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Buffering role of the intertidal anemone *Anthopleura aureoradiata* in cercarial transmission from snails to crabs

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ABSTRACT

In nature, parasite transmission from one host to the next takes place within complex biotic communities where non-host organisms can reduce transmission rates, for instance by preying on infective stages. We experimentally investigated the impact of four very different non-host organisms on the transmission of the microphallid trematode *Maritrema novaezealandensis* from its snail first intermediate host to its crustacean second intermediate host. We show that in laboratory mesocosms, accumulation of parasites in juvenile stalk-eyed mud crabs, *Macrophthalmus hirtipes* (Ocypodidae), was not reduced in the presence of cockles, *Austrovenus stutchburyi*, barnacles, *Balanus* sp., or the algae *Enteromorpha* spp., three organisms whose feeding mode or general abundance could negatively impact the parasite's infective stages (cercariae). In contrast, the presence of the anemone *Anthopleura aureoradiata* in the mesocosms caused a more than 4-fold reduction in the number of parasites acquired by crabs when compared to control mesocosms. Observations on fluorescent-dyed cercariae confirmed that they are ingested by anemones. Given the often high densities of anemones on mudflats, they may represent an important regulator of the abundance of *M. novaezealandensis*, and thus of the impact of this parasite on its hosts. These anemones may decrease cercarial transmission for many other trematode species as well. Our results stress the need for studies of parasite transmission in natural contexts rather than under simplified laboratory conditions.

1. Introduction

The impact of parasites on marine ecosystems is now well documented and widely accepted. Parasitism affects the fitness and ecological function of individual hosts, the dynamics of host populations, and even the diversity and stability of entire communities (e.g., Lafferty, 1993; Thomas et al., 1995; Mouritsen and Poulin, 2002, 2005). In most cases, however, the effects of parasitism depend on parasite abundance, i.e. on the mean number of parasites per host in the total population. Typically, lightly-infected hosts incur no measurable decrease in fitness, whereas heavily-infected ones experience substantial decreases in reproductive output or survivorship. For example, the impact of parasites that accumulate over time within a host, such as the cystacanth stages of acanthocephalans or the metacercariae of trematodes, is entirely dependent on parasite abundance (Goater, 1993; Thomas et al., 1995; Latham and Poulin, 2002; Fredensborg et al., 2004; Ferreira et al., 2005; Thieltges, 2006). Therefore, elucidating the factors determining local infection levels by particular parasites are important for our understanding of the role of parasitism in natural systems.

According to mathematical models, the input of infective parasite stages into a system, and the rates at which they are transmitted to hosts, are two key parameters determining local infection levels (Anderson and May, 1978; Tompkins et al., 2002). For trematodes, accumulation of metacercariae in crustaceans, molluscs or fish serving as second intermediate hosts will therefore depend on the rates at which infective larvae (cercariae) are produced and released by snail first intermediate hosts, and on their success at reaching and infecting the second intermediate host. While we know that temperature and food abundance for snails are the key factors regulating cercarial production (see Poulin, 2006), we know very little about the factors controlling transmission success of cercariae, especially in marine systems. The likelihood that a cercaria will find and infect its target host under laboratory conditions is generally-temperature dependent (Evans, 1985; Pechenik and Fried, 1995; McCarthy, 1999). However, in nature, cercariae and their hosts live within a complex biotic community, and the diversity of non-host organisms surrounding parasite infective stages and their target hosts can have a huge influence on whether or not infection will succeed, especially if non-host organisms prey on the infective stages (Thieltges et al., 2008). For example, the presence of the sea anemone, *Anthopleura aureoradiata*, on the shells of cockles decreases the rate at which cockles are infected by cercariae of the echinostomatid genera *Curtuteria* and *Acanthoparyphium* (Mouritsen and Poulin, 2003). The anemones intercept and consume cercariae before they enter the bivalves'

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siphons. This provides not only protection for the cockle on which they are attached, but also generates variability in infection levels among cockles within an area based on differences in the number of anemones harboured by individual cockles. Other reports on cerceriophagy, the predation of cercariae by various organisms, are available from freshwater systems (e.g. Oliver-González, 1946; Ruiz, 1951; Pellegrino et al., 1966; Knight et al., 1970; Holliman and Mecham, 1971; Fernandez et al., 1991; Banerjee, 1996; Schotthoefer et al., 2007). However, non-host organisms can also interfere with cercarial transmission without predation being involved: they can create physical barriers preventing host finding (Christensen, 1979), or they can act as decoys attracting the parasites away from suitable hosts (Thieltges et al., 2008). In marine systems, there have been few attempts to link the presence or diversity of other organisms in an area with the transmission rates of cercariae to their next host.

