

## Infectivity of *Himasthla* spp. (Trematoda) in cockle (*Cerastoderma edule*) spat

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The common cockle *Cerastoderma edule* is intermediate host to several species of digenean trematodes. However, little is known about the factors influencing the settlement of trematode larvae in cockles as well as their effects on the host. Aspects of the transmission ecology, behaviour and effects on juvenile host specimens of trematode larvae belonging to the genus *Himasthla* and utilizing mudsnails *Hydrobia ulvae* as their first intermediate host and various waterbirds as their definitive host have been studied. Cercariae of *Himasthla* spp. (more than 90% of the metacercariae were identified as *H. continua* post-experimentally) exhibited a host size-dependent selection within the host size range from 2 to 6 mm. Infection efficiency was reduced by the presence of substratum allowing cockles to burrow, suggesting that the foot and visceral region may be attacked by cercariae. No increased mortality due to parasite infections could be demonstrated within 5 d after infestation. The metacercariae within experimentally infected cockles were primarily located in the connective tissue within the foot and visceral region. Although some cockles were completely filled with metacercariae only small functional effects were detected, such as a slightly prolonged burrowing time of infected specimens.

### INTRODUCTION

Macrobenthic animals from intertidal flats are hosts to several digenean trematode species, which use either waterbirds or fish as their final hosts (see Lauckner, 1980, 1983). Bivalves are common second intermediate hosts to several of these digeneans and according to Lauckner (1983) some of these parasites may contribute to recruitment failure in ecologically and commercially important bivalves by killing their hosts during epizootics. However, there is generally a lack of data on the effects of trematodes on their marine invertebrate hosts (Sousa, 1991). Specimens of the common cockle *Cerastoderma edule* (L.), which is second intermediate host to at least ten trematode species in the Wadden Sea region (Lauckner, 1987), often contain high numbers of trematode larvae. Such trematodes may have severe pathological effects on bivalves—juveniles in particular (Lauckner, 1983, 1987, 1994). So, even a single *Himasthla elongata* Loos-Frank, 1967 larva has been reported to kill a cockle of about 2 mm in shell length (Lauckner, 1983). Considering the potential importance of such trematodes on their host organisms, experimental studies of factors influencing the parasite's settlement in cockles are required.

The aim of the present study was to examine experimentally the settlement of *Himasthla* spp. cercariae shed from the mudsnail *Hydrobia ulvae* (Pennant) and infecting *C. edule* and to measure short-term effects of the parasites on survival and burrowing characteristics of cockle spat. Infected specimens of juvenile cockles were also examined histologically to detect effects of parasites on host tissue.

### MATERIALS AND METHODS

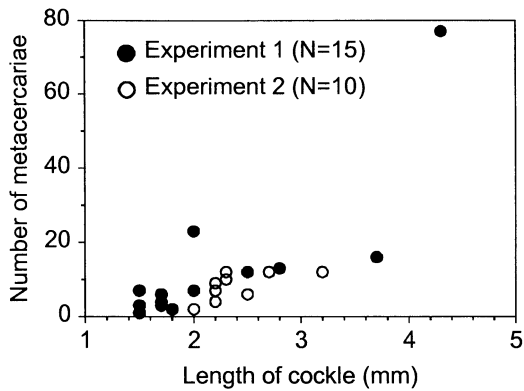
#### *Collection of Hydrobia ulvae and Cerastoderma edule*

Snails and juvenile cockles were collected at Banc d'Arguin in Arcachon Bay (44°40'N 01°10'W) during low-tide twice in June 1994. Surface sediment scraped by hand or using corers was sieved through a 1-mm mesh. Retained snails and juvenile cockles were brought alive to the laboratory. At least 1000 snails were collected in this way as the prevalence of *Himasthla* spp. in snails was low in June 1994 at this location (<1% of the collected snails were actively shedding cercariae).

