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Effect of infection by the metacercarial trematode *Renicola roscovita* on growth in intertidal blue mussel *Mytilus edulis*

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ABSTRACT: Trematode parasites can affect the molluscan hosts serving as first intermediate hosts in their complex life-cycles in manifold ways, but little is known about trematode-induced effects in second intermediate mollusc hosts. In 2 field experiments in 2 habitats and at 2 tidal heights (low and mid intertidal), controlled infection of blue mussels *Mytilus edulis* serving as second intermediate hosts for larval stages (metacercariae) of the trematode *Renicola roscovita* resulted in significant lower growth of parasitized compared to non-parasitized individuals. However, tidal height had a stronger effect on mussel growth than parasitism, without any interaction between the 2 factors. The negative effect of *R. roscovita* metacercarial infections on mussel growth is thought to result from direct tissue disruptions, interference of metacercariae (located in palps and visceral mass) with food intake ability, and growth of metacercarial cysts within the host. Mussel growth was negatively correlated with the number of metacercariae, but this relation was significant only at the mid and not at the low intertidal sites. This may indicate that parasites act as background stressors that affect their hosts depending on additional environmental stress such as (e.g.) food shortage, desiccation and heat, which all increase with the increasing aerial exposure. The results of this study show that trematode infections can be an important determinant of bivalve growth, with potential economic implications for mussel cultivation.

KEY WORDS: Trematodes · Bivalves · Growth · Parasites · Field experiment · Controlled infections

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INTRODUCTION

Trematode parasites have been shown to affect their marine mollusc hosts in manifold ways. In the complex life cycles of marine trematodes, molluscs serve as first intermediate hosts and, besides other invertebrates and fishes, also as second intermediate hosts. Final hosts of trematodes are vertebrates (Lauckner 1980, 1983). Particularly well studied are the effects of trematodes utilizing molluscs as first intermediate hosts. The extensive reproduction of the parasites inside the host tissue, often filling large parts of the host body, results in dramatic effects such as castration and enhanced mortality, and also affects host growth (Lauckner 1980, Mouritsen & Poulin 2002). Growth rates of gastropods serving as first intermediate hosts can be enhanced (gigantism) (Rothschild 1936, Mouritsen & Jensen 1994), reduced (Sousa 1983, Mouritsen et al. 1999) or not affected (Hughes & Answer 1982, Siddall et al. 1993, Mouritsen et al. 1999). In general, it is thought that in short-lived snails (e.g. *Hydrobia* spp.) castration by trematodes results in gigantism, while in longer-lived hosts (e.g. *Littorina* spp., *Cerithidea californica*, *Ilyanassa obsoleta*) no or negative effects occur (Sousa 1983, Mouritsen & Poulin 2002). However, factors other than life history characteristics of hosts seem to be important determinants of effects of trematode infections in first intermediate hosts, e.g. the trematode species involved, the host's food supply and exploitative competition between conspecifics (Mouritsen & Jensen 1994, Mouritsen et al. 1999, Mouritsen & Poulin 2002).

The effects of trematodes utilizing molluscs as second intermediate hosts are known to a much lesser extent. In this case, the effects seem to be less dramatic,

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since metacercariae do not reproduce in the host and thus are not as tissue destructive as their sporocyst counterparts in first intermediate mollusc hosts (Lauckner 1980, 1983, Mouritsen & Poulin 2002). However, in combination with other stressors, trematodes may affect survival of their second intermediate host (e.g. Wegeberg & Jensen 1999). The host's growth rates may also be affected: Lim & Green (1991) found enhanced growth in *Macoma balthica* parasitized by metacercariae of several species. In contrast, reduced growth was detected in *Cerastoderma edule* infected with *Himasthla interrupta* (Wegeberg & Jensen 2003) and in *Perna perna* infected with *Proctoeces* sp. (Calvo-Ugarteburu & McQuaid 1998). However, quantitative data on the effects of parasite species on their second intermediate mollusc hosts are largely lacking, and hence our knowledge on parasites as determinants of mollusc growth is limited. Another limitation is methodological: except for a few studies (e.g. Wegeberg & Jensen 2003), conclusions have been drawn from field observations or from experiments using parasitized and non-parasitized individuals collected in the field, with no controls for other potential factors underlying the infections or affecting growth. An appropriate solution to this limitation is controlled, artificial infection of experimental individuals.