Here, we experimentally investigate the impact of four non-host organisms, including the anemone *A. aureoradiata*, on the transmission of the microphallid trematode *Maritrema novaezealandensis* to its crustacean second intermediate host. *Maritrema novaezealandensis* is an abundant intertidal parasite whose ecology and lifecycle have been well studied (Martorelli et al., 2004; Fredensborg et al., 2005, 2006; Hay et al., 2005). After their release from their first intermediate host, the snail *Zeacumantus subcarinatus*, cercariae of *M. novaezealandensis* seek and infect a range of small crabs or amphipods (Martorelli et al., 2004). The mortality induced in crustacean hosts by this trematode is dependent on intensity (mean no. of parasites in infected hosts) of infection (Fredensborg et al., 2004), and thus transmission rates are crucial in determining the impact of this parasite on crustacean communities. Our study allows an evaluation of the respective effects of four very different intertidal organisms and potential inhibition mechanisms on the transmission success of a parasite that has been identified as a major player in the population dynamics and community structure of New Zealand intertidal areas (Fredensborg et al., 2005; Thompson et al., 2005). We hypothesise that the non-host organisms reduce the abundance of metacercariae in the crab hosts and test this using laboratory mesocosm experiments.

2. Materials and methods

2.1. Organisms

We collected *Zeacumantus subcarinatus* snails as source for cercariae of *Maritrema novaezealandensis* from the intertidal zone of Lower Portobello Bay in Otago Harbour, New Zealand, a location with a high prevalence of the parasite (Fredensborg et al., 2005). We screened for infected individuals by incubating snails at 25 °C with direct light for 2-3 hours. Only individuals that had single infections of the trematode species *M. novaezealandensis* were kept in aerated aquaria for later experimental infections of crabs.

We chose the stalk-eyed mud crab, *Macrophthalmus hirtipes* (Ocypodidae) as target second intermediate host for this study, as it is a known second intermediate host of *M. novaezealandensis* with nearly 100% prevalence and as many as 300 metacercariae per crab in localities where *Z. subcarinatus* snails are abundant (Fredensborg and Poulin, 2005). We collected juvenile crabs, with a carapace width range of 5 to 12 mm, in the intertidal zone of Hoopers Inlet on the Otago Peninsula, New Zealand, where crabs are abundant and where the trematode *M. novaezealandensis* is not present due to the absence of its snail first intermediate host (Fredensborg et al., 2004; Leung and Poulin, 2006).

We collected 4 non-host organisms for experiments on interference with cercarial transmission. These organisms were: (i) the anemone *Anthopleura aureoradiata*, a common inhabitant of the intertidal zone, often found attached to cockle shells; (ii) the cockle *Austrovenus stutchburyi*, a filter-feeding bivalve which can occur at very high densities, i.e. more than 200 m^{-2}, in intertidal areas; (iii) small specimens of barnacles, *Balanus* sp., found attached to hard substrates around mudflats; and (iv) the algae *Enteromorpha* spp., often growing in large mats on intertidal mudflats wherever it can find a substrate (Morton and Miller, 1973). We collected cockles with a proximate shell length of 2.9 cm, barnacles with a proximate base diameter of 0.3 cm from the intertidal zone of Lower Portobello Bay and anemones of approximately 0.5 cm in diameter from the intertidal zone of Hoopers Inlet. Throughout the duration of the experiments (October 2007 to January 2008), we continuously collected field-fresh organisms.

