

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 represented 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 partners 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 were initially considered as parasitisms that, with increasing knowledge, have been redefined as 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 2).

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 groves 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* overlapp 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 *Wilsoniella* (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 brizingid 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 californica*, 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. geryonicola*.

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 *Sphaerodorium 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 *Megatoura 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. geryonicola* 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. geryonicola* (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 laevigater*. 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 malidanid 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 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 Phanerozoia 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 *Acrocorda 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 chemoreception 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 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 heteronereis.

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. *Histriobdella homari* and *Ophryotrocha geryonicola*, 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. *Branchiosyllis 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 apheritid 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 pyrifer* (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 about 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 *Haematoceptes*, 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*, *Haematoceptes* and *Oligogonathus*, 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 *Oligogonathus* while in *Drilogonathus*, *Labrorostratus* and *Haematoceptes* 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 *Haematoceptes* than in *Drilogonathus*, *Oligogonathus* 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 about the possible sources of food for the endoparasitic oeononids and, thus, about 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 wood-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 claparede* (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 calamizid, *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 oenonids 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 oenonids, 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 oenonids 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 & Woodwick 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, Korringa 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 spongy 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 columellar 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 glycymerica* 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 species.

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 *Histriobdella 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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