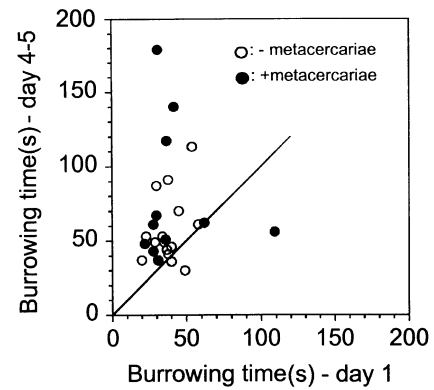
#### *Identification of parasitized snails*

In the laboratory snails were kept individually or in small groups (5–10) established in Petri dishes under light for 24 h at room temperature (22–24°C). During this period infected snails shed cercariae that were identified under a binocular microscope. To find the parasitized snails all specimens within the Petri dish in which cercariae had been observed were placed individually in Petri dishes for another 24 h period. Infected snails were kept together in small aquaria. Dissection of the parasitized snails after finishing the experiments revealed the presence of two *Himasthla* spp. among the snails. Identification of the larval stages is difficult but according to the size of the cercariae we suspect that both *H. continua* and *H. interrupta* were present (Loos-Frank, 1967; Wegeberg, 1998). One of the *Himasthla* shedding snails contained, in addition to rediae and cercariae, more than 15 metacercariae. Considering the low prevalence of parasites in the *Hydrobia* population it

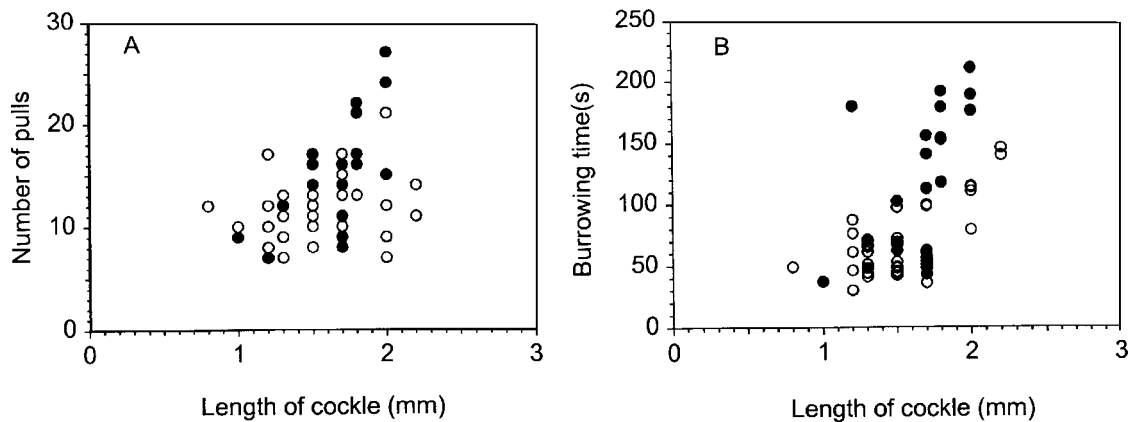




**Figure 2.** Distribution of metacercariae within juvenile cockles as a function of host length. In both experiments a group of cockles was incubated with about 200 *Himasthla* cercariae during 24 h.



**Figure 3.** Comparison of burrowing time(s) of infected and non-infected juvenile *Cerastoderma edule* (length: 1.8–2.2 mm) immediately after 24 h incubation period in Petri dishes with or without *Himasthla* cercariae (day 1) and again 4 or 5 d later (day 4/5). The cockles were kept without food during this period. The line indicates the relationship between the two variables if burrowing time was identical at the two times.



**Figure 4.** Burrowing behaviour of *Himasthla*-infected and non-infected *Cerastoderma edule* as a function of host length. All measurements were done 4 or 5 d after the cockles had been incubated in Petri dishes with cercariae. (A) number of pulls used by a cockle specimen to be positioned in its final position within the substratum; (B) burrowing time is the time spent from a cockle specimen starts to dig until it reaches its final position within the substratum; (●, with metacercariae; ○, without metacercariae).

