</i>	1 parasites / host
<i>Labrorostratus parasiticus</i>	1 parasites / host
<i>Labrorostratus prolificus</i>	33 parasites / host
<i>Labrorostratus sp.</i>	1 parasites / host
<i>Notocirrus sp.</i>	numerous parasites / host
<i>Notocirrus spiniferus</i>	53 parasites / host
<i>Pholadiphila turnerae</i>	1 parasites / host
<i>Proceraea sp.</i>	8-47 parasites / host colony
<i>Veneriservia pygoclava</i>	4-8 parasites / host

Table 8.- List of symbiotic species of boring polychaetes of the family Spionidae. TYPE: Type of relationship (O, obligatory; F, facultative).

SYMBIOTIC BORERS	AUTHORITY	HOST	SPECIES	TYPE	SOURCE
<i>Boccardia accus</i>	(Rainer)	Bivalve	<i>Atrina pectinata zetlandica</i>	F	Read 1975
“		Bivalve	<i>Chione stuchburyi</i>	F	Read 1975
“		Bivalve	<i>Ostrea</i> sp.	F	Read 1975
“		Bivalve	<i>Paphies subtriangularum</i>	F	Read 1975
“		Bivalve	<i>Perna canaliculus</i>	F	Read 1975
“		Gastropod	<i>Haliotis iris</i>	F	Read 1975
<i>Boccardia androgyna</i>	Read	Songe	<i>Ancorina alata</i>	O	Read 1975
“		Songe	<i>Ancorina</i> spp.	O	Read 1975
“		Songe	<i>Anchinoe</i> spp.	O	Read 1975
“		Songe	<i>Halichondria</i> spp.	O	Read 1975
“		Songe	<i>Tethya</i> spp.	O	Read 1975
<i>Boccardia anophthalma</i>	(Rioja)	Gastropod	<i>Muricanthus nigricus</i>	O	Blake 1980
<i>Boccardia berkeleyorum</i>	Blake & Woodwick	Gastropod	<i>Pododesmus macrochisma</i>	O	Blake 1980
<i>Boccardia chilensis</i>	Blake & Woodwick	Bivalve	<i>Atrina pectinata zetlandica</i>	F	Read 1975
“		Bivalve	<i>Chione stuchburyi</i>	F	Read 1975
“		Gastropod	<i>Haliotis iris</i>	F	Read 1975
<i>Boccardia knoxi</i>	Rainer	Bivalve	<i>Atrina pectinata zetlandica</i>	F	Read 1975
“		Gastropod	<i>Haliotis iris</i>	F	Read 1975
<i>Boccardia lamellata</i>	Rainer	Bivalve	<i>Atrina pectinata zetlandica</i>	F	Read 1975
<i>Boccardia outakouica</i>	Rainer	Bivalve	<i>Atrina pectinata zetlandica</i>	F	Read 1975
“		Bivalve	<i>Ostrea luritaria</i>	F	Rainer 1973
<i>Boccardia tricuspa</i>	(Hartman)	Bivalve	<i>Concholepas concholepas</i>	F	Carrasco 1974
“		Gastropod	<i>Haliotis</i> sp.	F	Blake 1980
“		Gastropod	<i>Muricanthus nigricus</i>	F	Blake 1980
<i>Boccardiella hamata</i>	(Webster)	Bivalve	<i>Crassostrea gigas</i>	F	Radashevsky 1993
“		Bivalve	<i>Mizuchopecten yessoensis</i>	F	Radashevsky 1993
“		Bivalve	Bivalve	F	Webster 1879a, b, Hartman 1951, Blake & Evans 1973
<i>Dipolydora alborectalis</i>	(Radashevsky)	Bivalve	<i>Crassostrea gigas</i>	F	Radashevsky 1993
“		Bivalve	<i>Crenomytilus grayanus</i>	F	Radashevsky 1993
