

Factors Affecting the Social Behaviour of Crustaceans Living Symbiotically with Other Marine Invertebrates: A Modelling Approach

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Abstract

Many crustacean species live symbiotically on, in, or with other marine macroinvertebrates. Characteristics of the macroinvertebrate hosts will have strong effects on the ability of crustaceans in defending host individuals and movements between hosts. Herein we developed a predictive model in order to examine how the "symbiotic environment" affects the social behaviour of symbiotic crustaceans. We considered two key vectors affecting the social behaviour of symbiotic crustaceans: A) their host monopolisation potential, and B) their intraspecific encounter rates. The monopolisation potential depended primarily on proximate factors such as the relationship between symbiont size and host size, host morphology, and weaponry of the symbiont species. The larger the symbiotic crustacean in relation to its host the higher is its potential to monopolise its host: relatively large symbiont species monopolised one host individual as solitary individuals or as heterosexual pairs while small species tended to share a host individual with many conspecifics. The tendency of symbionts to move between individual hosts was primarily affected by proximate factors such as predation pressure and host distribution and abundance.

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Movements between hosts have direct effects on intraspecific encounter rates as well as on the strength of these interactions. In species in which environmental conditions (e.g. high predation pressure, low host abundance) limited movements between hosts, the strength of intraspecific interactions increased: species with a high monopolisation potential tended to exclude conspecifics from their hosts. Some species with a low monopolisation potential increased their collective monopolisation potential by co-operating with genetically related individuals (excluding unrelated conspecifics from a host individual). In conclusion, among the factors examined herein, the ability to defend a host (monopolisation potential) and mobility (= the probability of intraspecific encounters) had strong effects on the social behaviour of symbiotic crustaceans. One additional factor that proved to be important was the reproductive mode of symbiotic crustaceans: most species that occurred in structured groups on their hosts engaged in extended parental care. Based on the results of this first analysis, we identify as one of the most important tasks for the future the examination of how proximate factors interact. Improved predictive models will foster our understanding of the behavioural diversity of symbiotic crustaceans (organisms).

Keywords: Crustacea, symbiosis, social behaviour, marine, ecology

1. Introduction

Background

Social behaviour of marine crustaceans that live symbiotically on or in other organisms has for a long time attracted the attention of biologists (see historical treatment of reports on crustacean symbionts in Arndt, 1933). Recently, this interest has resurged after the first eusocial marine invertebrate had been reported: a small shrimp species that inhabits the vast spongocoel spaces of tropical sponges (Duffy, 1996; Duffy et al., 2000). One of the main questions that researchers have asked is how the host environment affects the social behaviour of the crustacean symbionts. Knowlton (1980) has proposed that strong predation pressure favour the evolution of monogamy in the anemone-dwelling shrimp *Alpheus armatus*. Similarly, Duffy et al. (2000) have suggested that the strong predation pressure and the limited availability of hosts have favoured the evolution of eusocial behaviour in *Synalpheus* species. Thus, several environmental and host-related factors have an influence on the social behaviour of symbiotic crustaceans. Herein, we compare the social behaviour of a diverse and selective sample of symbiotic crustaceans and attempt to reveal whether similar association patterns occur in species characterised by similar environmental and host-related factors.

The adoption of a symbiotic life style represents one of the most important environmental adaptations of marine crustaceans (Ross, 1983). Among marine

crustaceans, a wide variety of taxa, including shrimps, crabs, amphipods, isopods, and copepods have been described as symbionts of macro-invertebrates all around the world, including tropical and temperate environments, and intertidal and subtidal regimens. Furthermore, the kind of symbiotic partnerships, regarding the cost and benefits for the symbionts, may vary widely. Relationships such as parasitism, mutualism and commensalism have been described between several marine macro-invertebrate species and their crustacean symbionts (Castro, 1988). Furthermore, macro-invertebrates used as hosts by marine crustaceans present a wide range of sizes, morphologies, habitats, and may vary widely in their general biology and ecology. Depending on the type of host inhabited, the form of association between host and symbiont, and the environment in which the host lives, symbionts will need to interact among themselves in different ways to procure refuges, food, or to reproduce and to care for their offspring. In this way, symbiotic environments can be expected to produce a wide range of social structures on their symbionts.

Several factors already studied in marine and terrestrial systems (such as resource distribution and predation pressure), have been suggested to influence the social behaviour of a species (see Wilson, 1975; Barash, 1982; Alcock, 1997). As an example for marine invertebrates, monogamous mating systems have been observed when predation pressure is high. Movements between refuges in search of sexual partners are suppressed when predation pressure is high. Each member of the species needs to share a refuge with a member of the opposite sex, in order to achieve and monopolise copulations (Knowlton, 1980). Furthermore, food distribution and abundance has been shown to affect the establishment of territories and their size in several terrestrial and marine vertebrate and invertebrate species (Barash, 1982; Abele et al., 1986; Alcock, 1997). To what extent these and other factors (host size and morphology, trophic relationships) are capable to affect the social behaviour of symbiotic marine and terrestrial invertebrate species remains to be explored.

A first indication that the symbiotic environment affects the social behaviour of symbiotic crustaceans is provided by the distinct association patterns in which these symbionts are found on/in their respective hosts. Some symbiotic species inhabit their hosts as solitary occupants, aggressively defending them against any conspecific intruder. This pattern is known for certain crabs that inhabit sea anemones (Baeza et al., 2001; Baeza unpublished data). Other species may inhabit their hosts as heterosexual pairs, rejecting any additional conspecific from their host individual (Knowlton, 1980; Huber, 1987; Baeza, 1999). Thus, in these species, two members of the opposite sex cooperate in defending their hosts. Many symbiotic crustaceans are also found in groups on their hosts (Thiel, 2000; Baeza and Thiel, 2000). These groups may be structured, i.e. be characterised by a distinct demographic pattern: one male may guard several females on its host individual (as suggested for

Gnathophylloides mineri, Patton et al., 1985) or a female (and male) may cohabit with its growing offspring in a host (for example *Leucothoe "ascidicola"*, Thiel, 2000). Unstructured aggregations in which no distinct demographic pattern is recognizable also have been reported for some symbiotic crustaceans (*Periclimenes anthophilus*, Nizinski, 1989).

Understanding whether and how host-related factors and other environmental parameters affect the social behaviour of symbiotic crustaceans represents an important step in elucidating their general ecology. The diverse examples of symbiotic crustacean species represent an interesting model to investigate how and to what extent factors in the marine environment affect the social behaviour of invertebrates. Here, we propose several features of the host environment that are likely to affect how conspecifics interact among themselves to procure refuge, food and other limiting resources. We raise predictions, we contrast these predictions with data from symbiotic crustacean species and finally, we propose a model predicting the social behaviour of a symbiont species according to the host and environment in which it may be found. Predictive models have proven very useful to understand the life history traits of symbiotic organisms (Roughgarden, 1975).