present parasite species have some difficulties to infect their host and above which, they are quite efficient. Offering cercariae a choice between various sizes of host specimens cercariae infect primarily the larger specimens (Figure 2). In one experiment, the largest cockle (~4.3 mm) contained 43% of all the recovered metacercariae resulting from a 24 h infection experiment with 15 cockle specimens in one container (Figure 2, experiment 1). In this particular experiment the variance to mean ratio ( $I=425.6$ ) indicates that the metacercariae were highly overdispersed among cockle individuals and strongly biased toward the largest specimen. Addition of sand to the dishes allowing cockles to burrow reduced the infection success of the cercariae. So, cockles incubated with sand obtained  $2.6 \pm 0.67$  (mean  $\pm$  SE) whereas those without substratum obtained  $7.6 \pm 1.27$  (ten cockles in each container and incubated with 100 hundred cercariae) (Mann–Whitney test,  $P < 0.05$ ).

#### *Short-term effects of metacercariae on host individuals*

No increased mortality of infected cockles compared with uninfected control specimens could be demonstrated

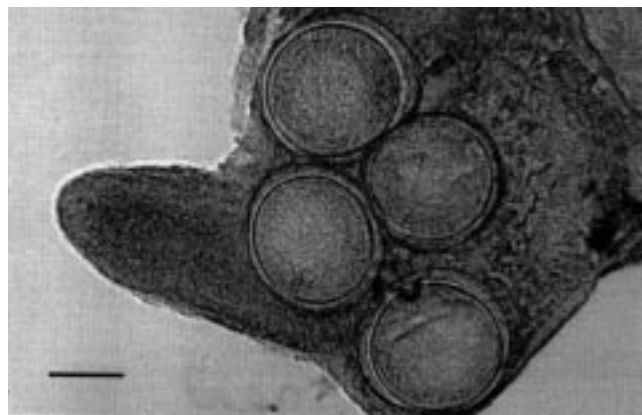
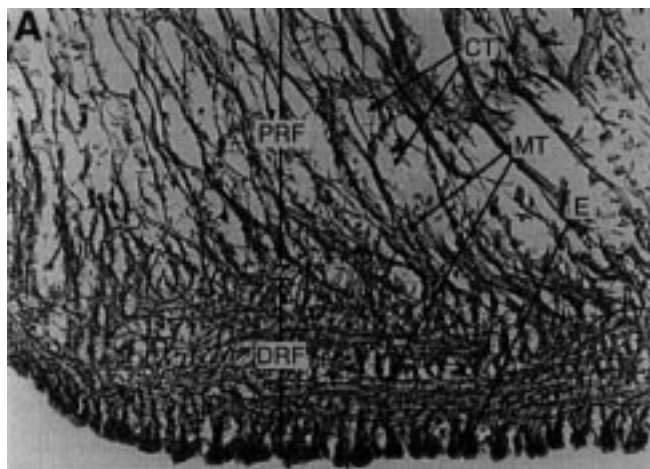
during our experiments (duration 4–5 d). Of 75 experimental animals, seven cockles died and only three of these were infected.

As the proper functioning of muscles in the foot of cockles is vital with respect to their ability to burrow and move around, we would expect that this ability is deterred by metacercariae located in the foot tissue. Newly (infection less than 24 h) and non-infected (control) cockles showed a linear increase in burrowing time with shell length (regression analysis,  $F_{1,44}=19.44$ ,  $r^2=0.31$ ,  $P < 0.001$ ). For both infected and non-infected cockles the burrowing time was significantly longer after 4–5 d post-infection than immediately after the 24 h infection experiment (Figure 3). To analyse the possible influence of parasites on the smallest cockles (<2.2 mm) three aspects of burrowing behaviour were distinguished and quantified 4–5 d post-infection, namely ‘response time’, ‘number of pulls’ and ‘burrowing time’. Using a stepwise regression analysis the influence of ‘shell length’ and ‘number of metacercariae’ on the three above mentioned parameters were tested (Table 1). Cockles that did not start to burrow within 10 min were ignored in the analysis of response time. This group constituted 9.3% of