“		Bivalve	<i>Mizuchopecten yessoensis</i>	F	Radashevsky 1993
“		Bivalve	<i>Modiolus kurilensis</i>	F	Radashevsky 1993
“		Bivalve	<i>Pododesmus macrochisma</i>	F	Radashevsky 1993

		Bivalve	<i>Swiftopecten swifti</i>	F	Radashevsky 1993
		Cirriped	<i>Balanus rostratus</i>	F	Radashevsky 1993
		Gastropod	<i>Acmaea pallida</i>	F	Radashevsky 1993
		Gastropod	<i>Crepidula derjugini</i>	F	Radashevsky 1993
		Gastropod	<i>Littorina squalida</i>	F	Radashevsky 1993
		Gastropod	<i>Nucella heyseana</i>	F	Radashevsky 1993
		Gastropod	<i>Tegula rustica</i>	F	Radashevsky 1993
<i>Dipolydora armata</i>	(Langerhans)	Cnidarian	<i>Leptastrea purpurea</i>	F	Okuda 1937
		Bryozoan	<i>Holoporella sardonica</i>	F	Laubier 1958
		Bryozoan	<i>Porella concina</i>	F	Laubier 1958
		Bryozoan	<i>Schizoporella armata</i>	F	Laubier 1958
<i>Dipolydora barbilla</i>	(Blake)	Gastropod	<i>Muricanthus nigricus</i>	F	Blake 1981
<i>Dipolydora bidentata</i>	(Zachs)	Bivalve	<i>Crassostrea gigas</i>	F	Radashevsky 1993
		Bivalve	<i>Crenomytilus grayanus</i>	F	Radashevsky 1993
		Bivalve	<i>Mizuchopecten yessoensis</i>	F	Radashevsky 1993
		Bivalve	<i>Modiolus kurilensis</i>	F	Radashevsky 1993
		Bivalve	<i>Pododesmus macrochisma</i>	F	Radashevsky 1993
		Bivalve	<i>Swiftopecten swifti</i>	F	Radashevsky 1993
		Gastropod	<i>Acmaea pallida</i>	F	Radashevsky 1993
		Gastropod	<i>Buccinum middendorffii</i>	F	Radashevsky 1993
		Gastropod	<i>Margarites sp.</i>	F	Radashevsky 1993
		Gastropod	<i>Muricanthus nigricus</i>	F	Blake 1981
		Gastropod	<i>Nucella hyseana</i>	F	Radashevsky 1993
		Gastropod	<i>Tegula rustica</i>	F	Radashevsky 1993
<i>Dipolydora carunculata</i>	(Radashevsky)	Bivalve	<i>Crassostrea gigas</i>	F	Radashevsky 1993
		Bivalve	<i>Crenomytilus grayanus</i>	F	Radashevsky 1993
		Bivalve	<i>Mizuchopecten yessoensis</i>	F	Radashevsky 1993
		Gastropod	<i>Acmaea pallida</i>	F	Radashevsky 1993
		Gastropod	<i>Nucella heyseana</i>	F	Radashevsky 1993
<i>Dipolydora commensalis</i>	(Andrews)	Decapod	<i>Clibanarius vittatus</i>	O	Dauer 1991
		Decapod	<i>Pagurus annulipes</i>	O	Dauer 1991
		Decapod	<i>Pagurus branchiomastus</i>	O	Radashevski 1989
		Decapod	<i>Pagurus capillatus</i>	O	Radashevski 1989
		Decapod	<i>Pagurus granosimanus</i>	O	Hatfield 1965
		Decapod	<i>Pagurus longicarpus</i>	O	Andrews 1891a, b, Hatfield 1965, Dauer 1991
		Decapod	<i>Pagurus middendorfi</i>	O	Radashevski 1989
		Decapod	<i>Pagurus pollicaris</i>	O	Dauer 1991
		Decapod	<i>Pagurus samuelis</i>	O	Blake 1969