Factors affecting the social behaviour of a symbiont species: The model

The social behaviour of a species comprises a complex set of different behavioural elements performed by interacting conspecifics (Wilson, 1975). Social behaviour may range from the way individuals protect the refuges they inhabit (social spacing system: territories, home ranges) to the way they interact with females and other conspecifics in order to achieve and monopolise copulations (mating systems: e.g. monogamy, harem polygamy), or how they care for and defend their growing offspring (parental care behaviour). The social behaviour of a particular symbiont species is commonly reflected in the way it associates with conspecifics. As pointed out above, several different patterns in which symbiotic crustaceans associate on their hosts can be distinguished: they may inhabit their hosts as solitary individuals, in heterosexual pairs, in structured groups or in unstructured aggregations.

Here, we propose that these association patterns of symbiotic crustaceans on their hosts are directly affected by two key vectors, the monopolisation potential of the symbiont and the encounter probability among symbiont conspecifics (Fig. 1). We suggest that both the monopolisation potential and the encounter probability be determined by several proximate factors that can be measured or estimated relatively easily. The proximate factors include those that determine the monopolisation potential (relationship symbiont size/host size, host morphology, symbiont weaponry) and the encounter probability of a

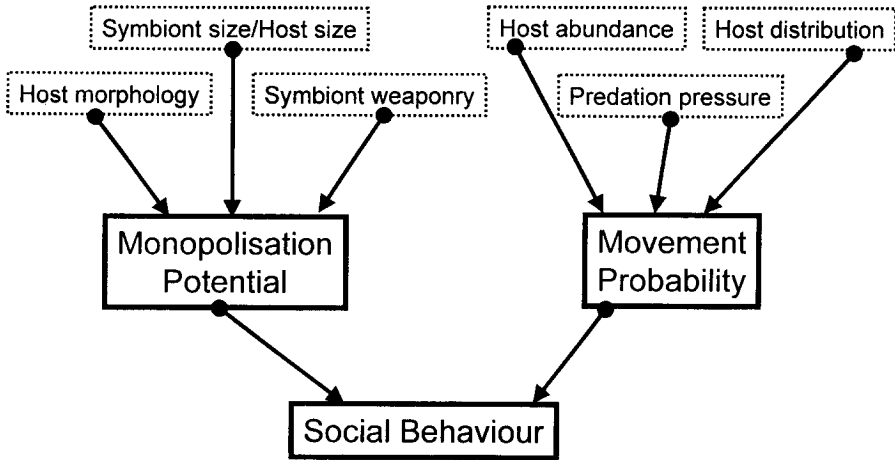


Figure 1. Conceptual model depicting proximate and mediating factors that shape the social behaviour of symbiotic crustaceans.

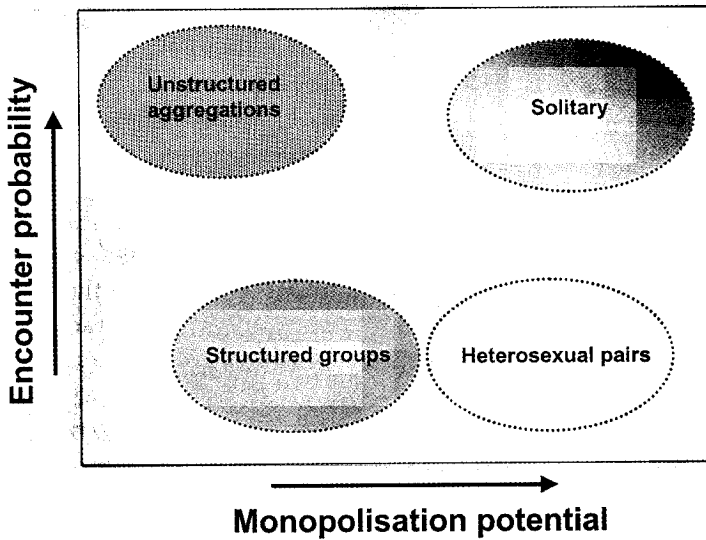


Figure 2. Predictions of the association pattern of symbiotic crustaceans in dependence of the mediating factors "monopolisation potential" and "encounter probability".

symbiont species (host abundance, host distribution, predation pressure). Since in our model only two key vectors affect the social behaviour of symbiotic crustaceans directly, the central result of this model will be a two-dimensional landscape (Fig. 2).

Based on theoretical considerations, we provide predictions about how the proximate factors should differ between crustacean species that display distinct association patterns (solitary, heterosexual pairs, unstructured aggregations, structured groups) (see also Fig. 2). Using available information on crustacean symbionts, we will examine in the following whether or not our predictions are valid. The main objective of this study is, however, to identify and examine simple measures that can be easily obtained and used to explain the association pattern (social behaviour) of symbiotic crustaceans. Following this step, we will propose simple measurements that should be reported in any future study on symbiotic crustaceans.

2. Material and Methods

We have surveyed many different studies on symbiotic crustaceans (see Appendix 2). In our survey we included studies devoted to the taxonomy, population biology, behaviour, ecology and host use pattern of symbiotic crustaceans. As outlined above, we distinguished six proximate factors that were scaled for the purpose of our model. Already the first proximate factor (relationship of symbiont size/host size) poses distinct problems – which body measure to use? Herein, we normally used the measurements that were given by the authors of each respective study. With respect to the hosts, we used the body measure that would best reflect the potential home range of their symbiotic crustacean (inhabitable space). For example, in brittle stars we used the total diameter (including the arms) rather than the diameter of the central disc, when we assumed that symbionts could roam anywhere on the brittlestar. However, when it was explicitly mentioned that the crustacean under investigation lived exclusively on the central disc, then we only considered the diameter of the central disc.

All other proximate factors that could not be measured were scaled arbitrarily. The factor "host morphology" was scaled from 1 to 10 such that highly complex hosts received the value of 10 while very simple hosts (or structures inhabited on a host) received the value of 1 (see Appendix 1). The same was true for predation pressure, depending on the environment which the symbiont and the host inhabited (Appendix 1). Scaling the proximate factors in this manner is a highly arbitrary procedure, and other authors may have proposed different scales. For the purposes of a first meta-analysis presented in this study, however, we believe that the scales we have developed are useful. Future studies may use different (or finer) scales or different factors depending on the purpose of each respective study, and furthermore on the information that is available.

