



Fouling of gastropods: a role for parasites?

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Received 5 August 1998; in revised form 8 October 1999; accepted 30 October 1999

Key words: Biomphalaria glabrata, Hydrobia ulvae, epibiosis, fouling, trematodes

Abstract

A sample of mud snails *Hydrobia ulvae* (Prosobranchia) from an intertidal population revealed that the shells of trematode-infected specimens were especially likely to be fouled with epibionts. Experimentally trematode-infected *Biomphalaria glabrata* (Pulmonata) appeared to be especially prone to develop epigrowth in comparison with uninfected conspecifics as well. These findings suggest an interaction between trematode infections and epibiosis in aquatic gastropods. The two most likely explanations for this are (1) that trematode infections weakens the snails' natural defences against epibionts, or (2) that the defences against epibionts also are effective against invading trematodes, causing snail specimens with a particularly good fouling defence to be less likely to become infected.

Introduction

Epibiosis, or the fouling by various epiphytes and epizoans, may be detrimental to aquatic organisms. In gastropods, epibionts are known to promote dislodgement, reduce growth rates, cause shell destruction, reduce fecundity and even cause direct mortality (Ishac & Bishai, 1968; Lauckner, 1980; Wahl, 1989, 1996; Kumar & Ayyakkannu, 1991). Consequently, many species especially prone to be fouled have developed antifouling mechanisms comprising both behavioural, mechanical, and chemical defences (see Bottjer, 1981; Wahl, 1989). The latter defence mechanism seems to be a widespread antifouling adaptation in which secondary metabolites, toxic to the epibionts, are incorporated into the tissues (Gerhart et al., 1988; Wahl, 1989).

Epibionts, however, are not the only symbionts aquatic gastropods have to face. Larval digenean trematodes are widespread among gastropods, and the frequency of parasitised specimens within a given snail population is often quite high (Lauckner, 1980). These

parasites usually infect and destroy the hepatopancreatic and gonadal tissue of the snail host, and through those activities they interfere with essential aspect of the host's metabolism (including allocation of secondary metabolites), cause behavioural changes, obstruct normal shell formation and reduce fecundity and survival (e.g. Lauckner, 1980; Huxham et al., 1993, 1995; Mouritsen & Jensen, 1994). Hence, the parasites seem to interfere with all basic defence mechanisms developed against epibionts, and we therefore hypothesise that snail specimens infected with trematodes are especially likely to become fouled. In order to test this prediction, we studied the relationship between trematode infections and epibiosis in two species of gastropods, *Biomphalaria glabrata* (Pulmonata) and *Hydrobia ulvae* (Prosobranchia). These two snail species are both phylogenetically and ecologically distantly related, the former being an annual, hermaphroditic and tropical freshwater snail, the latter a perannual, mainly temperate, marine species with separate sexes.

The analysed data are extracted from two different surveys that were not originally intended to clarify the present papers issue. This explains the restricted

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sample sizes and different methods used to elucidate the relationship between parasites and epibionts in the two species of snails (see below).

Materials and methods

Seemingly unfouled specimens of a laboratory strain of *Biomphalaria glabrata* (SmPR) were individually placed in 500 ml aquaria that were arranged in rows on a table, and each supplied with c. 20 small commercial aquarium stones (the likely source of foulers) and a 10 cm water column (untreated subsoil water). Some of the snails were exposed to *Schistosoma mansoni* miracidium larvae; the trematode species that causes 'bilharzia' in humans. The remaining part served as control individuals ($n=16$). Once a week, 2/3 of the water was replaced, and the snails were fed with dried and boiled lettuce and a protein source (the fish food 'Tetramin'). Following a 7 week period under a 12 h dark/12 h light (400 W halogen lamps producing about 4000 lux at the water surface of all aquaria) cycle, *Schistosoma*-infected snails were identified by the presence of cercarial emission ($n=8$). For both infected and control snails, the distribution of epibiota was drawn onto a snail sketch on graph paper and subsequently converted into percent coverage (to the nearest 5%).

