

Size-dependent pattern of metacercariae accumulation in *Macomona liliana*: the threshold for infection in a dead-end host

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Received: 21 May 2008 / Accepted: 13 August 2008 / Published online: 30 August 2008
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Abstract While bivalves can acquire trematode metacercariae over their lifetime, the rate at which this accumulation takes place is not necessarily linear. The present study found that the bivalve *Macomona liliana* acquires very few or no metacercariae until it reaches 30 mm in size, but thereafter the rate at which it becomes infected increases exponentially. It is likely that this ontogenetic change in infection rate is associated with the increased filtration capacity and siphon diameter of larger *M. liliana*. The echinostome metacercariae that infect *M. liliana* also infect a much more common sympatric bivalve, *Austrovenus stutchburyi*, in which they achieve much higher infection intensity. Due to its deeper burying depth, *M. liliana* most likely represents a dead-end host for the echinostomes: potential definitive hosts preferentially feed upon *A. stutchburyi* as they are located closer to the sediment surface than *M. liliana*. However, due to the low infection intensity and population density of *M. liliana*, its overall impact as a sink for echinostome populations in the ecosystem is probably negligible.

Introduction

Because bivalves are sessile animals, it is not possible for them to actively avoid parasite propagules, and, because trematodes infect bivalve hosts by entering the mantle cavity via the inhalant current (De Montaudouin et al. 1998; Wegeberg et al. 1999), the rate at which they accumulate trematode metacercariae should reflect their water filtration

capacity. The feeding rate of bivalves living in soft-sediment habitats is linked to water filtration rate, which in turn relates to the bivalves' size and burying depth. Generally, larger individuals are able to filter water more rapidly and bury deeper into the sediment than smaller individuals (Zaklan and Ydenberg 1997). Feeding rate is in turn affected by burying depth, with shallower-buried individuals being able to feed more efficiently (de Goeij and Honkoop 2003). Thus, like other aquatic organisms that filtrate food particles from water that contain infective stages, while larger size means greater filtration capacity and in turn higher feeding rate, it also imposes a cost of increased parasite infection rate (Hall et al. 2007).

According to the simplest null hypothesis, as it grows, a bivalve should accumulate trematode metacercariae gradually over time, and parasite load should increase steadily with host size. However, due to the relationship between bivalve size and filtration capacity, it is likely that the parasite load in fact increases exponentially with bivalve size. Recently, it has been found that *Macomona liliana*, a tellinid clam that lives in sympatry with the New Zealand cockle *Austrovenus stutchburyi* along the New Zealand coast, is infected with trematode metacercariae that encyst in its foot. Closer morphological inspection revealed that the metacercariae consisted of the echinostome species *Curtuteria australis* and *Acanthoparyphium* sp. that had previously been reported in *A. stutchburyi* (Allison 1979; Martorelli et al. 2006). While the transmission ecology and host–parasite interactions between the echinostomes and *A. stutchburyi* have been well studied (Thomas and Poulin 1998; Mouritsen 2002; Mouritsen and Poulin 2003, 2005; Babirat et al. 2004; Tompkins et al. 2004), the interactions between the echinostomes and *M. liliana* are less well understood. It is likely that any echinostome that infect *M. liliana* are lost from the parasite population. Compared with

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A. stutchburyi, *M. liliانا* are more cryptic and are buried deeper in the sediment, making them less accessible to shorebirds (the definitive hosts of echinostomes) than the abundant and shallower-burying *A. stutchburyi*. However, what percentage of the parasite population is lost due to the presence of *M. liliانا* has yet to be quantified. In this study, we use the New Zealand soft-sediment tellinid clam, *M. liliانا*, to investigate the relationship between parasite accumulation rate and host body size, and we quantify the role played by *M. liliانا* as a sink in the transmission ecology of the echinostomes.