2.2. Experiments

Experiments were carried out in laboratory mesocosms. Each mesocosm consisted of a plastic tank (23.4 × 18.4 cm), covered with a sand and silt mixture (2.5 cm depth) and filled with 740 ml of seawater. To each mesocosm, we randomly added four crabs. We acclimated all crabs and other organisms (barnacles, cockles, algae or anemones) overnight before introducing six infected snails per mesocosm the next day. All experiments ran for 48 hours under constant lighting, starting with the introduction of the snails. This design did not allow measuring the number of cercariae emitted by each snail during the experiment. However, these data are available from a previous study on the same parasite in the same snail population: under similar laboratory conditions as in the present study (i.e. at 18 degrees Celsius), the shedding rate was 81 ± 26 cercariae per snail per day (Fredensborg et al., 2005). There is indeed variability in the numbers of cercariae emitted daily by each snail, but with 6 snails and a two-day experiment, there were 12 daily snail outputs of cercariae per mesocosm, which should have limited inter-mesocosm variability in total cercarial emission. For logistical reasons we ran several series of experiments. Each series consisted of a control and a treatment (see below), both of which were started at the same time under the same conditions (room temperature and natural lightning). However, among series this resulted in slight differences in ambient conditions due to fluctuations in room temperature and lightning conditions. Another difference in conditions comes from the use of bubbler systems which were deployed in the first experiments, but then discontinued in subsequent experiments (see Table 1). These small changes may have caused variation in cercarial output or infection success among mesocosms. However, as we were only interested in comparing the effect of a single treatment versus its paired control, we consider our experimental design to be appropriate.

In a first series of experiments we tested the ability of the four non-host organisms to reduce transmission of cercariae from the snails to the crabs. In each of the first four experiments, we compared four replicate controls (tanks covered with a sand and silt mixture, filled

Table 1
Treatment type, mean abundance of metacercariae per crab and mean prevalence (proportion of infected crabs) in crabs, each including standard error (SE)

Treatment	Abundance	SE	Prevalence	SE	n replicate mesocoms	n total no. crabs dissected	Bubbler use
Control	33.4	6.4	100%	0.0	4	16	yes
Barnacles	35.8	8.0	100%	0.0	4	16	yes
Control	92.7	16.2	100%	0.0	4	15	yes
Cockles	70.5	14.6	100%	0.0	4	15	yes
Control	34.5	9.4	100%	0.0	4	12	yes
Algae	51.3	16.3	100%	0.0	4	15	yes
Control	7.3	2.3	67%	0.1	4	15	no
Anemones	1.3	0.6	38%	0.1	4	16	no
Control	4.9	1.3	77%	0.1	8	30	no
Anemones	1.1	0.4	50%	0.1	8	28	no
Control	4.5	1.0	75%	0.1	8	32	no
Cockles	6.8	1.5	91%	0.1	8	32	no

Also given are the number of replicate mesocoms, the total number of crabs dissected (differences result from the escape or death of a few crabs) and the use of bubbler systems in the different experimental runs.

with seawater and four crabs and six snails added as described above) with four replicate mesocosms for each of the following treatments: i) 200 barnacles attached to small rocks separated into groups of 50, ii) 12 cockles, iii) 20 anemones separated into four groups attached to rocks, and iv) algae, filling up the entire mesocosm. The densities of interfering organisms used in these experiments correspond roughly to typical densities observed in the field (Hopper et al., pers. obs.). After inspecting the results of the first series of experiments, only cockles and anemones appeared to be prospective transmission-interfering organisms (Table 1). Hence, we repeated the previous experimental series with these two organisms in the exact same manner, but increased the number of replicates to eight control and eight treatment mesocosms in a second series of experiments.

All experiments were terminated after 48 hours of exposure to cercariae shed by snails by removing all crabs from each mesocosm. Crabs were kept in fresh seawater for a maximum of 3 days during the dissection process. We measured each crab's carapace width with callipers and dissected them under a stereomicroscope by carefully lifting the carapace and then peeling off the gills onto a slide. Following this, we smeared the inside of the crab onto the slide, in order to retrieve all metacercariae. A coverslip was used to secure and stabilize the material for counting the metacercariae under a compound microscope. These were not fully formed metacercariae at this time, and thus appeared as cercariae without tail.