The blue mussel *Mytilus edulis*, an ecologically and commercially important epibenthic bivalve species, often occurs in mussel beds as well as in small clumps or as single individuals on hard bottoms and sand flats. In northern Europe, it is frequently parasitized by the trematode *Renicola roscovita* (Lauckner 1983, Buck et al. 2005). *R. roscovita* utilizes the periwinkle gastropod *Littorina littorea* as the first intermediate host for its life cycle and a range of bivalves as the second intermediate host (Lauckner 1980, 1983). Several thousand encysted metacercariae can occur in individual mussels, predominantly in the palps and the visceral mass (Lauckner 1983, Buck et al. 2005). A variety of factors such as salinity, temperature, current velocity, epigrowth and competition for substrate or food are known to influence mussel growth, with duration of emersion and contact with filterable food being probably the most important contributory factors in intertidal environments (Baird 1966, Okamura 1986, Seed & Suchanek 1992, Buschbaum & Saier 2001). Although it frequently occurs in mussels, the potential effects of this parasite species on growth of its host have not been studied. Using controlled infections of *M. edulis* with *R. roscovita*, this study tested the effects of infection by the trematode *R. roscovita* on growth of the blue mussel at 2 field sites and 2 tidal levels. One field site was a mussel bed, the other a sand flat. The latter site was chosen to examine the potential natural infection of non-parasitized mussels through a high abundance of periwinkles, the trematode's first intermediate host. On the sand flat no periwinkles were present and thus no natural infection by *R. roscovita* expected.

MATERIALS AND METHODS

Study site. Both experiments were conducted in a tidal inlet, Königshafen, on the north coast of the island of Sylt (North Sea, Germany) on a mussel *Mytilus edulis* bed and a sand flat. This tidal inlet is part of a tidal basin in the northern Wadden Sea. The tides in this basin are semidiurnal, with a mean range of 2 m. Salinity remains close to 30. Mean water temperature is 15°C in summer and 4°C in winter. Tidal flats comprise 33% of the area, with sand being the prevailing sediment type (72% of the total intertidal). *M. edulis* beds cover approximately 3% of the intertidal area.

Parasite and host material. Mussels *Mytilus edulis* (15 to 20 mm) were randomly collected from a buoy (not treated with antifouling paint) in front of the tidal inlet Königshafen, where experiments were conducted. Because of the absence of the intermediate snail hosts mussels at this site are known to be free of trematode infections. To confirm the absence of parasites, tissues from 50 mussels were placed between 2 large glass slides and examined for trematode infection under a dissection microscope. The remaining mussels were kept in a large flow-through aquarium (3 m diameter). To obtain parasitized snails for controlled infections, periwinkles *Littorina littorea* were randomly collected near the mussel bed. In the laboratory, these were placed in bowls filled with aerated sea water (approx. 20°C) and exposed to light for several hours. The water was then screened for the presence of emerged cercariae. *Renicola roscovita*-infected and uninfected periwinkles were then isolated and kept separately in large aerated aquaria (100 l) until the controlled infection was initiated.

Controlled infections and experimental design. Infection of mussels with metacercariae of *Renicola roscovita* was achieved by placing 5 mussels and 5 infected *Littorina littorea* in a bowl (400 ml) filled with sea water (approx. 20°C) and equipped with an air pump. In a second (control) treatment, 5 mussels and 5 uninfected snails were kept together in identical bowls to control for potential effects of snail presence on mussels. After 12 h, the snails in both treatments (parasitized and non-parasitized) were removed and the mussels were kept in the bowls for another 12 h to ensure encystment of metacercariae (authors' pers. obs.). Following this procedure, the mussels were kept in a large flow-through aquarium for a maximum of 3 d until the start of experiments.

At the start of the field experiments, infected and uninfected mussels were measured with a calliper to the nearest 0.1 mm. A single mussel was placed in a small cage (10 cm diameter, 10 cm height) made of polypropylene with a mesh size of 5 mm and mounted on a wooden board. On the mussel bed (entrance of the tidal inlet), I fixed 40 cages (20 replicates per treatment) with rods at the mean low water line (MLW) (low site) and 40 cages in the mid intertidal at the highest part of the bed (+0.5 m MLW) (mid site). The cages were placed approximately 50 cm apart on the top layer of mussels in a completely random design. On the sand flat (inner part of the tidal inlet), I fixed 30 cages (15 replicates per treatment) with rods on the sediment in the low intertidal (+0.2 m MLW) (low site) and 30 cages in the mid intertidal (+1 m MLW) (mid site). The cages were placed approximately 50 cm apart in a completely random design. The experiments started on 5 June 2004 and were terminated 10 wk later in August. Mean water temperature during the experiments was 15 to 21°C; salinity remained around 30. At the end of the experiments, the length of each mussel (maximum anterior–posterior axis) was measured with a calliper to the nearest 0.1 mm. The tissue of each mussel was carefully removed, placed between 2 large glass slides, and examined under a dissection microscope for trematode infection. All metacercariae were identified (Lauckner 1980, 1983) and counted.