Materials and methods

The *M. liliانا* used for this study were collected in February 2007 in Company Bay, Otago Harbor, South Island, New Zealand. *M. liliانا* were collected from the lower tidal range, along a 25-m-long transect parallel to the waterline. The transect was divided into five different sampling points, each sampling point located at 5-m intervals along the transect. At each sampling point, an area measuring 1 m² was dug to a depth of 15 cm and all *M. liliانا* found were collected. Five New Zealand cockles *A. stutchburyi* were also collected at each sampling point as a comparative sample. A total of 196 *M. liliانا* and 25 *A. stutchburyi* were collected from the site.

All animals were returned live to the laboratory where the maximum shell length of each cockle and *M. liliانا* was measured with digital calipers to the closest 0.1 mm. After the measurements were taken, all bivalves were dissected and inspected for parasites. Because the echinostome metacercariae were encysted in the foot, the foot muscle of each bivalve was removed and placed individually in a tube of pepsin digestive solution (6 g pepsin and 7 ml of 36–38% HCl in 1,000 mL of water) and incubated at 40°C for 20–30 h. The process partially dissolves most of the host tissue while leaving the metacercariae intact. After the incubation period, all the metacercariae in the tube were recovered and counted under a dissecting microscope.

Prior to statistical analysis, the numbers of metacercariae per bivalve were log-transformed. Statistical analyses were conducted using SPSS 11 statistical package. All statistical analyses conducted involved parametric tests.

Results

The shell lengths of *M. liliانا* collected for this study ranged from 13.4 to 52.4 mm, with a mean of 33.3 mm. The infection intensity by metacercariae ranged from 0 to 288, with a geometric mean of 20.4. The shell lengths of

the *A. stutchburyi* collected ranged from 25.0 to 39.6 mm, with a mean of 29.5 mm. The number of metacercariae found in *A. stutchburyi* ranged from 90 to 807 with a geometric mean of 387.5. When analyzed using an analysis of covariance with shell length as covariate and sampling point as a categorical variable, the infection intensity of metacercariae in *M. liliانا* was found to be strongly correlated with shell length ($F_{1, 190}=1,096.18$, $P<0.001$) while no difference was found among sampling points ($F_{4, 190}=1.88$, $P>0.05$). However, the relationship between shell length and infection intensity was not linear (Fig. 1): individuals with shell lengths below 30 mm harbor no or very few metacercariae, whereas infection intensity increases rapidly as a function of shell length in larger individuals.

Discussion

Previous studies have noted that infection intensity by trematode metacercariae in bivalves increases significantly with host size (De Montaudouin et al. 1998; Poulin et al. 2000; Leung and Poulin 2007); however, this study shows that the accumulation of parasites is not linear over the lifetime of the host. As seen in Fig. 1, there is a sudden increase in metacercariae load when *M. liliانا* exceeds approximately 30 mm in size. As discussed in the “Introduction,” the increase in filtration capacity as the bivalve grows can also lead to greater parasite accumulation rate; thus, at least for suspension-feeding filter feeders, there is a tradeoff between feeding rate and infection level.

Another factor to consider when examining the infection intensity of echinostomes in *M. liliانا* is the presence of *A. stutchburyi*, which can be considered as the main second intermediate host for echinostomes in this system. Each

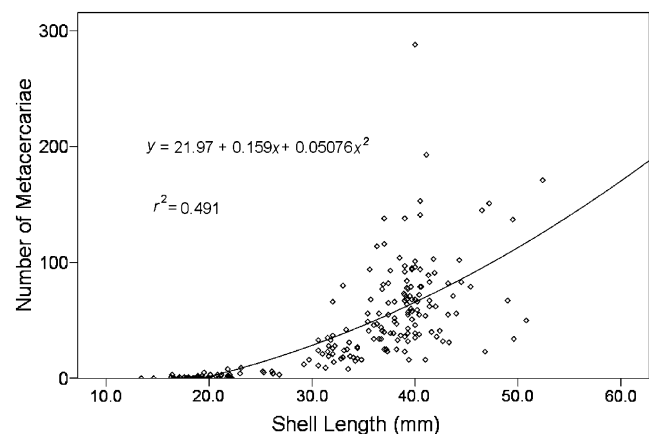


Fig. 1 Relationship between the number of echinostome metacercariae per host and the shell length of *M. liliانا*. A quadratic function has been fitted to these data purely to illustrate the nonlinear increase in infection intensity

