

SOME ASPECTS OF THE ECOLOGY OF *PACHYPYGUS GIBBER* (COPEPODA), AN ASSOCIATED ORGANISM OF *CIONA INTESTINALIS* (UROCHORDATA)

BECHEIKH S.***, THOMAS F.**, RAIBAUT A.** & RENAUD F.**

Summary :

The ecological parameters of the association between the Urochordata *Ciona intestinalis* and the copepod *Pachypygus gibber* are investigated. This associated organism displays an aggregated distribution on the host population, and preferential site location within host individuals. The sex ratio observed is female biased. Even though this copepod lives at the expense of its host's feeding, the mean abundance and variance to the mean abundance ratio β increase with host size, suggesting that the accumulation of this crustacean has no significant effect on either its host survival or growth. Although this associated copepod displays ecological features of parasites, it could be considered as a non costly partner.

KEY WORDS : ecology, population biology, parasitism, Copepoda, Urochordata.

Résumé :

ASPECTS DE L'ÉCOLOGIE DE *PACHYPYGUS GIBBER* (COPEPODA), ORGANISME ASSOCIÉ À *CIONA INTESTINALIS* (UROCHORDATA)
Nous avons analysé certains paramètres écologiques de l'association entre *Ciona intestinalis* (Urochordés) et le copépode *Pachypygus gibber*. Cet organisme associé présente une distribution agrégée au sein de la population hôte et au sein des individus hôtes. Le sexe ratio est biaisé en faveur des femelles. Bien que ce copépode se nourrisse aux dépens des ressources alimentaires de son hôte, l'abondance et le rapport variance sur moyenne β augmentent avec la taille de l'hôte, ce qui suggère que l'accumulation de ce crustacé n'affecte pas de façon significative la survie et/ou la croissance de son hôte. Si *P. gibber* présente des caractéristiques écologiques d'organismes parasites, il semble devoir être considéré comme un organisme associé, entraînant un coût restreint à son hôte.

MOTS CLÉS : écologie, biologie des populations, parasitisme, Copépode, Urochordés.

INTRODUCTION

Even though we do not know exactly the biological richness of the earth, all biologists seem to agree that parasitic organisms (i.e. Microparasites and Macroparasites in the sense of Anderson & May, 1979), which depend at least on one host for their ecological niche, constitute the majority of known species (Timm & Clauson, 1987). Therefore, we are led to conclude that the conquest of the living by the living represents a keystone parameter in the field of evolutionary biology. Indeed, all living species are involved with parasitism, either as parasites or as hosts (Barbault, 1988). The ecological relationships which link symbionts to their hosts extend from Mutualism, where the

two partners are obligate living associates, to Parasitoidism where the biological success of one depends on the death of the other and vice-versa (Renaud & De Meeûs, 1991). However, beyond the description of these organisms and their relationships, it is of fundamental importance to analyze ecological origins of parasitism in order to understand the mechanisms of transition between free living and parasitic species. Indeed, what are the ecological consequences of living at the expense of, and exploiting a host species? Consequently, the analysis of biological models in which individuals still possess characters of free living organisms on the one hand, and partial dependence for a host on the other hand, constitute suitable models to study essential information sources. With such models, we can expect to get information on: *i*) the dispersion patterns of these associated organisms within a host population; *ii*) the pathogenic potential they could represent for their hosts (i.e. are they parasites?) and *iii*) the biological consequences of living at the expense of another organism (i.e. location within host habitats, within host densities, evolution of the sex ratio). In this paper, these different ecological points are investigated and discussed through an association

* Station Méditerranéenne de l'Environnement Littoral, 1, quai de la Daurade, 34200 Sète, France.

** Laboratoire de Parasitologie Comparée (CC 105) UMR CNRS 55550, Université Montpellier II, Pl. E. Bataillon, 34095 Montpellier Cedex 5, France.