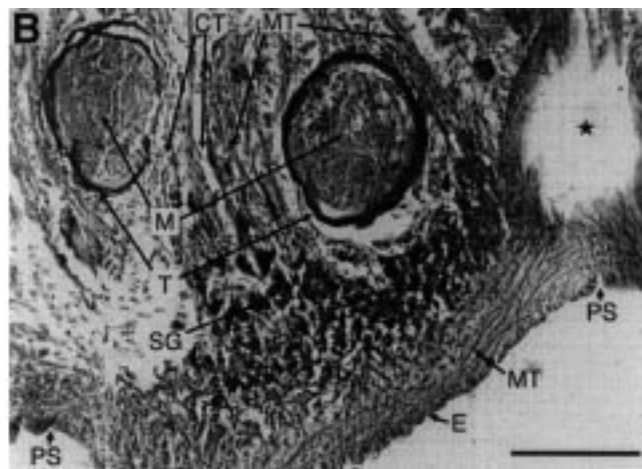
**Table 1.** Effect of the number of metacercariae and cockle length on burrowing characteristics (response time, number of pulls, burrowing time) of juvenile *Cerastoderma edule* experimentally infected by *Himasthla cercariae*. The standardized partial regression coefficients of the variables estimated by a stepwise multiple regression analysis are indicated as well as the correlation coefficient for the indicated variables in the regression equation ( $r^2$ ).

| Parameter       | Variables in the equation |               | $r^2$ |
|-----------------|---------------------------|---------------|-------|
|                 | Length                    | Metacercariae |       |
| Response time   | ns                        | ns            |       |
| Number of pulls | 0.32**                    | 0.41***       | 0.35  |
| Burrowing time  | 0.43***                   | 0.43***       | 0.48  |

Significance of  $F$ -values: \*\*,  $0.001 < P < 0.01$ ; \*\*\*,  $P < 0.001$ ; ns, non-significant.



**Figure 5.** Four *Himasthla* metacercariae located in the foot-visceral region of a *Cerastoderma edule* with a shell-length of 1.7 mm. Scale bar: 100  $\mu$ m.



**Figure 6.** Light micrographs of histological sections of the foot-visceral region of juvenile *Cerastoderma edule*: (A) from a non-infected cockle showing two patterns of arrangement of muscular fibres, loose in the proximal region of the foot (PRF) and dense in the distal region of the foot (DRF) as well as under the epithelium (E); MT, muscle tissue; CT, connective tissue. (B) From an infected cockle showing penetration sites (PS) of *Himasthla* in the epithelium, two metacercariae (M) each surrounded by a thick surface covering (T) and secretion granules (SG) in the vicinity of the parasite cysts (\*, metacercaria lacking due to a defect of the histological mounting). Scale bar: 100  $\mu$ m.

all individuals and infected individuals were not over-represented among them. Neither shell length or 'number of metacercariae' influenced the cockles response time. However, there was a significant positive impact of both factors on both 'number of pulls' and 'burrowing time' (Figure 4, Table 1).

In several of the infected specimens the metacercariae occupied a large fraction of the foot and visceral region (Figure 5). To examine if metacercariae could have any mechanical deteriorating effect on muscle fibres, experimentally infected specimens were subjected to a histological analysis. The cockles were kept alive two days after infection and hereafter preserved. The histological sections revealed the presence of metacercariae in the connective tissue separating the bundles of muscular tissue in the foot (Figure 6). As this tissue is rather loosely organized and only contains few cells, metacercariae are probably doing little tissue damage to their host specimen. The metacercariae were surrounded by a thick surface covering without evidence of cells. In the cockle tissue

close to metacercariae secretion granules could be seen (Figure 6). As the surface layer of the metacercariae showed the same colour as the secretion granules when coloured with erythrosin, the tunic is supposed to be at least partly a result of some host response to the presence of cercariae. The only possible signs of the penetration sites were seen in the epithelium forming the outer tissue layer in the foot. At such places both the epithelium and the underlying muscle tissue were thinner than normal and in a regenerating phase (Figure 6).