<i>Dipolydora concharum</i>	(Verrill)	Bivalve	<i>Mercenaria mercenaria</i>	F	Blake 1969
“		Bivalve	<i>Mercenaria stimpsoni</i>	O	Radashevsky 1993
“		Bivalve	<i>Mizuchopecten yessoensis</i>	O	Mori et al. 1985, Radashevsky 1993
“		Bivalve	<i>Pandora wardiana</i>	O	Radashevsky 1993
“		Bivalve	<i>Plecopecten magellanicus</i>	F	Blake 1969
“		Gastropod	<i>Buccinum verkruzeni</i>	O	Radashevsky 1993
“		Gastropod	<i>Crepidula derjugini</i>	O	Radashevsky 1993
“		Gastropod	<i>Cyprina islandica</i>	O	Blake & Evans 1973
“		Gastropod	<i>Neptunea bulbacea</i>	O	Radashevsky 1993
“		Gastropod	<i>Neptunea constricta</i>	O	Radashevsky 1993
“		Gastropod	<i>Neptunea lyrata</i>	O	Radashevsky 1993
“		Gastropod	<i>Neptunea polycostata</i>	O	Radashevsky 1993
“		Gastropod	<i>Turritella fortilirata</i>	O	Radashevsky 1993
<i>Dipolydora elegantissima</i>	(Blake & Woodward)	Bivalve	<i>Tivela stultorum</i>	O	Blake & Woodward 1971, Blake 1980
<i>Dipolydora rogeri</i>	(Martin)	Sponge	<i>Cliona viridis</i>	O	Martin 1996
<i>Dipolydora socialis</i>	(Schmarda)	Bivalve	<i>Plecopecten magellanicus</i>	F	Blake & Evans 1973
<i>Dipolydora trilobata</i>	(Radashevsky)	Bivalve	<i>Crassostrea gigas</i>	F	Radashevsky 1993
“		Bivalve	<i>Crenomytilus grayanus</i>	F	Radashevsky 1993
“		Bivalve	<i>Modiolus kurilensis</i>	F	Radashevsky 1993
“		Bivalve	<i>Pododesmus macroshisma</i>	F	Blake & Woodward 1971
“		Cirriped	<i>Balanus rostratus</i>	F	Radashevsky 1993
“		Cirriped	<i>Semibalanus cariosus</i>	F	Radashevsky 1993
“		Gastropod	<i>Acmaea pallida</i>	F	Radashevsky 1993
“		Gastropod	<i>Buccinum middendorffii</i>	F	Radashevsky 1993
“		Gastropod	<i>Margarites</i> sp.	F	Radashevsky 1993
“		Gastropod	<i>Nucella heyseana</i>	F	Radashevsky 1993
“		Polychaete	<i>Cruzigera zygonophora</i>	F	Radashevsky 1993
<i>Polydora allopuris</i>	Light	Cnidarian	<i>Allopora californica</i>	O	Light 1970a
<i>Polydora biocipitalis</i>	Blake & Woodward	Bivalve	<i>Mesodesma donacium</i>	F	Blake & Woodward 1972, Blake 1983
<i>Polydora brevipalpa</i>	Zachs	Bivalve	<i>Mizuchopecten yessoensis</i>	F	Imajima & Sato 1984, Mori et al. 1985, Radashevsky 1993
<i>Polydora ciliata</i>	(Johnston)	Bivalve	<i>Mytilus edulis</i>	F	Michaelis 1978, Ramberg & Schram 1982
“		Bivalve	<i>Mizuchopecten yessoensis</i>	F	Mori et al. 1985
“		Bivalve	<i>Mya arenaria</i>	F	Blake & Evans 1973, Ramberg & Schram 1982
“		Bivalve	<i>Ostrea carunculata</i>	F	Blake & Evans 1973
“		Bivalve	<i>Ostrea edulis</i>	F	Korringa 1951, Blake & Evans 1973, Ramberg & Schram 1982
