

Effects of the trematode *Microphallus turgidus* on locomotion and prey capture in the grass shrimp *Palaemonetes pugio*

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Abstract

The grass shrimp, *Palaemonetes pugio*, is common in estuaries and marshes along the east coast of the USA and is frequently infected with metacercariae of the trematode, *Microphallus turgidus*. To test whether or not *M. turgidus* has an effect on intermediate host behaviour, the length of time spent swimming and walking over 1 min and 3 min intervals and prey (*Artemia*) capture rates of uninfected grass shrimp and those infected with 1–10, 11–20 or 21–30 metacercarial cysts were compared. Uninfected shrimps spent significantly more time swimming than infected shrimps during the first minute of observation. There were no differences between the control and infected groups in terms of swimming at 3 min, walking at 1 and 3 min, or in numbers of prey captured. These results indicate that *M. turgidus* may induce little or no change in grass shrimp locomotion nor in prey capture behaviour. This is in contrast to other parasites that modify intermediate host behaviour to enhance their transmission to definitive hosts. Furthermore, these data support earlier studies indicating that *M. turgidus* does not affect the growth and survival of *P. pugio*.

Introduction

Transmission to new hosts is vital to the survival of parasites, many of which facilitate this process by influencing the behaviour of their hosts (Moore, 2002). Moreover, parasites with complex life cycles are known to modify the behaviour of their intermediate host to assure transmission to the definitive host. Parasite-induced alterations of host behaviour include increased or decreased levels of activities such as locomotion, changes in foraging behaviour, and modification of predator–prey relationships of their hosts (Brown & Thompson, 1986; Mesa *et al.*, 1994; Maynard *et al.*, 1998; Levri & Fisher, 2000). In contrast, some trematodes may not necessarily induce any behavioural changes in their intermediate

host (Thomas *et al.*, 1995). The wide array of parasite-induced effects on host behaviour prompts further behavioural studies involving other host–parasite systems.

The grass shrimp, *Palaemonetes pugio*, is a shallow water crustacean occurring frequently along the Atlantic coast of the USA (Anderson, 1985). These shrimps are hosts to a variety of parasites, including the trematode *Microphallus turgidus* (Heard & Overstreet, 1983). *Palaemonetes pugio* serves as the second intermediate host, with aquatic birds, among other vertebrates, serving as definitive hosts for *M. turgidus* (Heard & Overstreet, 1983).

Several investigators have reported evidence that shows an increase in the parasite load with host size is not detrimental to host survival (Anderson & Gordon, 1982; Rousset *et al.*, 1996). Thomas *et al.* (1995) studied the effects of *Microphallus hoffmanni* on the amphipod *Gammarus aequicauda* and reported that the mean parasite abundance increased with host size, suggesting that

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accumulation of this parasite had no significant effect on the survival of its crustacean host. In addition, similar observations by Pung *et al.* (2002) were reported on the effects of *M. turgidus* on the grass shrimp *P. pugio*. In this study, the prevalence of metacercarial cysts of *M. turgidus* in grass shrimp *P. pugio* from 11 field localities along the Georgia coast was reported to be around 75% and the intensity of infection ranged between 1 and 105 cysts; additionally, parasite density increased with the body length and weight of *P. pugio* (Pung *et al.*, 2002).

It is not known whether the locomotion and feeding behaviours of *P. pugio* are significantly influenced by *M. turgidus*. Consequently, the present investigation examined the effects of *M. turgidus* on the shrimp's activity levels (swimming, walking) and the number of prey captured, using *Artemia* as prey. Based on the observation that the parasite may not have an effect on grass shrimp survival (Pung *et al.*, 2002), we hypothesized that *M. turgidus* would not reduce the activity levels of grass shrimp or their ability to capture prey.

Materials and methods

Grass shrimps were collected with a dip net from a tidal marsh creek in Savannah, Georgia, and were transported to the laboratory. Thereafter, shrimps were examined under a dissecting microscope ($10\times$ total magnification) and the number of metacercarial cysts, visible through the transparent integument of the shrimp, was counted. Shrimps were grouped according to intensity of infection for each study: four experimental groups of 20 shrimps each were used in the locomotion studies (uninfected controls, 1–10 cysts, 11–20 cysts, and 21–30 cysts), and three groups of 13 shrimps (uninfected controls, 1–10 cysts, and 11–20 cysts) were used for feeding studies. Shrimps were acclimatized separately for 1 week in 20 ppt salt water prior to experimentation and each shrimp was used in only one trial. Experiments were conducted using similar-sized (mean body length 30 ± 5 mm) non-ovigerous individuals.