Correspondence: F. Renaud. Tel: 67-14-37-09 - Fax: 67-14-46-46 - E-mail: renaud@crit.univ-montp2.fr

between one host (*Ciona intestinalis* L. 1767, Urochordata) and one copepod (*Pachypygus gibber* Thorell, 1859) which, at least *in vitro*, can develop into the adult stage without its host (Hipeau-Jacquotte, 1988). So, it is necessary to examine the ecology of the relationship of such organisms in order to shed light on the ecological origin of parasites.

MATERIAL AND METHODS

BIOLOGICAL MATERIAL

A large sample of *Ciona intestinalis* ($n = 2,200$) was collected during 1994-95 in the Thau lagoon (Sète, Southern France; 43° 25' N, 3° 35'E). In the laboratory, the lengths of *Ciona* were immediately measured, and they were dissected in order to count adults (i.e. males and females) and larvae of the associated copepod *Pachypygus gibber* that they harbor. The reproduction of this copepod occurs within the host, eggs are released and hatch outside. After seven larval moults, the infective larvae (i.e. copepodid) enter the host and develop into adults.

DATA ANALYSIS

Host size classes were used to study the relation between copepod load and *Ciona* size because the relationships between size and age are unknown for this organism. For this purpose, *Ciona* were grouped in 17 length classes, the first 16 of which had a 5 mm range and consist of at least 43 individuals. Class 17 included all individuals larger than class 16 (i.e. 80 mm). The nomenclature used to describe copepod distributions was that of Margolis *et al.* (1982). The prevalence (P) is the proportion of *Ciona* harboring at least one copepod. The mean abundance (A) corresponds to the ratio of the total number of copepods sampled by the total number of *Ciona* analysed. We also calculated the variance to mean abundance ratio β , a measure of the parasite aggregation. The mean intensity (I) corresponds to the mean number of copepods per infected *Ciona* ($I = A/P$).

Anderson & Gordon (1982) and Rousset *et al.* (in press) have developed a method to analyse host-parasite relationships based on changes in mean parasite abundance and β with host age. Because length of *Ciona* increases during life on the one hand, and all *Ciona* were collected in the same biotope on the other hand, we assumed that some correlations exist between size and age for these organisms.

Statistical tests were performed following Sokal & Rohlf (1981) and Siegel & Castellan (1988). Biological association coefficient between males and females was assessed using the phi coefficient ($r\phi$, Janson & Vege-

lius, 1981; Scherrer, 1984). Thus, we calculated $r\phi$ as follows:

$$r\phi = (ad - bc) / \sqrt{(a+b)(a+c)(c+d)(b+d)}$$

where a , b , c and d correspond to the number of *Ciona* with: *i*) at least one male and one female copepod simultaneously (a), *ii*) with at least one female and no male b , *iii*) with at least one male and no female (c), *iiii*) with no copepod (d). Following Scherrer (1984), the significance of the association was tested using χ^2 with 2 degrees of freedom.

All tests are two-tailed and made using the program Logithecq 5.1 (Boy, 1994, Station Biologique de la tour du valat, Le Sambuc, 13200 Arles, France).

RESULTS

DISTRIBUTION ON HOST POPULATION

Table I shows the different parameters (i.e. prevalence, mean abundance and mean intensity) of the association between the copepod and its host. The frequency distribution of *P. gibber* within its host (Fig. 1) conforms to a negative binomial distribution (Kolmogorov-Smirnov test, $P > 0.05$). The values of k (i.e. the aggregation coefficient) is 0.60. Fixing the effect of host size, we find a weak influence of the date of capture on the mean abundance. Indeed, residuals from regression of copepod mean abundance as a function of host size are negatively correlated with the date of capture ($r = -0.07$, $P < 0.01$). Mean copepod abundance increased steadily with host size (Fig. 2*a*). The maximum mean number of copepods reached 4.9. The variance to the mean abundance ratio, β , describes the degree of aggregation of *P. gibber* in its host population. This ratio, following abundance, also increases with host size (Fig. 2*b*). Such a phenomenon is also observed while considering separately the mean abundance and β of adult and larvae copepods.