“		Gastropod	<i>Littorina littorea</i>	F	Blake 1980, Ramberg & Schram 1982

<i>Polydora cornuta</i>	Bosc	Phanerogam	<i>Zostera marina</i>	F	Michaelis 1978
<i>Polydora curiosa</i>	Radashevsky	Gastropod	<i>Acmaea pallida</i>	F	Radashevsky 1994
<i>Polydora glycymerica</i>	Radshevsky	Bivalve	<i>Glycymeris yessoensis</i>	O	Radashevsky 1993
“		Bivalve	<i>Scapharca boughtoni</i>	O	Radashevsky 1993
<i>Polydora haswelli</i>	Blake & Kudenov	Bivalve	<i>Crassostrea commercialis</i>	O	Blake & Evans 1973, Blake & Kudenov 1978
<i>Polydora hoplura</i>	Claparède	Bivalve	<i>Atrina pectinata zetlandica</i>	F	Read 1975
“		Bivalve	<i>Crassostrea gigas</i>	F	Blake & Kudenov 1978
“		Bivalve	<i>Ostrea edulis</i>	F	Korringa 1951, Blake 1980
“		Bryozoan	<i>Schizoporella auriculata</i>	F	Laubier 1959
<i>Polydora latispinosa</i>	Blake & Kudenov	Bivalve	<i>Pecten alba</i>	O	Blake & Kudenov 1978
“		Bivalve	Oysters	O	Blake & Kudenov 1978
<i>Polydora vulgaris</i>	Mohammad	Bivalve	<i>Pinctada margaritifera</i>	F	Mohammad 1972, Blake 1980
<i>Polydora websteri</i>	Hartman	Bivalve	<i>Aequipecten gibbus</i>	F	Blake & Evans 1973
“		Bivalve	<i>Crassostrea commercialis</i>	F	Blake & Evans 1973
“		Bivalve	<i>Crassostrea gigas</i>	F	Blake & Evans 1973
“		Bivalve	<i>Crassostrea virginica</i>	F	Blake & Evans 1973
“		Bivalve	<i>Hinnites multirugosus</i>	F	Blake & Evans 1973
“		Bivalve	<i>Mercenaria mercenaria</i>	F	Blake & Evans 1973
“		Bivalve	<i>Mesodesma deauratum</i>	F	Blake & Evans 1973
“		Bivalve	<i>Modiolus modiolus</i>	F	Blake & Evans 1973
“		Bivalve	<i>Mytilus edulis</i>	F	Blake & Evans 1973
“		Bivalve	<i>Ostrea lurida</i>	F	Blake & Evans 1973
“		Bivalve	<i>Ostrea permollis</i>	F	Blake & Evans 1973
“		Bivalve	<i>Ostrea</i> sp.	T	Blake 1969
“		Bivalve	<i>Patinopecten caurinus</i>	F	Blake & Evans 1973
“		Bivalve	<i>Pecten irradians</i>	F	Blake & Evans 1973
“		Bivalve	<i>Plecopecten magellanicus</i>	F	Blake 1971, Blake & Evans 1973
“		Gastropod	<i>Crepidula fornicata</i>	F	Blake 1971
“		Gastropod	<i>Littorina littorea</i>	F	Blake 1971
“		Gastropod	<i>Muricanthus nigricus</i>	F	Blake 1980
“		Gastropod	<i>Thais lapillus</i>	F	Blake 1971
<i>Polydora wobberi</i>	Light	Cnidarian	<i>Lophogorgia</i> sp.	O	Light 1970b
<i>Polydora woodwicki</i>	Blake & Kudenov	Gastropod	<i>Haliotis ruber</i>	F	Blake & Kudenov 1978

Table 9.- List of symbiotic species of boring polychaetes of the families Sabellidae and Cirratulidae. TYPE: Type of relationship (O, obligatory; F, facultative).