Statistical analysis. Parasite recruitment to the mussel bed was unexpectedly low (indicated by similar infection rates of the originally non-parasitized mussels at the 2 experimental sites) during the experiment so that data from both sites could be used for analysis. Results are shown as mean (±SE) infection intensity (number of parasite individuals per infected host) (sensu Bush et al. 1997) (see Fig. 1). To compare growth rates between treatments, analysis of covariance (ANCOVA) was applied with $\log_{10}$ (initial mussel length) as covariate and tidal height and parasitism as fixed factors in a 2-factor crossed design. Shell growth was $\log_{10}$-transformed prior to all analyses to meet assumptions of normality and homogeneity of variances (visual inspection and Cochran's *C*-test). Relations between parasite load ($\log_{10}$ + 1) and growth ($\log_{10}$) were analyzed by linear regression. All calculations were carried out with the software STATISTICA (StatSoft).

RESULTS AND DISCUSSION

In both experiments, parasite infection and tidal height had a significant effect on mussel growth, but there were no interactions (Fig. 1, Table 1). Non-parasitized mussels grew better than mussels infected with *Renicola roscovita*, and mussels at the low intertidal sites grew better than mussels at the mid intertidal sites. On the mussel bed, growth of parasitized individuals at the mid site (7.8 ± 0.3 mm) was 14% lower than that of non-parasitized individuals (9 ± 0.3 mm). Parasitized mussels at the low site (11.9 ± 0.2 mm) grew 5% less than non-parasitized mussels (12.5 ± 0.4 mm). On the sand flat, growth of parasitized mussels at the mid

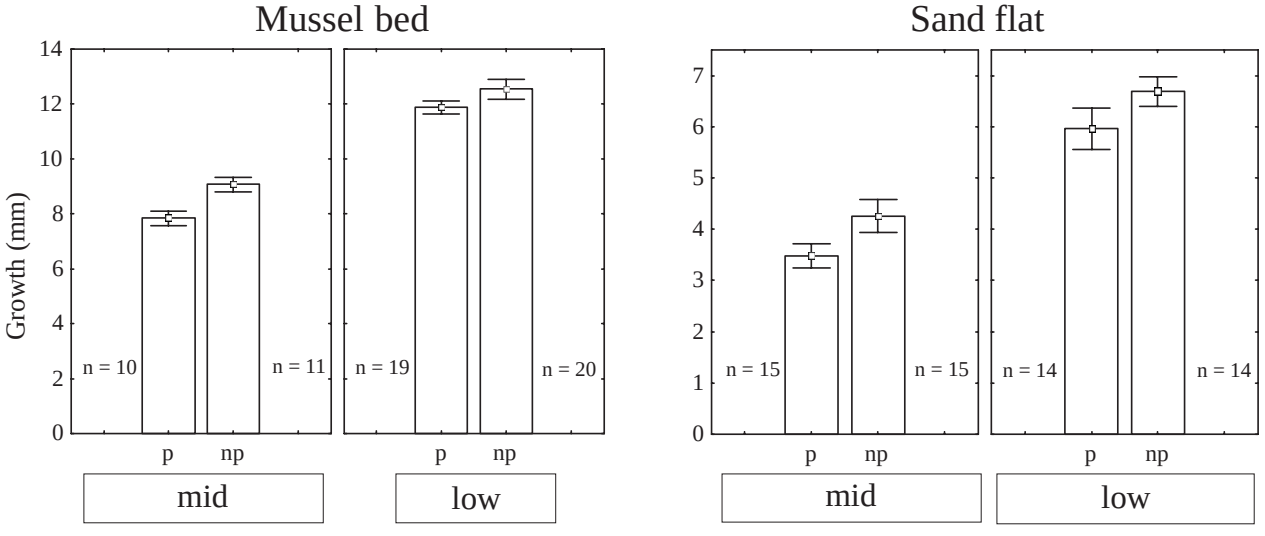

Fig. 1. *Mytilus edulis*. Mean (±SE) growth of mussels parasitized (p) with metacercariae of *Renicola roscovita* and non-parasitized (np) mussels at low and mid intertidal sites in 2 experiments (mussel bed, sand flat) at the end of 10 wk exposure. Due to cage loss, final replicates (n = no. of mussels per treatment) differed between treatments