2.3. Observations on anemone-cercariae interaction

To ascertain whether anemones actually feed on cercariae, we further observed the interactions of anemones with cercariae under a black-light microscope using fluorescent-stained cercariae. Cercariae were stained and incubated at 25 °C in a mixture containing 10 ml filtered seawater and 100-µl Bodipy 558 dye (Molecular Probes, Inc). Cercariae were rinsed after one hour in the stain mixture. We took three groups of 40 stained and rinsed cercariae and placed them into three separate wells of a tissue-culture plate, each containing an anemone, *Anthopleura aureoradiata*. We also used two control groups of anemones: three anemones with unstained, incubated cercariae, and another three with incubated, filtered seawater. We used these controls to distinguish between potential natural biofluorescence in anemones and fluorescence acquired by feeding on dyed cercariae. The fate of cercariae was observed under the microscope and the anemones dissected after exposure to the cercariae.

2.4. Statistical analysis

We tested for differences in the number of metacercariae acquired by crabs with t-tests (using the standard least squares regression procedure of the statistics software JMP 7.0 (SAS, Cary, North Carolina)). Mesocosms were considered to be the replicate unit with the average number of metacercariae per crab per mesocosm being the dependent variable. Each experimental series (control versus treatment) was analyzed separately. Differences in crab length between the control and experimental treatments of each experimental series were tested with t-tests as above.

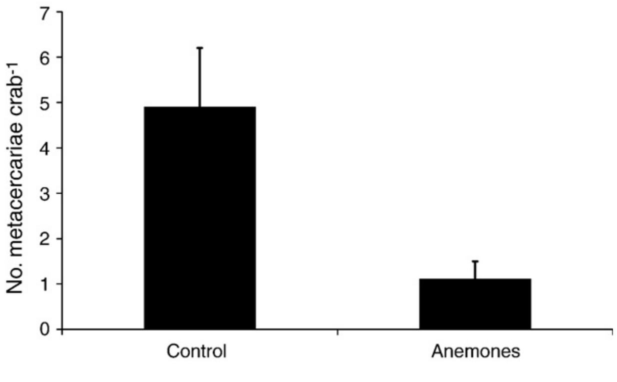

Fig. 1. The mean number of metacercariae (+/- SE) per crab (*Macrophthalmus hirtipes*) in the control containing zero anemones, and the experimental treatment containing 20 anemones, *Anthopleura aureoradiata*. Means are based on 8 replicates, with each mesocosm containing four crabs.

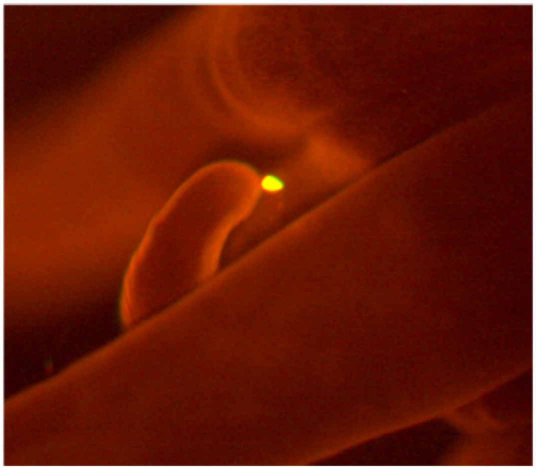

Fig. 2. Image of a fluorescent-dyed cercaria caught on the tentacle of the anemone, *Anthopleura aureoradiata*, under a black-light stereomicroscope.

3. Results

In the first series of experiments, we did not detect any reduction of metacercarial load in the crabs caused by the four non-host organisms (barnacles: $F_{1,7}=0.87$, $p=0.87$; cockles: $F_{1,7}=0.55$, $p=0.49$; algae: $F_{1,7}=0.047$, $p=0.84$; anemones: $F_{1,7}=1.68$, $p=0.24$) (Table 1).

In the second series of experiments, cockles had no effect on the average number of metacercariae found per crab ($F_{1,15}=1.46$, $p=0.25$) (Table 1). However, anemones had a significant effect on metacercarial load in crabs ($F_{1,15}=6.32$, $p=0.025$) (Table 1, Fig. 1) with a more than 4 times lower load in crabs from the mesocosms with anemones compared to crabs from the controls (Table 1, Fig. 1). In both experimental series there was no significant difference in crab size between the experimental and control treatments ($p>0.05$).