Relatively few of the studies that we reviewed provided complete

information on all the different factors outlined above. When the information we were seeking was not explicitly given in the primary literature, but could be obtained from other studies or from invertebrate zoology and marine ecology textbooks, we estimated the respective values for each proximate factor to the best of our knowledge from secondary literature.

Following completion of the data matrix (see Appendix 2), we examined the different factors in two separate steps. As a first step we considered each proximate factor separately. We tested whether a specific proximate factor differed among crustacean species displaying distinct association patterns using one-way ANOVA for the factor "relative size" and non-parametric Kruskal-Wallis ANOVA for all other factors (Sokal and Rohlf, 1981). Relative size was calculated using the equation

$$\text{Symbiont size/host size} \times 10$$

and these values were square root transformed before analysing them with a one-way ANOVA. The statistical analysis of each proximate factor individually allowed us to discriminate which of the six proximate factors was a good predictor for the social behaviour (the association pattern) of the symbiotic crustaceans that entered the model. In a second step, for each species for which values of all six proximate factors were available, the monopolisation potential and the encounter probability was calculated by adding up the proximate factors. Using these two key vectors, we examined whether and how their combination affects the intraspecific association pattern of symbiotic crustaceans.

3. Results and Discussion

For most crustacean symbionts, we were able to obtain values for the three proximate factors that determined their monopolisation potential. However, in many cases this information could not be extracted from the primary literature on the respective crustacean symbionts, but had to be searched for in additional secondary literature.

In particular, values on environmental factors such as host abundance, host distribution and predation pressure, i.e. the factors that are considered important for the encounter (=movement) probability of crustacean symbionts, were often sorely missing in the primary literature (see Appendix 2).

Importance of proximate factors on social behaviour of crustacean symbionts

Relationship "symbiont size /host size"

Prediction: "In symbiont species that live in unstructured aggregations, the relationship symbiont size/host size will be small." When the host is small

compared to the symbiont (=relationship symbiont size/host size is large), there is a higher probability/need to monopolise this host. Simultaneously, the possibility increases that a symbiont can defend its host. We thus should expect that the symbiont size/host size ratio is large in species that live as solitary individuals, in heterosexual pairs or in structured groups on their hosts.

Our data compilation indicated that all crustacean symbionts were smaller than their hosts. In some cases, size differences between symbionts and their hosts were considerable – for example the amphipod *Maxillipius commensalis* reaches an average body length of 2 mm while its gorgonian host may reach a height of more than 800 mm (Thomas, 1996; J.D. Thomas, personal communication). Other crustacean symbionts were relatively large in comparison to their hosts – for example several alpheid shrimp species with an average body length of 40 mm lived on anemones with a disc diameter of approximately 120 mm. In most crustacean symbionts that inhabited their hosts in heterosexual pairs, the relationship "symbiont size/host size $\times 10$ " exceeded 0.50 (Appendix 2). In contrast, in many species that lived in unstructured aggregations this relationship did not exceed 0.50 (Appendix 2). In our present model, the relationship symbiont size/host size only has a limited utility in predicting the social behaviour of crustacean symbionts (Fig. 3A). This relationship was significantly smaller in species that inhabited their hosts in unstructured aggregations than in those that lived as single individuals on their hosts (one-way ANOVA, $F_{3,70} = 3.5$, $P = 0.02$), but no other significant differences were found. This is surprising at first view. One might have expected that the relationship between symbiont size and host size has a stronger effect on the association pattern. The fact that this relationship has only a limited effect may be due to different degrees of trophic dependence on hosts. At present, information about trophic relationships of symbionts is unavailable for most species, but nevertheless this factor is considered as important and should be included in the future. In a species that feeds on its host, fewer individuals may be able to cohabit on a single host (Yanagisawa and Hamaishi, 1986) than in a species that only utilises its host for protection. Similarly, the measures that we utilised herein (mainly body length) may not be appropriate. It may be more adequate to utilise other measures, such as biomass, volume or body surface of the inhabitable surface in the future. Thus, addition of the trophic dependence of the respective crustacean symbionts may be better suited to describe the relationship between symbionts size (biomass, body surface) and the size of its host.

Host morphology

Prediction: "Hosts of symbiont species that live in unstructured aggregations will have a complex morphology." It is expected that morphologically complex or heterogeneous hosts are difficult to defend against intruders. On the other

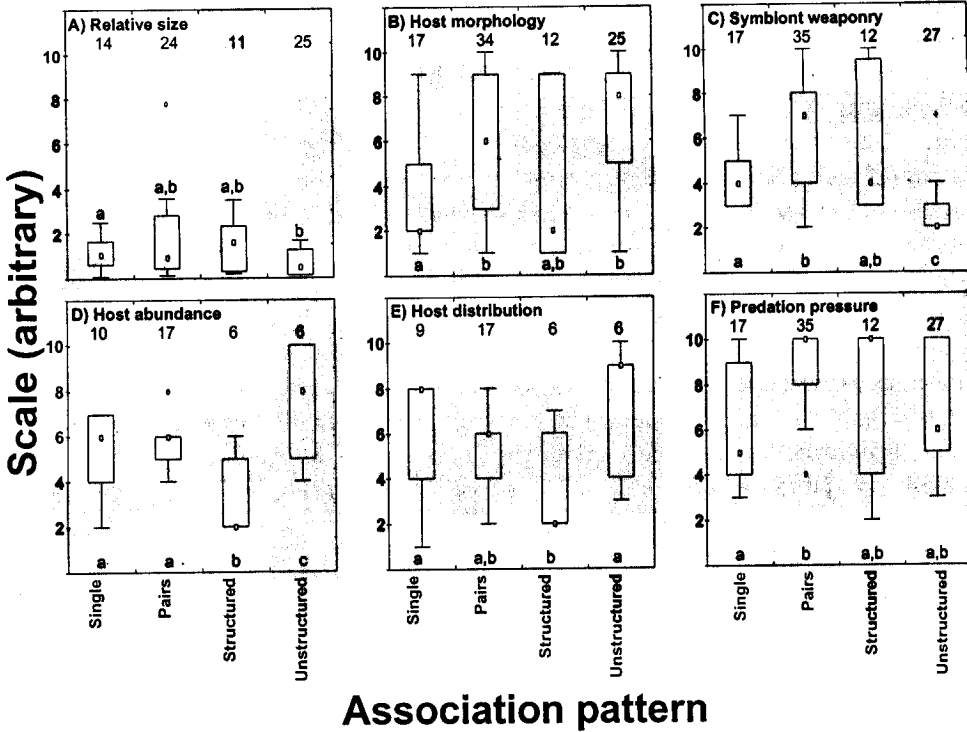


Figure 3. Box plots of values for respective proximate factors (a-f) for different association patterns of crustacean symbionts. Box-plots show medians, 25%- and 75%-percentiles and ranges, outliers are marked by a filled circle; values are calculated based on the matrix presented in Appendix 2; (similar letters indicate no significant differences at $p > 0.05$).

hand, very simple and less complex hosts that can be easily defended may harbour structured groups, pairs or solitary individuals of symbionts.