cockle can be infected with hundreds or even more than a thousand metacercariae (Poulin et al. 2000; Leung and Poulin 2007). It has been calculated that cockles can take up most of the available cercariae because the cockle population at the low tidal mark can filter the water column 8–19 times for each immersion period (Mouritsen et al. 2003). The study that led to this figure was also conducted at Company Bay, where the sample for the present study was collected. In effect, the cockles “compete” with each other as well as other potential hosts in the system such as *M. liliana* for cercariae in the water column (Mouritsen et al. 2003).

While the echinostome cercariae can successfully infect and encyst in *M. liliana*, any parasite entering *M. liliana* is most probably lost in a dead-end host, as oystercatcher definitive hosts are unlikely to feed on this deep-burying bivalve. While shorebirds are known to feed on *M. liliana* (Thursh et al. 1994; Cummings et al. 1997), it is also known that the frequency at which they feed upon *M. liliana* is dependent upon the presence and density of *A. stutchburyi*, which appears to be the preferred prey (Cummings et al. 1997). Incidentally, the presence of large numbers of echinostome metacercariae in the foot of *A. stutchburyi* further facilitates their accessibility to shorebirds (Thomas and Poulin 1998). The higher density of *A. stutchburyi* at locations such as Company Bay means that any potential shorebird hosts will be more likely to prey upon *A. stutchburyi* than *M. liliana*, making the former species the more reliable transmission route. This situation is similar to an example from the North Sea region, where the trematode *Renicola roscovita*, which usually utilizes the mussel *Mytilus edulis* and the European cockle *Cerastoderma edule* as second intermediate hosts, is also found to infect two introduced species of bivalves—the American razor clam *Ensis americanus* and the Pacific oyster *Crassostrea gigas* (Krakau et al. 2006). While *E. americanus* seems to be a viable alternative transmission route for *R. roscovita* as they are readily consumed by birds like oystercatchers, the shells of *C. gigas* are far too strong to be crushed by potential bird hosts; thus, any *R. roscovita* that infect *C. gigas* are lost from the system (Krakau et al. 2006). Therefore, while *M. liliana* can potentially act as an alternative transmission pathway, due to environment and circumstance, in this system, it may act more as a decoy or dead-end host (Thieltges et al. 2008) and thus as a sink for parasite populations. Based on the mean infection intensity found here and on the density of *M. liliana* at the site, we can estimate that there should be 796 metacercariae per square meter encysted in *M. liliana*. Similarly, using the corresponding values for *A. stutchburyi* from the study conducted by Mouritsen et al. (2003), we get an estimate of approximately 29,218 metacercariae in total per square meter. Thus, there may be no more than 3% of the echinostomes lost inside the dead-end host.

The presence of alternative hosts has been shown to disrupt the transmission dynamics of parasites (Tefler et al. 2005; Krakau et al. 2006; Kopp and Jokela 2007; Meisner et al. 2007). However, while the presence of *M. liliana* can have serious consequences for the cercariae that enter this bivalve as they will have a lower probability of transmission to the appropriate definitive host due to the low infection intensity and population density of *M. liliana*, its overall ecological role in the transmission of echinostomes is probably negligible. While the presence of echinostome metacercariae in cockles can result in altered host phenotype with consequences at the ecosystem level (Mouritsen and Poulin 2005), this is not the case for *M. liliana*. In addition to highlighting the nonlinear relationship between host size and parasite accumulation rate, this study also shows that not all potential hosts in an ecosystem are necessarily equally affected by a particular parasite.

Acknowledgements The experiments conducted for this study comply with the current laws of New Zealand.

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