For locomotion studies, a randomly selected shrimp from one of the groups described above was placed in a transparent 20 l aquarium, filled with 10 l seawater with a salinity of 20 ppt, and allowed to acclimatize for 5 min after which the length of time spent swimming or walking over 1 and 3 min time periods was recorded. Thereafter, a stopwatch was used to quantify swimming and walking for 1 and 3 min. One-way analysis of variance was employed to compare uninfected and infected groups for each of the activities.

For prey capture studies, the brine shrimp *Artemia* sp. was used as prey. During experimentation, an individual grass shrimp that had been fed or starved for either 24 h or 48 h was placed in an opaque tank (length, 10 cm; height, 10 cm) filled with 2.5 l saltwater, and allowed to acclimatize for 5 min. Pilot studies showed that an individual shrimp starved for 48 h consumed an average of two *Artemia* in 5 min. Thus, five *Artemia* were introduced with one grass shrimp during each experiment and the number of *Artemia* consumed after 5 min was recorded. One-way analysis of variance was performed to test for significant differences between the

total number of prey consumed by uninfected and infected shrimps.

Results and Discussion

During the present experiments, individual shrimps occasionally rested but this behaviour was not accounted for, and only swimming and walking were quantified. Infected shrimps spent significantly less time swimming than uninfected shrimps during the first minute of observation (fig. 1, $P = 0.019$). However, no significant differences were found between uninfected and infected shrimps with respect to the length of time spent in swimming at 3 min, or walking at 1 min and 3 min (figs 1 and 2, $P > 0.05$). During the prey capture experiments, although uninfected shrimps consumed more *Artemia* than fed individuals, no significant differences in prey capture rates were found between uninfected and infected individuals at the three feeding intervals (fig. 3, $P > 0.05$).

It is well known that parasite-induced modification in host behaviour increases the chance for parasite

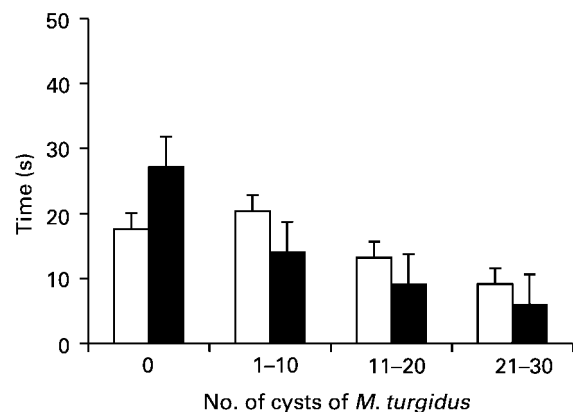


Fig. 1. Length of time uninfected and *Microphallus turgidus*-infected grass shrimp, *Palaemonetes pugio*, spent either walking (□) or swimming (■) during the first minute of observation. Each value is a mean plus 1 SEM.

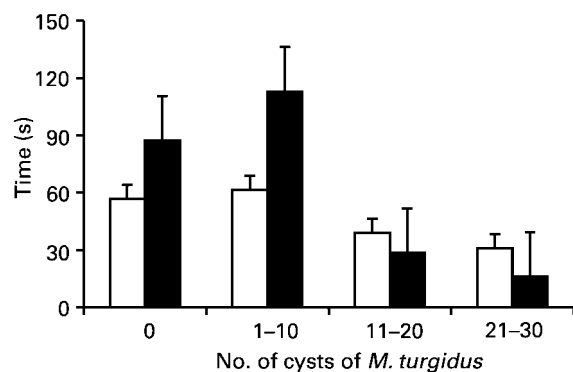


Fig. 2. Length of time uninfected and *Microphallus turgidus*-infected grass shrimp, *Palaemonetes pugio*, spent either walking (□) or swimming (■) during the three minutes of observation. Each value is a mean plus 1 SEM.