The factor host morphology had a significant effect on the association pattern of crustacean symbionts (Fig. 3B). Significant differences were found between the different categories of association patterns (solitary, in pairs, structured groups, unstructured aggregations) with respect to the host morphology (Kruskal-Wallis test: $H_{3,N=88}=10.1965$, $P=0.017$). Hosts inhabited by symbiont species as solitary individuals are less complex than hosts inhabited by symbiont species as heterosexual pairs or unstructured aggregations (post-hoc Newman-Keuls test: $P < 0.05$, Fig. 3B).

These simple hosts inhabited by crustaceans that live as solitary individuals may be relatively easy to control and defend. Symbionts either can

easily move from one side of the host to the other, there attacking any potential intruder (Baeza, unpublished data), or they can easily block entrances to the host structure inhabited, as is the case in pinnotherid crabs (Báez and Martínez, 1976). In contrast to these solitary species, those that inhabit hosts in unstructured aggregations or as heterosexual pairs live on hosts of rather complex morphology. Complexity in morphology probably impedes efficient supervision of the entire host by a single individual. The impossibility to control highly complex hosts may also be reflected by the high diversity of symbiont assemblages that can be found on them (Gotelli et al., 1985; Spotte and Bubucis, 1996). The consequence of inefficient host control could be that any symbiont individual could immigrate to or emigrate from a host individual without any impediment by conspecifics. Two (or more) symbiont individuals may also co-operate in order to improve their control efficiency of a host individual – this could explain the fact that many symbiont species live in relatively stable heterosexual pairs on complex hosts (Fig. 3B).

Surprisingly, the range of host complexity inhabited by symbionts living in structured groups vary widely, and no significant differences were found to hosts, which are inhabited by symbionts as solitary individuals on the one hand, or in pairs and unstructured aggregations on the other hand (post-hoc Newman-Keuls test: $P > 0.05$). This pattern may represent a mixture of small structured groups (i.e. family groups as in ascidian-dwelling amphipods, Thiel, 2000), in which hosts monopolisation is achieved by only one or two individuals of the species (e.g. parents), and large structured groups such as eusocial species inhabiting sponges with a complex spongocoel system. In order to maintain the stability of a small structured group, it is probably necessary to efficiently control hosts in order to prevent frequent immigration or emigration – this is easier to achieve on simple hosts rather than on highly complex hosts. Indeed, in *Caecognathia robusta* as well as in *Paracerceis sculpta*, similarly structured groups (=harem-like aggregations) occur (Shuster, 1987; Barthel and Brandt, 1995). In these two species, hosts are highly complex but males guard females in simple spaces that are easily defendable by single individuals. In the other case of large structured groups, host complexity is very high, as in the sponges that are inhabited by the eusocial *S. regalis*. Apparently in this (and other snapping shrimp) species, all individuals from a single host individual co-operate in defending the host (Duffy, 1996). Finally, shrimps such as *Gnathophylloides mineri* are an example of structured aggregations living on complex hosts. This shrimp occurs in aggregations on its sea urchin host, *Tripneustes ventricosus* (Patton et al., 1985). Females outnumber males and apparently gather on urchins with males (op.cit.). Consequently, groups of *G. mineri* would be structured as a result of the gregarious behaviour of females.

More sophisticated future studies that examine the importance of host morphology may utilise a less subjective measure such as fractal dimensions

similar to what has been done with some success in order to study the effect of macroalgal morphology on the composition of epifauna (Davenport et al., 1999).

Symbiont weaponry

Prediction: "Symbiont species that live in unstructured aggregations will have small and weak weaponry." The weaponry of a symbiont is important for defence of a host individual against intra- and inter-specific intruders. Consequently, we expect that species with strong weaponry are capable to live in structured groups, pairs or as solitary individuals on/in their hosts, while species with poorly developed weaponry might inhabit their hosts in unstructured aggregations.

Symbiont weaponry had a significant effect on the association pattern displayed by symbiotic crustaceans (Fig. 3C; Kruskal-Wallis test: $H_{3,N=91}=39.967$, $P < 0.0001$). As predicted, symbiotic crustaceans inhabiting their hosts in unstructured aggregations present the weakest weaponry (post-hoc Newman-Keuls test: $P < 0.005$). Weaponry of symbionts living as heterosexual pairs was stronger than that of symbionts living as solitary individuals (post-hoc Newman-Keuls test: $P < 0.005$), but similar as that displayed by symbionts living as structured groups (post-hoc Newman-Keuls test: $P > 0.005$). Furthermore, no significant differences in weaponry were found between symbionts living as solitary individuals and in structured groups (post-hoc Newman-Keuls test: $P > 0.005$). Thus, weaponry of symbiotic crustaceans may be considered as an important factor in determining their social behavior. Species that inhabit their hosts as solitary individuals, in pairs, or in structured groups are characterised by highly powerful weapons (Fig. 3C), which allow them to exclude unrelated intraspecific or possibly even interspecific competitors.

Similar as for the previous factors, the scale for symbiont weaponry as we presented it herein shall be viewed only as a first step in order to compare different organisms. Although crustacean armature appears highly diverse, it relies on very simple principles, most commonly represented by the chelae. Crustaceans compete merely by mechanic power with conspecifics, and this can be summarised in the simple statement: "the larger a chela, the more powerful the competitor." Crustaceans do not possess any other means to attack potential contenders, such as poison, traps, or likes. Even crustaceans from taxa as different as for example leucothoid amphipods and snapping shrimp are directly comparable with respect to their weaponry. Snapping shrimp possess very powerful chelae and few crustacean contenders of similar size can successfully compete with them.

The scale, which we provided herein, is rather arbitrary, and since chelae are the primary weapon in most crustaceans, direct comparisons between chelae

are probably more adequate. We propose that future studies measure the size of the chelae of their respective crustacean study organisms, and that future scales of symbiont weaponry are directly based on the comparison of the chela size.

The relationship chela size/body size for each respective symbiont species could provide indication for intraspecific competitive potential, and the degree to which some individuals would be capable to monopolise a host against conspecifics. Species with a relatively large chela are more likely to interact in intraspecific combats (and to monopolise a host) than species with relatively small chela. The chela size will in the future also allow for better interspecific comparisons assuming that species with large chela are able to expulse interspecific competitors from their hosts. Several observations suggest that interspecific exclusion may occur among crustacean symbionts – some symbiont species never occur together on the same host individual (Millar, 1971).