Table 1. *Mytilus edulis*. Results of analysis of covariance (ANCOVA) with log initial shell length as covariate for effects of tidal height (low, mid), and parasites R*enicola roscovita* (parasitized, non-parasitized) as fixed factors on log growth. Significant p-values are in boldface

Parameter	df	MS	*F*	p
Mussel bed				
Tidal height (T)	1	0.313	155.8	**<0.001**
Parasites (P)	1	0.015	7.6	**<0.01**
T × P	1	0.003	1.5	=0.23
Log initial length	1	0.016	8.1	**<0.01**
Total	55	0.002		
Sand flat				
Tidal height (T)	1	0.639	45.7	**<0.001**
Parasites (P)	1	0.059	4.2	**<0.05**
T × P	1	0.003	0.2	=0.66
Log initial length	1	0.006	0.4	=0.51
Total	55	0.014		

site (3.5 ± 0.2 mm) was 18% lower than that of non-parasitized mussels (4.3 ± 0.3 mm). Growth of parasitized mussels at the low site (5.7 ± 0.4 mm) was 11% lower than that of non-parasitized mussels (6.7 ± 0.3 mm). Loss of cages due to storms caused a reduction in the original numbers of replicates (Fig. 1). The growth of individual mussels ($\log_{10}$) was only significantly and negatively correlated with the number of *R. roscovita* metacercariae present ($\log_{10}+1$) at the mid-intertidal sites (mussel bed: $r^2 = 0.32$, $p < 0.001$; sand flat: $r^2 = 0.14$, $p < 0.05$) but not at the low-intertidal sites (mussel bed: $r^2 = 0.04$, $p = 0.22$; sand flat: $r^2 = 0.06$, $p = 0.20$).

Controlled infections proved to be successful, since all artificially infected mussels bore metacercariae of *Renicola roscovita* (mean = 334 ± 270 metacercariae mussel^{-1}). Metacercariae occurred predominantly (>90% of total *R. roscovita* metacercariae per host) in the palps and the visceral mass of infected individuals. Prior to the experiments, the mussels had been free of parasites (confirmed by microscopic examination of 50 sub-sampled individuals). Natural infections with *Renicola roscovita* in the non-parasitized treatments during the experimental period occurred on the mussel bed in 61% of the mussels. However, intensities were generally low (2.3 ± 2.2 metacercariae infected mussel^{-1}). In the mid-intertidal of the sand flat, natural infections with *Himasthla continua* occurred in 73% of parasitized and non-parasitized mussels (2.5 ± 1.4 metacercariae infected mussel^{-1}).

Controlled infection with metacercariae of *Renicola roscovita* resulted in up to an almost 20% lower growth increment in parasitized *Mytilus edulis* compared to non-parasitized mussels within a period of 10 wk. This effect was independent of tidal height and experimental site. There are 3 mechanisms that are likely to be responsible for the observed growth reduction in infected mussels: (1) the invasion of the mussel tissues by cercariae with subsequent encystment, since metacercariae lead to tissue destruction and local inflammation (Lauckner 1983, Villalba et al. 1997), thus imposing a physiological burden on the mussels; (2) the encystment by metacercariae of *R. roscovita* in *M. edulis* predominantly in the palps and the visceral mass (Lauckner 1983, Buck et al. 2005, authors' pers. obs.), which both play an important role in the feeding and metabolic processes of bivalves (Hawkins et al. 1998); (3) growth of *R. roscovita* during the encysted metacercarial stage (Lauckner 1980, 1983, author's pers. obs.) which could result in a higher defense response of mussels and a higher energy demand by *R. roscovita* compared to non-growing metacercarial cysts of other trematode species. These characteristics of *R. roscovita* metacercariae may explain the greater effect of *R. roscovita* on bivalve growth compared to the trematode *Himasthla interrupta* on growth of *Cerastoderma edule* in controlled experiments, where only a very subtle effect on growth was observed (Wegeberg & Jensen 2003). *H. interrupta* does not grow in its second intermediate host and inhabits other tissues (mainly the foot), and thus does not interfere with it's host's feeding. In another marine bivalve species serving as second intermediate host, the green mussel *Perna perna*, large metacercariae of *Proctoeces* sp. caused a more notable reduction in growth, probably because of the immense size of the latter parasite (Calvo-Ugarteburu & McQuaid 1998). However, enhanced growth due to metacercarial infection has also been observed (e.g. in *Macoma balthica*: Lim & Green 1991). This indicates that a variety of factors determine the magnitude of trematode-induced effects on bivalve growth, e.g. size and tissue location of parasites, food supply of the host, and exploitative competition with conspecifics. Differences in food supply could have been responsible for the difference in growth of mussels at the 2 experimental sites, with the supply presumably being lower on the sand flat, which is located in the inner part of the tidal inlet at a slightly higher tidal level than the mussel bed site.