## DISCUSSION

The experiments conducted in this study illustrate some aspects of the ecology of echinostomatid trematode cercariae, especially their settlement in juvenile cockles. Being non-feeding organisms (lecithotrophic larvae) cercariae rely on their stored energy reserves during the free-swimming stage. As a result the longevity of cercariae decreases with increasing temperature (Evans,

1985; Pekkarinen, 1987). The infectivity, in contrast, seems to increase with temperature, at least until a certain threshold temperature differing between species (Evans, 1985; Rea & Irwin, 1992; Greve, 1997). According to Loos-Frank (1967) *Himasthla* cercariae (*H. continua* and *H. interrupta*) may live for about two days at 18–20°C but they are only infective during the first 12 h. In the present Petri dish experiments the parasites generally exhibited a high infection success within 24 h at room temperatures, and it seems unlikely that further infection with remaining cercariae would occur after this period.

The parasites exhibited a high infection success, in particular among juvenile cockles larger than 3 mm, but a more varying success among the smaller host specimens. The small volume of the foot–visceral region in small cockles is probably an important factor contributing to this. Cercariae may have troubles to grasp cockles with a foot–visceral region not too different in size from themselves (Lauckner, 1983; Wegeberg, 1998). Typically the length of the cercariae belonging to either *H. continua* or *H. interrupta* is within the range 400–450 µm (Wegeberg, 1998). In comparison, the width of the foot–visceral mass is less than 500 µm in a cockle with a shell length of 1.7 mm (Figure 5). In addition, avoidance behaviour of the cockles differ with their sizes in relation to cercaria size. So, in small cockles, the cercariae may trigger an avoidance response, whereas the larger cockles probably are less sensitive to these cercariae. The three *Himasthla* sp. found in cockles differ in their sizes and have varying success in different sizes of host individuals (Wegeberg, 1998).

The present experiments showed a positive host size-dependent settling intensity in cockle spat. The increasing pumping rate of cockles with size (Vahl, 1972) may cause a disproportionate and passive attraction of cercariae to the larger specimens within a group of cockles. A similar mechanism has been reported to explain a higher frequency of other trematode species within larger cockles in comparison with smaller ones (Bowers & James, 1967). Entrance of cercariae through the inhalant siphon is a common mechanism for *Himasthla* cercariae to find their host (Montaudouin et al., 1998; Wegeberg, 1998). Inside the mantle cavity they may locate and penetrate the foot and visceral region. However, this mechanism was not supported by preliminary observations in the present experiments. All cercariae observed entering through the inhalant syphon were expelled. However, the behaviour of cockles may change if food particles are being inhaled at the same time. The experiments with and without substratum as well as the observations of cercariae attacking the exposed foot–visceral region suggest that parasites may penetrate in this direct way as also reported by Lauckner (1983) and Loos-Frank (1967). Under natural circumstances cockles do often crawl on the surface of their substratum (Jensen, 1985), and this behaviour may, in particular, be critical to cockles if cercariae are in the surrounding water, though, under natural conditions, infection success may be much lower considering the whole scenario of abiotic and biotic factors interfering with the parasites ability to reach their hosts. In particular, water currents may reduce the efficiency of cercariae under field conditions. However, experiments in flume tanks with *H. elongata* do show that

even in flowing water they maintain a high infection rate (Montaudouin et al., 1998). Considering cercariae's restricted range of settlement sites it is questionable how they manage to spot host organisms *in situ*. Various mechanisms may actually facilitate a successful transmission between the intermediate hosts. As an example, parasites may manipulate their host's behaviour so that the transmission success increases (Curtis, 1990). Parasite-induced behavioural characteristics have been reported both for first and second intermediate host organisms (see Moore & Gotelli, 1990). Shedding of cercariae may also be restricted to a certain set of environmental variables ensuring a high survival and infection success (Théron, 1984; Rea & Irwin, 1992; Combes et al., 1994). As an example, shedding of *Himasthla* cercariae primarily takes place at high temperatures (personal observations), which typically will occur in small tidal pools remaining on intertidal flats during low water. This will diminish the flushing rates and thus improve the chances of successful settlement of cercariae. Furthermore, it has been reported that echinostomatid cercariae may locate their target host by responding to chemical secretions produced by their host (McCarthy, 1990).