SITE LOCATION WITHIN A HOST

Copepods were found in two sites within their hosts: site 1 is the wall of the gill cavity, and site 2 is the bottom of the gill cavity and oesophagus. They appear

	Adult Copepods	Larvae Copepods	(Adult + Larvae) Copepods
Prevalence	56.7 %	24.8 %	63 %
Mean abundance	1.94 (3.18)	46 (1.12)	2.40 (3.79)
Mean Intensity	3.42 (3.58)	1.85 (1.57)	3.80 (4.18)

Table I. — Ecological characteristics of the association between *P. gibber* and *Ciona intestinalis*. Standard Deviations are given in brackets.

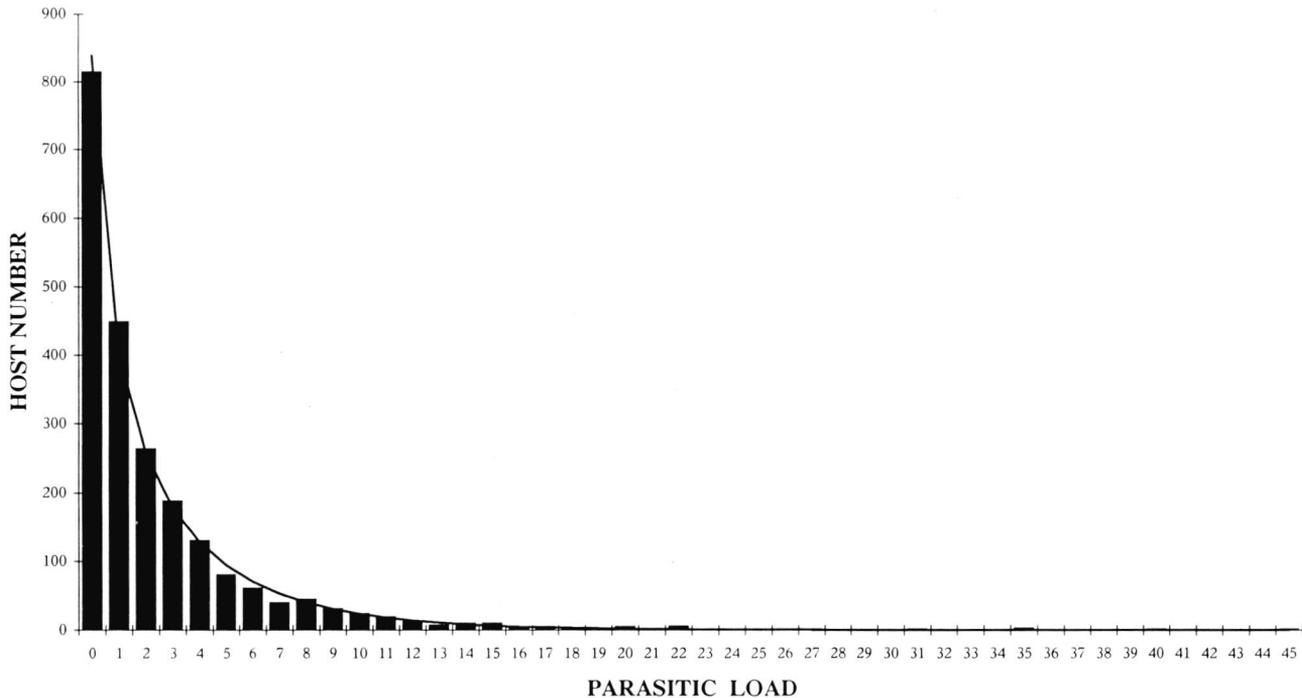


Fig. 1. — Frequency distribution of parasites on their host and adjustment to the negative binomial distribution ($k = 0.60$).

to exhibit a preference for site 1 (mean \pm SD, zone 1: 1.4 ± 3.3 ; zone 2: 1 ± 2.28 ; Wilcoxon's signed-ranks tests for paired comparisons, $z = -3.765$, $P < 0.001$). However, we did not observe a difference between site 1 and site 2 location for the ratio of adult to larvae copepods (Fisher exact test, $P = 0.11$).