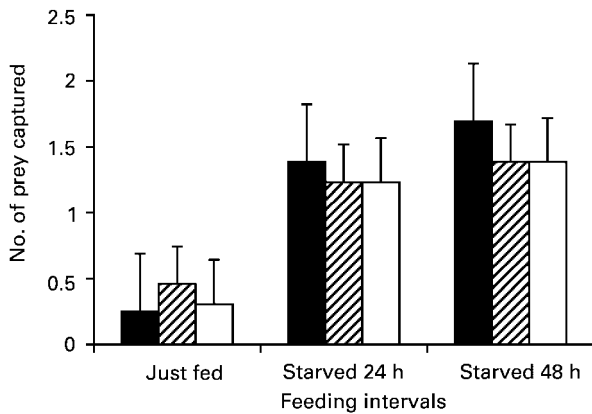


Fig. 3. Number of *Artemia* (prey) captured by uninfected (■) and *Microphallus turgidus*-infected (▨, 1–10 cysts; □, 11–20 cysts) grass shrimp, *Palaemonetes pugio*, either fed immediately prior to exposure to the prey or starved for 24 h or 48 h. Each value is a mean plus 1 SEM.

survival and transmission or ensure completion of its life cycle.

Crustaceans may exhibit a wide array of parasite-induced behavioural changes, and these behavioural modifications may eventually depend on a particular host–parasite association. While little or no changes in locomotion and feeding activities were reported between uninfected and infected shrimps as a result of *M. turgidus* infection, other investigators working with different crustacean–parasite systems have reported varied results. For example, the amphipod *Echinogammarus stammeri* infected with the acanthocephalan *Pomphorhynchus laevis* displays positive phototrophism and are more vulnerable than uninfected amphipods to predation by the definitive fish host (Maynard *et al.*, 1998). Brown & Thompson (1986) reported that *Gammarus pulex*, also infected with *P. laevis*, showed a greater tendency to swim in open water, thereby increasing the risk of predation by fish.

The grass shrimp *P. pugio* serves as the definitive host for the isopod *Probopyrus pandalicola* (Anderson, 1985). It has been shown that isopod-infected grass shrimps have lower activity levels than uninfected shrimps and capture fewer *Daphnia*; yet, when *Artemia* is offered as prey, there is no difference in consumption rates between uninfected and infected *P. pugio* (Bass & Weis, 1999). In the present study, *Daphnia* was not incorporated in the prey capture experiments and this aspect may be investigated in a future study.

Several investigators have reported on the effects of *Microphallus* spp. on the behaviour of intermediate hosts. These trematodes are reported to alter the foraging behaviour of its snail host, *Potamopyrgus antipodarum*, thereby increasing predation by their final (waterfowl) host (Levri & Fisher, 2000). *Microphallus papillorobustus* induces strong behavioural alterations in the amphipod *Gammarus insensibilis*, making the intermediate host more vulnerable to predation by aquatic birds, which serve as definitive hosts (Helluy, 1984; Thomas *et al.*, 2002). Conversely, *M. hoffmanni* does not seem to alter the behaviour of its gammarid amphipod host *G. aequicauda*,

as parasite accumulation does not appear to affect host survival (Thomas *et al.*, 1995). The present findings compare well with the latter study in that *M. turgidus* does not seem to affect the locomotory and feeding behaviours of the shrimps, demonstrating the lack of parasite-induced behavioural changes in *P. pugio*. These results were not unexpected because in an earlier field study the density of *M. turgidus* metacercariae was found to increase with body length and weight of *P. pugio*, with the highest parasite density in the largest individuals, thus suggesting that the parasite does not affect the survival of its grass shrimp host (Pung *et al.*, 2002). Similar observations have been made for the shrimp *Macrobrachium ohione*, also infected with *M. turgidus* (Bridgeman, 1969).

A possible explanation of the lack of parasite-induced behavioural changes in infected grass shrimps may be related to the location of cysts within the intermediate host. According to Thomas *et al.* (2000), trematodes encysting in the abdomen of the gammarid *G. insensibilis* have no particular effect on the host; however, one trematode species encysts in the cerebral ganglia of the gammarid and strongly alter its behaviour in a way that increases its predation risk by aquatic birds, the definitive hosts. We encountered *P. pugio* harbouring up to 40 metacercarial cysts of *M. turgidus* during our study, and these metacercariae were typically located within the abdominal muscle tissue of the shrimps. If an abdominal muscle-dwelling trematode fails to induce behavioural changes in gammarids, it is possible that other crustaceans like *P. pugio* may not exhibit defined parasite-induced behaviours for reasons mentioned above. However, this rationalization for the lack of behavioural alterations in infected grass shrimps needs further experimentation.

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