An unbiased sample of 230 specimens of *Hydrobia ulvae* was collected from an unimodal size-distributed intertidal population in the Danish Wadden Sea, March 1990 (see Jensen & Mouritsen, 1992). The snails were measured and divided into three groups according to the degree of epibiosis on their shells: little fouled (<1/3 of the shell covered), intermediately fouled (1/3–2/3 coverage) and heavily fouled (>2/3 coverage). Epibionts were not attempted identified. The snails were subsequently dissected for the presence of larval trematodes. Snails with metacercarial infections may be more active on the sediment surface than uninfected snails and snails with cercarial infections (Huxham et al., 1995). Hence, snails with metacercarial infections can be expected to be particularly fouled and were, therefore, excluded in the present analysis.

Statistical analysis were carried out using SPSS (Statistical Package for the Social Science) (Norusis, 1993). Prior to One-way ANOVA, the prerequisites of homogeneity of variance and normality were tested and confirmed.

Results

The uninfected control specimens of *Biomphalaria glabrata* were significantly less fouled (median coverage: 23%; $n=16$) than trematode infected individuals (median coverage: 67%; $n=8$) (Mann-Whitney test, $Z=-2.72$, $p=0.006$). Epibionts were identified to be green algae (*Stigeoclonium* spp., *Scenedesmus* spp., *Monoraphidium* spp.) and blue-green algae (*Lyngbya* spp.). Average shell diameter of infected and control snails was 8.2 ± 0.7 (SD) and 8.3 ± 0.9 mm, respectively.

The proportion of infected *Hydrobia ulvae* was not randomly distributed among the three categories of fouling ($\chi^2=12.59$, $df=2$, $p<0.003$, Figure 1), demonstrating that the group of almost unfouled *Hydrobia ulvae* was significantly less likely to be infected with trematodes than their more fouled conspecifics. The snails were naturally infected by various species of digenean trematodes (mostly microphallids, echinostomids and plagiogochiids).

Because older (and hence usually larger) snails are more likely to be infected than younger (smaller) specimens (Lauckner, 1980), and because fouling is evenly likely to be a function of time (Wahl, 1989), a positive relationship between abundance of epibionts and prevalence of trematode infections is to be expected also under the assumption of independence between the occurrence of trematode infections and epibiosis. However, if this apply to the present data, snails from the group of heavily fouled and frequently infected *H. ulvae* should also be significantly larger than their conspecifics from the group of little fouled and less frequently infected snails. This could not be demonstrated, since the size-distribution of snails in the three categories of fouling did not differ significantly (One-way ANOVA, $F_{2,229}=2.11$, $p=0.12$; mean shell height among groups: 3.6–3.8 mm).

Nevertheless, in order to further exclude the possible influence of size/age as well as sex on epibiont cover, randomly selected pairs of infected and uninfected snails with similar sex and size (length deviation <0.2 mm) was tested against each other using epigrowth score as the variable (0, 1 and 2, corresponding to little, intermediately and heavily fouled, respectively). The analysis demonstrated that infected specimens were significantly more fouled than uninfected (Wilcoxon matched-pairs signed-rank test, $Z=3.01$, $n_{\text{pairs}}=74$, $p<0.003$).