PARASITE SEX RATIO

Figure 3 shows the evolution of the sex ratio with host size. Except for the first three classes, the sex ratio is always female biased. Moreover, this sex ratio increases with host size ($r = 0.24$, $n = 660$, $P < 0.001$).

Within the host population, we observed a significant positive association between adult male and female copepods ($r = 0.46$, $P < 0.001$) on the one hand, and between female and male larvae copepodids ($r = 0.12$, $P < 0.001$) on the other hand.

DISCUSSION

Generally for evolutionists, symbiotic associations (Parasitism, Commensalism and Mutualism) are defined in terms of cost-benefit ratio with regard to host fitness (Boucher, 1985; Renaud & De Meeüs, 1991; Poulin & Vickery, 1995). Only those which reduce host fitness are considered as parasites. The increase of the mean abundance and of the ratio β (Fig. 2a and b) is in accordance with

previous data (Heussner 1983) and shows that this associated copepod does not affect its host survival either through accumulation (Anderson & Gordon, 1982; Rousset *et al.*, in press), or prevalence (Rousset *et al.*, in press). Indeed, when the host mortality rate is intensity dependent (i.e. accumulation), curves of the host age as a function of the parasite intensity are convex, as a consequence of the death of the most heavily infected hosts (Anderson & Gordon, 1982; Rousset *et al.*, in press). A similar pattern is expected under host mortality induced by parasite prevalence (Rousset *et al.*, in press). Hipeau-Jacquotte (1988) provides some evidence that *P. gibber* is able to feed on the same planktonic algae as those filtered by its host (i.e. *Paulova lutheri*). Thus, this organism is potentially detrimental for its host growth through reduction of food availability. In addition, *Ciona* might develop regulation mechanisms (i.e. expulsion) against this competitor. However, both reduction of host growth and/or parasite regulation should be detected by the models described above (Rousset *et al.*, in press). So, it seems that *P. gibber* does not affect: *i*) host survival, *ii*) host growth, or *iii*) host resistance mechanisms. Unless this copepod affects its host's fecundity, it does not represent a costly partner (i.e. parasite), and thus should be considered, as already suggested by Dudley (1966) for Notodelphyidae copepods living in the branchial pharynx of an ascidian, as a commensal.

Moreover, Hipeau-Jacquotte's (1988) *in vitro* experiments revealed that this copepod was able to reach