Our observations on anemone-cercariae interactions confirmed that ingestion of cercariae by anemones does occur. Under the black-light stereomicroscope we noticed that cercariae became stuck on the anemone's tentacles (Fig. 2). In addition, when we dissected the anemones, we discovered several (2-4) cercariae inside the anemone.

4. Discussion

The transmission of parasites from one host to another host does not occur in an ecological vacuum: it takes place in the midst of a diverse community of non-host organisms that may interfere with transmission in many different ways. Our study supports the idea that species interactions involving non-host organisms are important to cercarial transmission in a marine community. However, our study shows that not all non-host organisms are of equal importance in this respect.

The anemone, *Anthopleura aureoradiata*, was the only organism in this study capable of decreasing the abundance of cercariae in the second intermediate host crab, *Macrophthalmus hirtipes.* In contrast, we did not find any effect of barnacles, cockles and dense mats of algae on cercarial transmission in this particular system. We had originally considered all four non-host organisms to be important, based on their biological properties: barnacles, cockles, and anemones should unintentionally or intentionally filter feed the cercariae out of the water column, and algae should act as a physical obstacle in the way of the swimming cercaria.

Due to the experimental design, metacercarial load in the crabs was higher in the first three experimental runs compared to the other runs (see Table 1). This difference in metacercarial load is due to the use of air bubblers in the first three experiments for the trials with barnacles, cockles and algae only; the use of bubblers likely increased dispersal of cercariae and contact with hosts, resulting in higher infection values in those experiments. Variations of metacercarial loads in crabs among controls of the different experimental runs result from slightly varying ambient conditions as the experimental runs were conducted at different times. However, ambient conditions were exactly the same for all paired mesocosms per single experimental run (control versus treatment), thus allowing testing for the effect of the non-host organisms.

It is unclear why one filter-feeding species, the anemone *A. aureoradiata*, has a substantial impact on cercarial transmission by feeding on cercariae, whereas two other sympatric filter-feeders, barnacles and cockles, have no measurable effects on the number of cercariae successfully reaching crabs. Perhaps the latter two species show some size-selective feeding preferences that exclude cercariae as prey. It would be interesting to elucidate the reasons why certain filter feeders consume cercariae while others do not. The fact that algae had no effect on transmission to the crab hosts contrasts with several prior studies reporting that certain types of plant material interrupt cercariae in their swimming paths (Christensen, 1979, Thieltges et al., 2008). Different species of algae and different species of trematodes could be used for future studies, though the fact that *Enteromorpha* spp. is the dominant taxon in our study system suggests that algal interference is unlikely to be a major factor.

The observations on the fate of cercariae using a black-light microscope and fluorescent-stained cercariae showed that *A. aureoradiata* can indeed consume the cercariae (Fig. 2), whether actively or not. In addition, we noticed several cercariae dying after being stuck to the tentacles of the anemone. These observations support findings of a prior field study on the role of the same anemone species in reducing the abundance of another trematode, *Curtuteria australis*, in its bivalve second intermediate host within the same New Zealand intertidal system (Mouritsen and Poulin, 2003). Given the sometimes huge densities of anemones on mudflats, they possibly represent an important regulator of the abundance of the trematodes *C. australis* (Mouritsen and Poulin, 2003) and *M. novaezealandensis* (present study), and thus of the impact of these parasites on their hosts. The combined findings of these two studies suggest that this species of anemone could impact cercarial transmission for a number of other trematode species as well. In contrast to the cockle-anemone mutualism that was found by Mouritsen and Poulin (2003), no reciprocally beneficial relationship between the anemone and the crab *Macrophthalmus hirtipes* was found in this study, as the anemones occasionally consume the smaller sized crabs (Hopper et al., pers. obs.). However, predation of anemones on crabs seems to be rare, and the benefits of being in proximity to a high-density field of anemones probably outweigh the occasional costs. The case of the anemone *A. aureoradiata* supports the idea that species interactions involving non-host organisms may be crucial to cercarial transmission in marine communities (see Thieltges et al., 2008). It also reinforces the need for studies of parasite transmission in natural contexts rather than under simplified laboratory conditions.

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