Overdispersion of larval trematodes among host animals is the rule (Esch & Fernandez, 1993). Various suggestions have been forwarded to explain such patterns. In this case a simple size dependent mechanism seems to be operating. All host individuals examined in this study were easily infected, but in cases where groups of cockles were placed together size could be identified as an important determinant of infection intensity. Within the spectrum of cockles used, a small difference in length implied a considerable difference in volume and thus potential target area. As the amount of water being pumped by cockles increases logarithmically with their weight (Vahl, 1972) this could also be a mechanism by which cercariae might become concentrated around the largest cockle specimens in a closed container.

Infected juvenile cockle individuals exhibited a reduced burrowing efficiency compared with non-infected specimens, as indicated by the significant impact of parasites on burrowing characteristics of the smallest cockles. However, this effect was not evident immediately after infection but 4 d afterwards. It could indicate that starvation combined with parasites is particularly detrimental to cockles. Earlier studies have similarly suggested an impact of parasites on adult bivalves burrowing ability (Swennen, 1969; Lauckner, 1983; Lim & Green, 1991; Jonsson & André, 1992), but the cause-and-effect relation in studies of naturally infected bivalves is not straightforward. The mechanism by which the present parasites influence host burrowing ability is unknown but it could be related to some of the damages exerted by cercariae penetrating their host specimens. These include: (1) destruction of muscle fibres as cercariae pass through the muscle layers situated beneath the epidermis of the viscero–pedal mass as suggested by our histological analysis; (2) tissue lysis caused by cercarial enzymes (Lauckner, 1983); and (3) loss of body fluids through the penetration holes.

No parasite-induced host mortality during short-term experiments with *H. continua* were found. From the experimental data it is obvious that under present laboratory

conditions small juvenile cockles (0.8–2.2 mm) survive being parasitized even if they are filled with metacercariae in the connective tissue of their foot–visceral region. It could be argued that the experimental period was too short to produce any significant mortality. However, other experiments with echinostomatid cercariae utilizing snails as their second intermediate host have revealed that parasite-induced mortality primarily occurred during the first four days post-infection (Fried et al., 1995). Furthermore, as *Himasthla* metacercariae remain relatively inactive in cockles (Lauckner, 1971) it can be expected that the most severe damage to their host individual occur during and shortly after penetration of the cercariae. The extent of the damage provoked will probably depend on the influx of cercariae. For other host–parasite systems in which the metacercariae grow inside their host, they can be a significant mortality agent (Mouritsen & Jensen, 1997).

In contrast with this study showing that *H. continua* is relatively harmless to juvenile cockles, *H. elongata* cercariae have been reported to be lethal to juvenile bivalves (Lauckner, 1983). Size differences among cercariae and metacercariae belonging to *H. elongata* and those belonging to either *H. continua* or *H. interrupta* could perhaps contribute to the difference in their host effects. Metacercariae of *H. interrupta*, *H. continua* and *H. elongata* are on average 164, 195 and 248 µm in diameter (A.M. Wegeberg, personal communication), respectively.

Under *in situ* conditions infected cockles may potentially suffer more than under controlled laboratory conditions. As an example, the presence of environmental stress factors such as oxygen depletion may be more severe to parasitized than non-parasitized cockles (Wegeberg, 1998). Furthermore biotic factors may also be important *in situ*. So, parasitized cockle individuals being more exposed to epibenthic predators because of their deterred burrowing ability may be subjected to higher mortality rates than unparasitized specimens. Actually, the negative influence of parasites on the cockles burrowing time could be a result of an adaptive strategy of the parasites to facilitate their transmission to their final bird host. Surface dwelling cockles represent an easy accessible food resource to birds, the parasites definitive host. Several reports have indicated that various species of trematodes actually may manipulate their host in order to facilitate the transmission to the next host (see review by Moore & Gotelli, 1990). However, often it remains an unresolved question to what extent altered host behaviour is a result of a parasite strategy or just a sort of pathological host response. Nevertheless, compensatory mortality induced by predators taking advantage of surface dwelling cockles could be a possible mechanism by which these trematodes might cause recruitment failure among cockles.

Dr Xavier de Montaudouin is acknowledged for help in the laboratory and in the field. Thanks to T. Greve and A.M. Wegeberg for valuable discussions. Financial support was given by 'Université Bordeaux 1' to K.T.J.

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Submitted 1 December 1997. Accepted 1 June 1998.