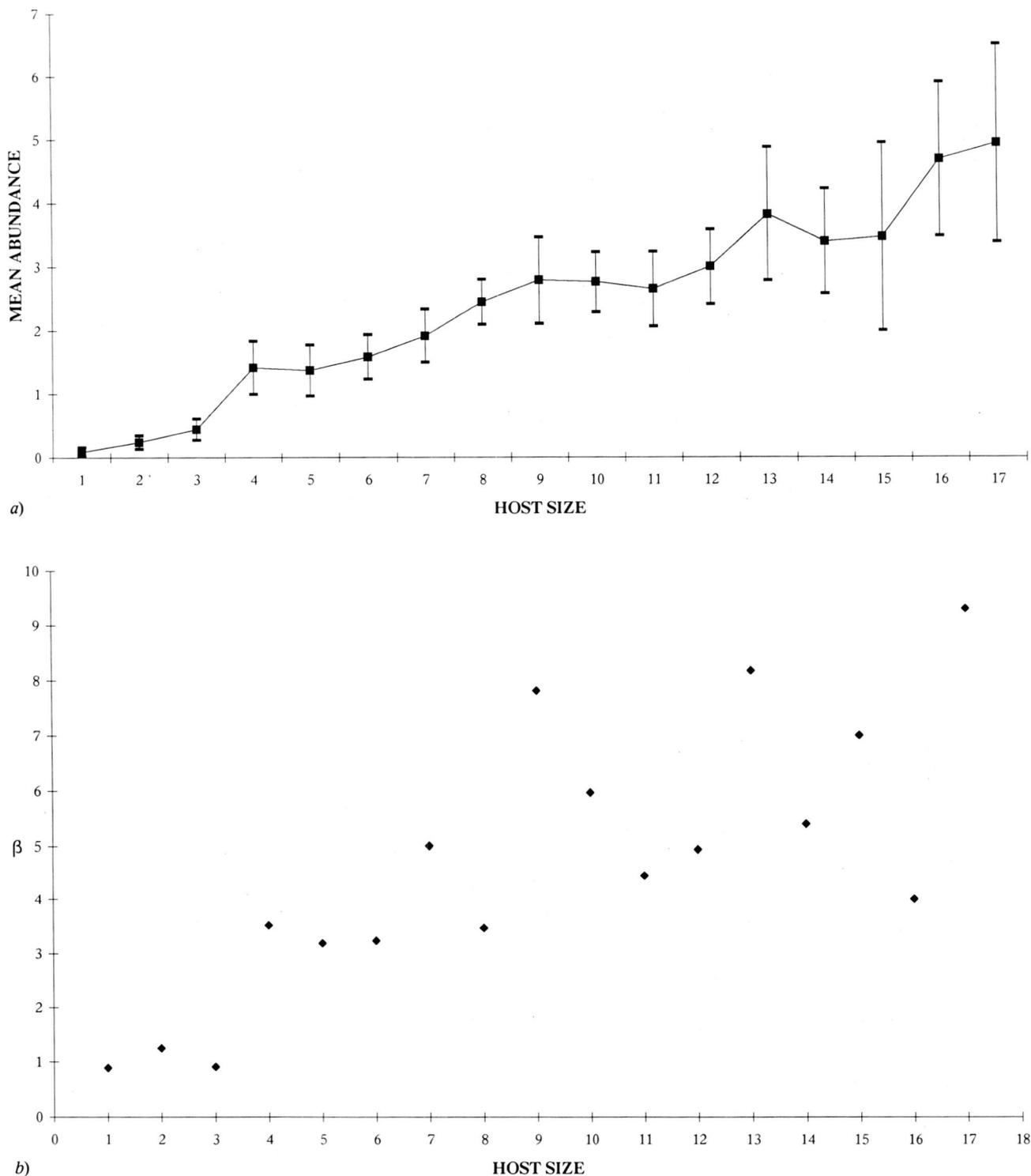


Fig. 2. — Relation between *Ciona* size and *P. gibber* abundance (a) and degree of aggregation β (b).

the adult stage without host colonization. So, it seems that *P. gibber* is not totally dependent on *Ciona*. This host can thus represent biological sites where the copepod find feeding (i.e. alga) and mating opportunities (i.e. sexual partners). We might thus consider the possibility of increasing fitness through generation time for copepod genotypes which are localized in *Ciona*. This situation could represent an evolutionary

path toward parasitism or mutualism through a first step of commensalism (Renaud & De Meeüs 1991). Interestingly, *P. gibber* displays an aggregated distribution within the host population, a pattern commonly observed in parasitic associations (Crofton, 1971; May, 1985). This situation could suggest that aggregated distribution occurs also for non-parasite associated organisms (Heip & Engels, 1977).