It could be criticised that "symbiont weaponry" was considered herein as a proximate factor that directly affects the monopolisation potential and consequently also the social behaviour of a symbiotic crustacean (compare model in Fig. 1). One may assume that fighting structures that can be used to defend a host are also exposed to natural selection, and this certainly may occur (Caldwell and Dingle, 1975). However, we are not aware of any case where natural selection in a symbiotic crustacean would have led to the evolution of a strong fighting structure. Most crustaceans that have adopted a symbiotic life style have similarly developed (or undeveloped) fighting structures as free-living congeners (see for example janirid isopods, caprellid amphipods, porcellanid crabs, alpheid shrimp, all of which comprise symbiotic and free-living species). Thus, in most cases symbiont weaponry probably has evolved independently from the symbiotic life-style of a symbiont. However, following the adoption of the symbiotic life, this weaponry probably has played an important role in determining the capability of a symbiont species to monopolise a host individual and consequently also its social behaviour.

Finally, we would like to emphasise that we are not aware of any study comparing the weaponry of crustaceans that have adopted a symbiotic life style with that of their free-living counterparts. Neither has the size and strength of the weaponry received much attention in previous studies on the social behaviour of symbiotic crustaceans (for an exception see Knowlton and Keller, 1982). We suggest that future studies place more emphasis on this factor since our analysis indicates that it may play an important role in determining the social behaviour of symbiotic crustaceans.

Host abundance and host distribution

Prediction: "Hosts of symbiont species that live in unstructured aggregations will be very abundant." Furthermore: "Hosts of symbiont species that live in unstructured aggregations will occur in dense patches." Thus, it can be expected

that symbiotic crustaceans inhabiting abundant (densely aggregated) hosts live in unstructured aggregations or as solitary individuals on/in their hosts, while symbionts inhabiting scarce (uniformly spaced) hosts cohabit in structured groups or pairs.

Host abundance differed significantly between the different association patterns of symbiotic crustaceans (Fig. 3D; Kruskal-Wallis test: $H_{3,N=39}=10.21$, $P=0.012$). Hosts that harboured unstructured aggregations of symbiotic crustaceans displayed significantly higher abundance than hosts that were inhabited by symbionts as solitary individuals, heterosexual pairs, or structured groups (post-hoc Newman-Keuls test: $P<0.05$). On the other hand, hosts that harboured structured groups of symbionts displayed the lowest abundance (post-hoc Newman-Keuls test: $P<0.05$). Hosts on which symbiotic crustaceans dwelled as heterosexual pairs were as abundant as hosts harbouring single individuals of symbionts (post-hoc Newman-Keuls test: $P>0.05$).

Host distribution also had a significant effect on the association pattern of symbiotic crustaceans (Fig. 3E; Kruskal-Wallis test: $H_{3,N=38}=8.29$, $P=0.04$). Hosts on which symbionts live in structured groups are less aggregated than hosts on which symbionts inhabit as single individuals or in unstructured aggregations (post-hoc Newman-Keuls test: $P<0.05$).

In general, while host abundance appears to be of some importance in determining the association pattern of symbiotic crustaceans, host distribution appeared to be less important (Figs. 3D and E). Host abundance was highest in species that lived in unstructured aggregations of conspecifics (Fig. 3D). Groups of symbionts that do not show any demographic structure may be the consequence of frequent movements between hosts, which are facilitated when hosts are abundant. Indeed, several crustacean species that live in unstructured groups have been reported to move frequently between hosts, which are usually very abundant. *Periclimenes pedersoni*, which lives in unstructured aggregations on sea anemones, apparently change frequently between hosts (Mahnken, 1972; Chace, 1958; Spotte and Bubucis, 1996). Similarly, the porcellanid crab *Liopetrolisthes mitra* inhabits the sea urchin *Tetrapygus niger* in unstructured aggregations (Baeza and Thiel, 2000), as well as the isopod *Iais pubescens* on its host the isopod *Exosphaeroma gigas* (Thiel, unpublished). Both symbiont species move easily between host individuals, which usually live in dense aggregations (Zander, personal communication; Thiel, unpublished) supporting the notion that host abundance has an influence on the movement probability of symbiotic crustaceans and thereby also on their intraspecific encounter probability and association pattern.

Surprisingly few studies provided estimates about host abundance and distribution (see low values of n in Fig. 3D and E, Appendix 2), which may severely affect the discriminatory power for these factors. In the future, when measuring the abundance of host individuals, the use of traditional methods

(e.g. quadrat counts) can provide a useful first approximation, and can be done relatively easily. When determining host abundance and host distribution, though, it is important to consider the potential movement range of the respective symbionts. Clearly, a harpacticoid copepod may have a different activity range than a small shrimp species. In our present scale, we thus referred to host abundance and distribution as a distance between hosts, scaled according to the body length of the respective crustacean symbiont. Consequently, the same host in the same environment may receive different abundance and distribution values depending on whether it is considered host for a harpacticoid copepod or for a small shrimp species.

Predation pressure

Prediction: "Symbiont species that occur in unstructured aggregations will be found in environments with low predation pressure." On the other hand, structured groups or heterosexual pairs are probably found in environments with high predation pressure. These predictions are based on the assumption that increasing predation pressure will affect the movement rate of symbionts among hosts negatively.

Predation pressure had a significant effect on the association patterns of symbiotic crustaceans (Kruskal-Wallis test: $H_{3,N=91}=15.17$, $P=0.0017$; Fig. 3F). However, only species that inhabit their hosts as heterosexual pairs experience a significantly higher predation pressure than species that dwell on/in their hosts as single individuals (Fig. 3F; post-hoc Newman-Keuls: $P<0.05$).

These results partly confirm what previous studies had indicated (Knowlton, 1980), namely that crustacean symbionts live in heterosexual pairs when predation pressure is high and movements in search of mating partners are risky. In species that live as solitary individuals on their hosts, predation pressure is comparatively low facilitating movements between hosts in search of mates.

Predation pressure is a factor that is difficult to scale. In the future, more objective and comparable measures could be obtained for predation pressure by exposing a certain number of the respective crustacean symbionts in their respective habitats and determine the disappearance rates of the exposed individuals (Smith and Herrnkind, 1992; Ruiz et al., 1993; Peterson and Black, 1994; Aronson and Heck, 1995). This method would have the advantage that the predation pressure could be determined for each respective species individually, and that the disappearance rates could be compared among species (and habitats).