Although parasitism by *Renicola roscovita* metacercariae had a negative effect on mussel growth at both experimental sites, tidal height had a stronger effect, as indicated by the larger *F*-values in the ANCOVAs (Table 1). The importance of tidal height for mussel growth is well known, with long periods of immersion allowing almost continuous feeding (Baird 1966, Buschbaum & Saier 2001). In addition, mussels at higher intertidal sites are subject to harsher environmental variables such as desiccation and temperature, than mussels at lower intertidal sites (Widdows & Shick 1985). This may be reflected in the significant negative rela-

tions of mussel growth with metacercarial load at the mid-intertidal sites compared to the non-significant correlations at the low-intertidal sites. Trematode infection may act as a stressor, with the strength of its effects depending on the presence of additional environmental stressors (Lafferty & Kuris 1999). For example, infection of *Cerastoderma edule* by *Himasthla elongata* have been shown to reduce survival of infected individuals under oxygen depleted conditions, but not under normal environmental conditions (Wegeberg & Jensen 1999).

Renicola roscovita is common in blue mussels throughout European coastal waters, and is often found in 100% of mussels on intertidal mussel beds (Lauckner 1983, Svärdh & Thulin 1985, Buck et al. 2005). Thus its effect on mussel growth is likely to affect a large fraction of *Mytilus edulis* populations. The parasite loads in my experiments were lower than the several thousand metacercariae per individual host reported for many intertidal mussel beds (Lauckner 1983, Svärdh & Thulin 1985, Buck et al. 2005). Significant negative regressions between metacercarial intensity and mussel growth at the mid-tide level indicate that effects are intensity dependent. Hence, at sites with very high *R. roscovita* loads, growth reduction should be severe. This may be a strategy by the parasite to enhance its transmission to its final bird host (Poulin 1995), since mussels may thus remain within the prey size range of the parasite's final host for a longer period of time. Common bird predators such as the eider *Somateria mollissima* and the oystercatcher *Ostralegus haematopus* are known to prefer smaller mussels (Nehls 1989, Hilgerloh 1997). However, growth reduction could also be a side effect of *R. roscovita* infection, arising from the 3 mechanisms discussed earlier (Poulin 1995). Whatever the reason, a growth reduction of up to almost 20% indicates that trematode parasites can be an important determinant of bivalve growth. This may have economic implications for mussel cultivation, which may be better situated at subtidal offshore sites, where *R. roscovita* infection does not occur (Buck et al. 2005). Alternatively, intertidal sites without the first intermediate host, *Littorina littorea*, may be suitable. Ecologically, the parasite mediated negative linkage to *L. littorea* is of interest because positive effects of the periwinkles are also reported for mussels—notably the scraping off of detrimental epigrowth such as barnacles (Buschbaum 2000). The effect of parasites on mussel growth may be lower than that of other factors such as salinity, temperature, current velocity, epigrowth and competition, all of which are known to influence mussel growth (Baird 1966, Okamura 1986, Seed & Suchanek 1992, Buschbaum & Saier 2001). However, parasite reduced growth may also indicate that parasites function as 'background' or superimposed stressors that may exert stronger effects in the long run. The 10 wk duration of my experiments was too short to reveal long-term effects of parasites such as enhanced mortality rates. However, controlled infection and subsequent field experiments are a promising approach for revealing parasite induced, hidden determinants of bivalve growth.

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