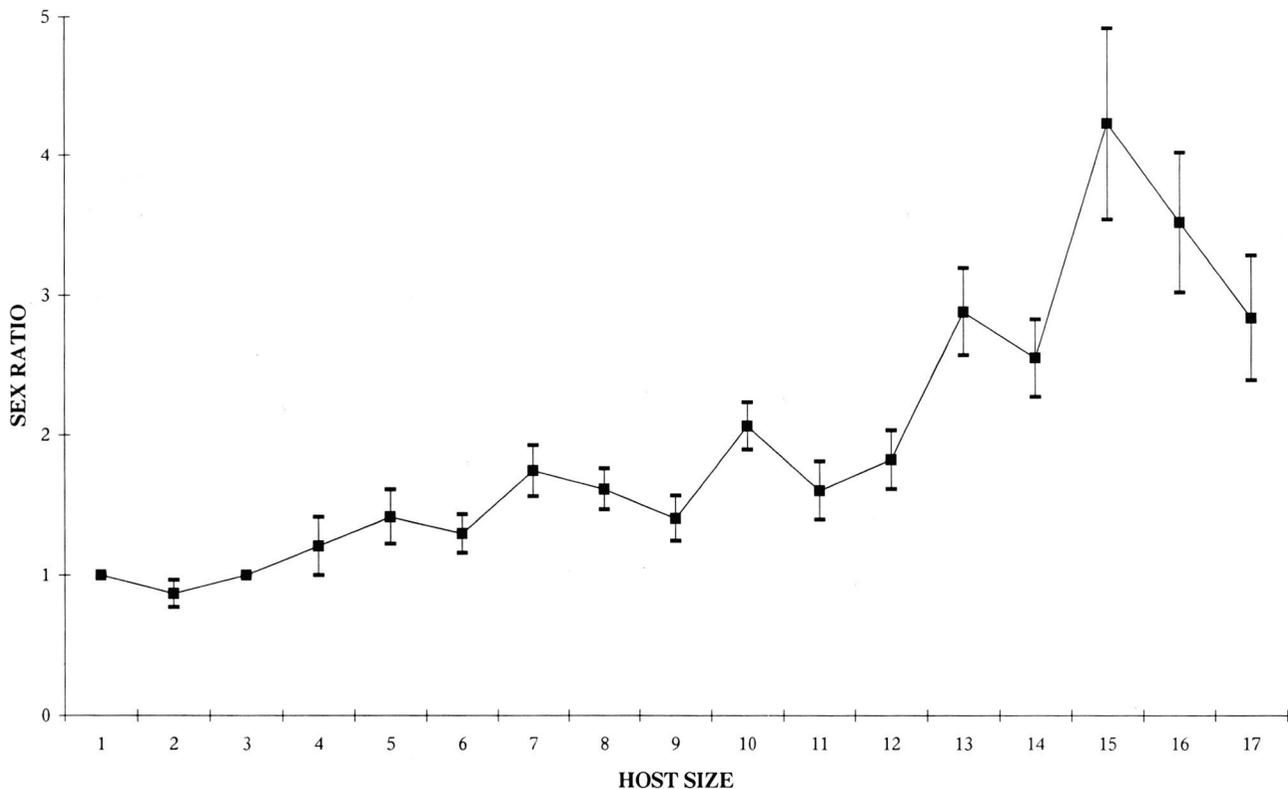


Fig. 3. — Relation between *P. gibber* sex ratio and *Ciona* size. Only *Ciona* presenting at least simultaneously one male and one female of *P. gibber* are taken into account in the analysis ($n = 660$ *Ciona* analysed).

Another point of the particular biology of this Crustacean must be underlined. Indeed, as already reported by Heussner (1983), we found a female biased sex ratio. Several mechanisms could explain such a phenomenon: *i*) the sex ratio is naturally biased, *ii*) female survival is superior to male survival, or *iii*) the first individual which colonizes one host develops to a female, while the second becomes a male until females are fertilized within a host (i.e. we observed female accumulation within host). Thus, this particular biology of *Pachypygus gibber* might be the reflection of the colonization of one host (i.e. *Ciona*), an evolutionary consequence which differentiates associated and free copepod species.

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