Monopolisation potential and encounter probability

For 34 symbiotic crustaceans we could gather sufficient information on all six proximate factors such that it was possible to calculate their monopolisation potential and encounter (=movement) probability. The resulting two-dimensional landscape (Fig. 4) coincides relatively well with the predictions (compare Fig. 2). In the upper left corner, we mostly find species that live in unstructured aggregations on their hosts. Opposite from this corner, on the right side of the figure, we find species that inhabit their hosts either as solitary individuals, or in some sort of specific association with conspecifics. In other words, species with a low monopolisation potential and a high encounter probability indeed occur in unstructured aggregations. Unexpectedly, we found one species with a low monopolisation potential that apparently lives in structured groups, *Gnathophylloides mineri* (the square at the left side in Fig. 4). As has been outlined in the above, the groups of *G. mineri* may be the result of the active aggregation behaviour of this species, and groups are only loosely structured compared to the distinct family-offspring groups of *Synalpheus* spp. and *Leucothoe ascidicola*. Particularly interesting is the case of the *Synalpheus* species. Single individuals of this species have a low monopolisation potential, primarily due to the fact that their hosts are very large and have many

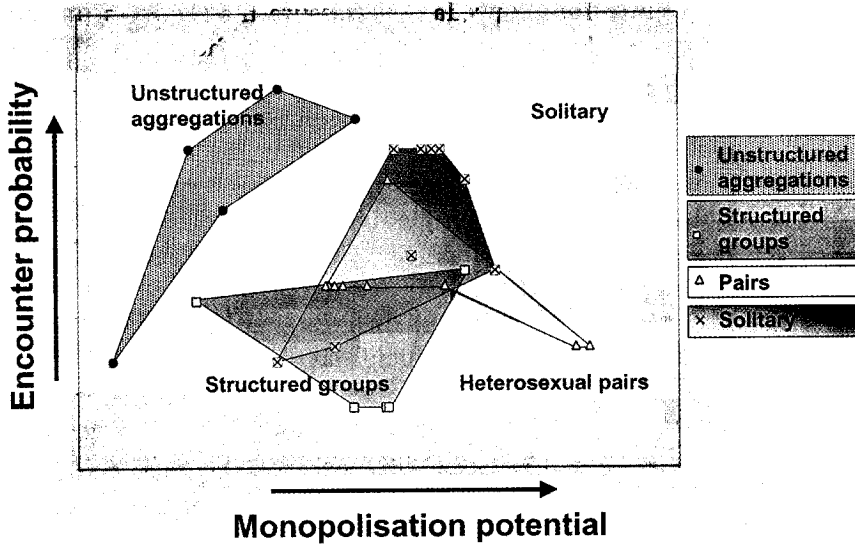


Figure 4. Relationship between "monopolisation potential" and "encounter probability" for the symbiotic crustaceans for which values were available for all proximate factors; values are calculated based on the matrix presented in Appendix 2; shaded areas connect all species with the respective association patterns.

different openings (Fig. 4; compare also Appendix 2). However, they achieve a very high collective monopolisation potential by joining forces – members within a colony co-operate (Duffy, 1996). The individuals from a colony are all closely related to each other (Duffy, 1996) which apparently is the result of very long-lasting extended parental care. In this context it is interesting to note, that extended parental care apparently is the primary cause for the development of structured groups of symbiotic crustaceans (Appendix 2). Future predictive models should include the reproductive mode of symbionts, since it may help explain the association pattern of several species that occur in structured groups of conspecifics on their hosts.

4. Conclusion

The model introduced herein presents the first attempt to investigate factors shaping the social behaviour of crustacean symbionts across a wide number of crustacean species. Many of the factors included herein had been discussed by previous authors but to our knowledge no meta-analysis had been conducted so far. Clearly, our contribution can only serve as a first step in this direction, and many aspects of our model can be substantially improved in the future as we have outlined above. The patterns may become more distinct when the different factors will be scaled according to more subjective guidelines. And furthermore the model will become more complete when more information is included in the data matrix. The inclusion of additional factors and vectors may also help to focus the results of our model in the future. For example the reproductive biology of crustacean symbionts (direct or indirect development, presence or absence of extended parental care) and the trophic dependence of symbionts on their hosts play an important role in determining the association pattern of crustacean symbionts. The relationship "symbiont size/host size" and the symbiont weaponry play an important role in determining the social behaviour of symbiotic crustaceans. The analysis of most proximate factors was shown to partly explain the association pattern of symbiotic crustaceans. The complete model showed relatively good agreement with the main predictions (compare Fig. 2). Proximate factors probably interact in a highly complex manner and a better understanding of these interactions may improve our model substantially. Thus, future studies should particularly focus their attention on the way how proximate factors interact.

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Appendix 1: Crustacean symbionts and their hosts, scale for proximate factors

Host morphology

- 1 Simple small cavities, with a single entrance, e.g. cloaca inhabited by entocomensals
- 2 Simple cavities or short tunnels with two openings or entrances, e.g. clams, mussels, sea cucumbers
- 3 Large tunnels with at least two openings or entrances, e.g. U-shaped tubes or burrows
- 4 Two-dimensional structures such as disks, e.g. sand dollars
- 5 Simple cylinders with poorly structured additional ramifications, e.g. sea anemones with few thick tentacles
- 6 Complex cylinders with highly structured ramifications, e.g. sea anemones with many fine tentacles
- 7 Spheres (sometimes flattened) without complex surfaces, e.g. sea urchins with small spines, sponges with >2 openings
- 8 Spheres with complex surfaces, e.g. sea urchins with very large spines, sponges with several openings
- 9 Head-like structures with sculptured surfaces (*Pocillopora* corals), or several tubes interconnected, (Sponges)
- 10 Highly ramified structures, with many branches, e.g. black corals, gorgonians or similar species

Symbiont weaponry

- 1 No apparent structures to compete with conspecifics or other species, e.g. small isopods, small copepods
- 2
- 3 Weak structures useful to push away other individuals, e.g. some isopods, copepods, also some pinnotherids
- 4 Moderate, e.g. some decapods with weak chelae such as *Pinnixa*, some amphipods
- 5
- 6 Moderately strong, useful to expel conspecifics, e.g. some shrimp with strong chelae, some amphipods
- 7 Strong, useful to expel competitor, some decapods with strong chelae, e.g. porcellanid crabs
- 8 Very strong, useful to expel competitor, some decapods with strongly developed chelae, e.g. brachyuran crabs
- 9
- 10 Extremely strong, useful to expel other competing species, e.g. e.g. alpheid shrimp