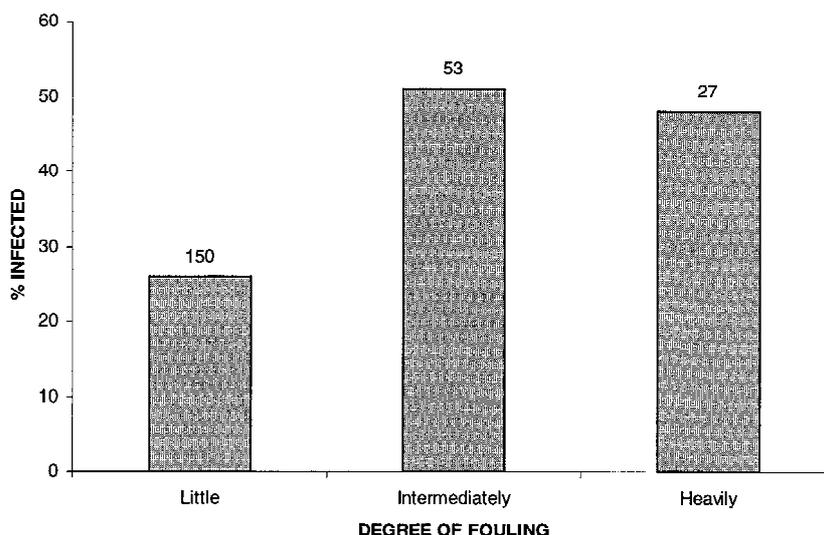


Figure 1. The proportion of trematode infected *Hydrobia ulvae* distributed on categories according to the abundance of epibionts on their shells. Sample size is given above the columns. The snails were classified as little fouled (<1/3 of shell covered), intermediately fouled (1/3–2/3 covered), and heavily fouled (>2/3 covered).

Discussion

The present results show a positive relationship between epibiosis and trematode infections thereby supporting our above formulated hypothesis. Through their severe impact on the general physiology of the snail (e.g. Lauckner, 1980, and see 'Introduction'), the trematodes may weaken the defence mechanisms developed to avoid epibiosis causing infected specimens to be especially fouled. This means that apparent population dynamic consequences of fouling to some extent can be ascribed to the act of the parasites as the ultimate factor. However, at least two alternative interpretations, evenly consistent with the present results, can be stated. 1. The defence mechanisms against epibionts are also effective against parasites. Assuming genetic variation within the population regarding the ability to resist epibiosis, snail specimens with a good defence may be less likely to become infected with trematodes. The significance of this interpretation is that the picture of the intimate gene-for-gene coevolutionary arms-race envisaged to be going on between a generalised host and its parasites (e.g. Holmes, 1983) is somewhat weakened in the case of aquatic gastropods and associated parasites: also the epibionts may significantly participate as a third party. Moreover, because trematodes as opposed to epibionts usually cause a complete castration of their snail host (e.g. Sousa, 1983), genotypes expressing a particularly poor anti-fouling defence should become rare within

the population. The presence of trematodes may thus accelerate the evolution of effective anti-fouling mechanisms. 2. Through a reduction of the snail's general condition, the occurrence of epigrowth may weaken the immuno-defence system against trematode infections causing fouled specimens to be especially likely to become infected. Our data on *Biomphalaria glabrata*, however, do not support this interpretation because these snails were attempted infected prior to the development of epigrowth. Moreover, under the likely assumption that an epibiosis-based reduction of snail condition is a continuous function of the degree of fouling, we would also expect a steady increase in the frequency of infected snails with increasing degree of fouling. Such a pattern is not supported by the *Hydrobia* data (see Figure 1).

The above interpretations are not mutually exclusive, and mentioned interactions could in principle occur simultaneously within a given snail population, or be of differential importance in different species. Nevertheless, since *Biomphalaria glabrata* and *Hydrobia ulvae* must be considered phylogenetically and ecologically quite separate species, we suspect that the demonstrated connection between trematode infections and fouling is a rather widespread phenomenon within aquatic gastropods. However, *in lieu* of the restricted amount of data presented here, this expectation needs to be further substantiated in future studies.

Acknowledgements

We are grateful to the Danish Bilharziasis Laboratory (DBL), Chalottenlund, for providing the *Biomphalaria* snails and the *Schistosoma* larval trematodes. We also thanks Helle Nielsen, University of Copenhagen, for the identification of epiphytes, and Lone T. Mouritsen, Peter Middelfart and referees for encouragements and constructive comments on an earlier draft. The study was partly supported financially by the Carlsberg Foundation (grant to Kim N. Mouritsen).

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