SYMBIOTIC BORERS	AUTHORITY	HOST	SPECIES	TYPE	SOURCE
SABELLIDAE					
<i>Caobangia abboti</i>	Jones	Gastropod	<i>Antimelania asperata</i>	O	Jones 1974
“		Gastropod	<i>Balanocochlis glans</i>	O	Jones 1974
“		Gastropod	<i>Brotia dactylus</i>	O	Jones 1974
“		Gastropod	<i>Brotia pageli</i>	O	Jones 1974
“		Gastropod	<i>Brotia pontificalis</i>	O	Jones 1974
“		Gastropod	<i>Brotia pontificalis agrestis</i>	O	Jones 1974
“		Gastropod	<i>Brotia pontificalis pageli</i>	O	Jones 1974
“		Gastropod	<i>Stenomelania</i> sp. 1	O	Jones 1974
“		Gastropod	<i>Stenomelania</i> sp. 2	O	Jones 1974
<i>Caobangia billeti</i>	Giard	Gastropod	<i>Melania aubryana</i>	O	Jones 1974
<i>Caobangia brandti</i>	Jones	Gastropod	<i>Brotia pseudosulcospira pseudosulcospira</i>	O	Jones 1974
“		Gastropod	<i>Brotia pseudosulcospira armata</i>	O	Jones 1974
“		Gastropod	<i>Brotia binodosa binodosa</i>	O	Jones 1974
“		Gastropod	<i>Brotia binodosa subgloriosa</i>	O	Jones 1974
“		Gastropod	<i>Anulotaia cf mekongensis</i>	O	Jones 1974
“		Gastropod	<i>Cipangopaludina chinensis</i>	O	Jones 1974
“		Gastropod	<i>Mekongia jullieni</i>	O	Jones 1974
“		Bivalve	<i>Hyriopsis delaporteii</i>	O	Jones 1974
<i>Caobangia ceylonica</i>	Jones	Gastropod	<i>Ganga abbreviata</i>	O	Jones 1974
“		Gastropod	<i>Paludomus hanleyi</i>	O	Jones 1974
“		Gastropod	<i>Tanalia aculeata</i>	O	Jones 1974
<i>Caobangia indica</i>	Jones	Gastropod	<i>Antimelania menkiana</i>	O	Jones 1974
“		Gastropod	<i>Hemimindra stephanus</i>	O	Jones 1974
<i>Caobangia morrisoni</i>	Jones	Gastropod	<i>Brotia</i> sp. 1	O	Jones 1974
“		Gastropod	<i>Brotia</i> sp. 2	O	Jones 1974
“		Gastropod	<i>Brotia testudinaria</i>	O	Jones 1974
<i>Caobangia smithi</i>	Jones	Gastropod	<i>Brotia costula siamensis</i>	O	Jones 1974
“		Gastropod	<i>Brotia cf baccata</i>	O	Jones 1974
“		Gastropod	<i>Brotia gloriosa</i>	O	Jones 1974
“		Gastropod	<i>Brotia</i> sp. 3	O	Jones 1974

“		Gastropod	<i>Paludomus conica</i>	O	Jones 1974
<i>Pseudofabricia</i> sp.	Kudenov	Gastropod	<i>Haliotis</i> sp.	F	Oakes & Fields 1996
<i>Pseudopotamilla reniformis</i>	(Müller)	Bivalve	<i>Plecopecten magellanicus</i>	F	Blake 1969
CIRRATULIDAE					
<i>Dodecaceria concharum</i>	Oersted	Bivalve	<i>Ostrea edulis</i>	F	D. Martin personal observations
<i>Dodecaceria fimbriata</i>	(Verrill)	Bivalve	<i>Placopecten magellanicus</i>	F	Blake 1969, M.E. Petersen personal communication
“		Bivalve	<i>Mercenaria mercenaria</i> ,	F	Blake 1969
“		Bivalve	<i>Crepidula fornicata</i>	F	Blake 1969