Host abundance

- 1 Very rare, other host individuals farther away than 50 body lengths of the symbiont
- 2 Rare, other host individuals within 50 body lengths of the symbiont
- 3 Few, at least one other host individual within 20 body lengths of the symbiont
- 4 Some, at least one other host individual within 10 body lengths of the symbiont
- 5 Several, several other host individuals within 10 body lengths of the symbiont
- 6 Frequent, at least one other host individual within 5 body lengths of the symbiont
- 7 Common, several other host individuals within 5 body lengths of the symbiont
- 8 Abundant, at least one other host individual between one & two body lengths of the symbiont
- 9 Very abundant, almost always at least one other host individual within one body length of the symbiont
- 10 Extremely abundant, almost always several other host individuals within one body length of the symbiont

Host distribution

- 1 Hosts widely dispersed in complex habitat, chance of finding other host individual very low
- 2 Hosts very widely distributed, next host individual not perceivable by symbionts without leaving their host
- 3 Host widely distributed, but perceivable by symbionts from their hosts
- 4 Hosts relatively uniformly distributed, but always several body lengths between host individuals
- 5 Hosts occur in patches, in which they are uniformly distributed, always several body lengths between hosts
- 6 Hosts aggregated, but host individuals never touching each other
- 7 Some hosts in small aggregations, others solitary
- 8 Dense host aggregations, some (5-10) host individuals aggregated, many aggregations nearby
- 9 Very dense host aggregations, many (10-100) hosts within one aggregation, touching each other
- 10 Extremely dense aggregation, many (>100) host individuals within one aggregation, touching each other

Predation pressure

- 1 Polar waters, subtidal
- 2 Deep sea
- 3 Temperate, soft bottom, intertidal
- 4 Temperate, soft bottom, subtidal
- 5 Temperate, hard bottom, intertidal
- 6 Temperate, hard bottom, subtidal
- 7 Tropical, soft bottom, intertidal
- 8 Tropical, soft bottom, subtidal
- 9 Tropical, hard bottom, intertidal
- 10 Tropical, hard bottom, subtidal

Appendix 2: Crustacean symbionts and their hosts, values for proximate factors, and references

Crustacean species	Host species	size (mm)	structure measured	alternative hosts	size (mm)	structure measured	Host morphology (multiplied by 10)	Symbiont weaponry	Host abundance	Host distribution	Predation pressure	Association pattern	References		
<i>Inachus phalagium</i>	<i>Anemona sulcata</i>	15	CW	Anthozoa	150	D	1.00	6	7	3	7	6	S	Writz & Diesel, 1983	
<i>Stenothynchus seticornis</i>	<i>Diadema antillarum</i>	50	CL	Echinoidea	300	D	1.67	6	4	4	10	S	Hayes et al., 1998; Stanton 1977		
<i>Polyonyx bella</i>	<i>Chaetopterus variopedatus</i>	5	CW	Polychaeta	600	T	0.08	3	7	10	S	S	Hsueh and Huang, 1998		
<i>Pinnotheres ostreum</i>	<i>Crassostrea virginica</i>	10	CW	Bivalvia	200	SL	0.50	2	3	7	8	4	S	O'Beim & Walker, 1999; Christensen & McDermott 1959	
<i>Pinnotheres tsingtaoensis</i>	<i>Sarguinolaria acuta</i>	7	CW	Bivalvia	60	SL	1.17	2	3	9	S	S	Soong 1997		
<i>Pinnotheres novaehollandiae</i>	<i>Loxechinus albus</i>	8.4	CW	Bivalvia	45	SL	1.87	2	3	7	8	4	S	Palmer 1995	
<i>Pinnaxodes chilensis</i>	<i>Macra</i> spp	16.2	CL	Echinoidea	100	D	1.62	1	3	7	8	6	S	Baez & Martinez 1976	
<i>Pinnaxodes floridensis</i>	<i>Theleothuria princeps</i>	11	CW	Holothuroidea	140	BL	0.79	2	3	9	S	S	Wells & Wells 1961		
<i>Pinnotheres maculatus</i>	<i>Mytilus edulis</i>	8	CL	Bivalvia	60.9	SL	1.31	2	3	7	8	4	S	Tablado & Lopez 1995; Bierbaum & Ferson 1986	
<i>Pinnotheres pisum</i>	<i>Mytilus edulis</i>	8.13	CW	Bivalvia	50	SL	1.63	2	3	7	8	4	S	Haines et al., 1994	
<i>Pinnixa chaetopterana</i>	<i>Chaetopterus variopedatus</i>			Polychaeta	600	T	0.00	3	4	5	3	S	Grove and Woodin, 1996		
<i>Pinnixa tumida</i>	<i>Paracudina chilensis</i>			Holothuroidea							4	S	Takeda et al., 1997		
<i>Pinnixa cylindrica</i>	<i>Arenicola cristata</i>	18.4	CW	Polychaeta	300	T	0.61	3	3	3	S	S	McDermott 1962		
<i>Alloporelloides spinifrons</i>	<i>Phymacis clematis</i>	10	CL	Anthozoa	40	D	2.50	5	7	4	5	S	Baeza and Stotz, 1998		
<i>Echinoecus pentagonus</i>	<i>Echinotrix calamaris</i>			Echinoidea							1	7	10	S	Castro, 1971
<i>Zebrida adamsii</i>	<i>Toxopneustes pileolus</i>	14	CW	Echinoidea	150	D	0.93	8	5	2	1	6	S	Yanagisawa & Hamaishi, 1986	
<i>Harrisia albolineata</i>	<i>Comaster gracilis</i>	10	CW	Crinoidea	200	D	0.50	9	5	4	S	S	Ng & Lim, 1980		
<i>Athanas indicus</i>	<i>Echinometra mathaei</i>	8	BL	Echinoidea	30	D	2.67	8	6	6	10	P	Gherardi, 1991		
<i>Trapezia intermedia</i>	<i>Pocillopora</i> spp.	10	CL	Scleractinia	200	D	0.50	9	8	6	10	P	Huber, 1987		
<i>Trapezia digitalis</i>	<i>Pocillopora</i> spp.	8	CL	Scleractinia	200	D	0.40	9	8	6	10	P	Huber, 1987; Tsuchiya & Taira 1999		
<i>Trapezia ferruginea</i>	<i>Pocillopora</i> spp.	9	CL	Scleractinia	200	D	0.45	9	8	6	10	P	Castro, 1978; Tsuchiya & Taira 1999		
<i>Trapezia formosa</i>	<i>Pocillopora</i> spp.	10	CL	Scleractinia	200	D	0.50	9	8	6	10	P	Gotelli et al., 1985		
<i>Trapezia corallina</i>	<i>Pocillopora</i> spp.	8	CL	Scleractinia	200	D	0.40	9	8	6	10	P	Gotelli et al., 1985		
<i>Trapezia cymodoce</i>	<i>Pocillopora</i> spp.	11	CW	Scleractinia	120	D	0.92	9	8	6	10	P	Tsuchiya & Yonaha 1992; Tsuchiya & Taira 1999		
<i>Trapezia guttata</i>	<i>Pocillopora</i> spp.	8	CW	Scleractinia	120	D	0.67	9	8	6	10	P	Tsuchiya & Yonaha 1992; Tsuchiya & Taira 1999		
<i>Trapezia areolata</i>	<i>Pocillopora</i> spp.	11	CW	Scleractinia	120	D	0.92	9	8	6	10	P	Tsuchiya & Yonaha 1992; Tsuchiya & Taira 1999		
<i>Planes minutus</i>	<i>Caretta caretta</i>	15	CW	Vertebrata	400	BL	0.38	4	7	2	8	P	Dellinger et al., 1997		
<i>Alpheus armatus</i>	<i>Bartholomea annulata</i>	40	BL	Anthozoa	120	D	3.33	6	10	4	10	P	Knowlton, 1980; Knowlton and Keller, 1982, 1983, 1985		
<i>Alpheus immaculatus</i>	<i>Bartholomea annulata</i>	35	BL	Anthozoa	120	D	2.92	6	10	4	10	P	Knowlton, 1980; Knowlton and Keller, 1982, 1983, 1985		
<i>Alpheus polyisticus</i>	<i>Bartholomea annulata</i>	35	BL	Anthozoa	120	D	2.92	6	10	4	10	P	Knowlton, 1980; Knowlton and Keller, 1982, 1983, 1985		
<i>Alpheus roquensis</i>	<i>Heteractis lucida</i>	35	BL	Anthozoa	120	D	2.92	6	10	4	10	P	Knowlton, 1980; Knowlton and Keller, 1982, 1983, 1985		
<i>Alpheus idiocheles</i>	<i>Helopora coerulea</i>	35	BL	Scleractinia	200	D	2.92	6	10	4	10	P	Knowlton, 1980; Knowlton and Keller, 1982, 1983, 1985		
<i>Alpheus lottini</i>	<i>Pocillopora damicornis</i>	40	BL	Scleractinia	200	D	2.00	9	10	6	10	P	Vannini, 1985; Tsuchiya & Yonaha 1992		

Crustacean species	size (mm)	structure measured	Host species	alternative hosts	size (mm)	structure measured	Symb. Size / Host size (multiplied by 10)	Symbiont weaponry	Host abundance	Host distribution	Predation pressure	Association pattern	References	
<i>Hippolyte nicholsoni</i>	8	BL	<i>Pseudopteropegia americana</i>		1000	BL	0.20	10	4	10	A	A	Spoite et al., 1995	
<i>Neopontonides chacei</i>	8	BL	<i>Pseudopteropegia americana</i>		1000	BL	0.08	10	4	10	A	A	Spoite et al., 1995	
<i>Porcellana sayana</i>	10	CW	<i>Dardanus</i> spp.	+++	80	SL	1.25	4	7	10	A	A	Werding, 1983	
<i>Liopetrolisthes mitra</i>	8	CL	<i>Tetrapygus niger</i>	+	60	D	1.33	8	7	10	9	6	A Baeza and Thiel, 2000	
<i>Tuleariocaris zanzibarica</i>	40	BL	<i>Diadema setosum</i>	-	300	D	1.33	8	3	8	9	10	A Fricke and Hentschel, 1971; Fricke, pers. comm.	
<i>Thor arborescens</i>	10	BL	<i>Telmatactis cricoides</i>	+	120	D	0.83	6	2	10	A	A	Wirtz, 1997	
<i>Dissodactylus primitivus</i>	8.5	CW	<i>Meoma ventricosa</i>		145	D	0.59	8	4	8	A	A	Telford 1978	
<i>Leucothoe "spongicola"</i>	8	BL		+	100	H	0.80	3	5	4	10	A	A	Thiel, 2000
<i>Caprella stella</i>	5	BL	<i>Ophidiaster ophidianus</i>	++	150	D	0.33	8	3	6	A	A	Wirtz and Vader, 1996	
<i>Panambus typicus</i>	5	BL	<i>Ophiura</i> spp.	+++	120	CL	0.50	3	3	4	A	A	Volbehr and Rachor, 1997	
<i>Stenothoe symbiotica</i>	6	BL	<i>Stenocionops spinimana</i>		800	H	0.03	10	3	4	3	10	A	Thomas and Cairns, 1984; Thomas, pers. comm.
<i>Maxillipus commensalis</i>	2	BL	<i>Echinogorgia</i> sp.	++	48	D	1.31	8	2	8	9	6	A	Stebbins 1989
<i>Colidotea rostrata</i>	6.3	BL	<i>Strongylocentrotus purpuratus</i>	+	15	BL	1.33	5	2	5	5	A	A	Hahtela and Naylor, 1965
<i>Jaera hopeana</i>	2	BL	<i>Sphaeroma serratum</i>	+	15	BL	1.33	5	2	3	A	A	Rotzmeil, 1975	
<i>Iais californiensis</i>	2	BL	<i>Sphaeroma quoyanum</i>	-	20	BL	1.00	5	2	10	5	A	A	Thiel, in prep.
<i>Iais pubescens</i>	2	BL	<i>Exosphaeroma gigas</i>	+	50	D	0.10	9	2	4	A	A	Humes and Hendler, 1999	
<i>Ophypsyllus latus</i>	0.5	BL	<i>Ophiocomella ophiactoides</i>	-	50	D	0.12	9	2	4	A	A	Humes and Hendler, 1999	
<i>Ophypsyllus reductus</i>	0.6	BL	<i>Ophiocoma echinata</i>		75	D	0.08	9	2	4	A	A	Humes and Hendler, 1999	
<i>Pseudanthessius deficiens</i>	0.6	BL	<i>Ophioderma brevispinum</i>	+	30	H	1.00	1	2	6	A	A	Gage, 1966	
<i>Notolepithys ailmani</i>	3	BL	<i>Asciella aspersa</i>	+++	60	H	0.33	1	2	6	A	A	Svavarsson et al., 1993	
<i>Doropagus pulex</i>	2	BL	<i>Polycarpa pomaria</i>		60	H	0.33	1	2	6	A	A	Svavarsson et al., 1993	
<i>Gunentophorus globularis</i>	2	BL	<i>Polycarpa pomaria</i>		70	H	0.14	1	2	6	A	A	Svavarsson, 1990	
<i>Lichomolgus canui</i>	1	BL	<i>Halocynthia pyriformis</i>											

CL - carapace length
 CW - carapace width
 SL - shell length
 BL - body length
 D - diameter
 H - height
 A - area (cm²)
 T - Tube length (mm)

S - solitary individuals
 P - pairs
 G - structured groups
 A - unstructured aggregations