

# Phototactic responses of the cercaria of *Echinoparyphium recurvatum* during phases of sub-maximal and maximal infectivity

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## Abstract

Phototactic responses of cercariae of the echinostome *Echinoparyphium recurvatum* (Digenea: Echinostomatidae) were investigated during phases of sub-maximal and maximal infectivity using a simple light/dark choice chamber. The phototactic responses of a total of 400 cercariae were examined in 20 replicate experiments during their sub-maximal infectivity dispersal phase (0.5 h post-emergence from the first intermediate host *Lymnaea peregra*) and during their maximal infectivity phase (2.5 h post-emergence). Cercariae in the sub-maximal infectivity dispersal phase were found to be positively phototactic, significantly larger numbers of them occurring on the light side of a light/dark choice chamber  $P < 0.001$ . Cercariae in the maximal infectivity phase were found to be negatively phototactic, significantly larger numbers of them being found on the dark side of the choice chamber,  $P < 0.001$ . This report of 'phototactic switching' demonstrated by the cercariae of *E. recurvatum* from a positively phototactic dispersal phase to a negatively phototactic infection phase constitutes the first record of such behaviour in the cercaria of an echinostome.

## Introduction

Previous studies have shown that the cercariae of certain species of echinostome digeneans show a marked period of low infectivity toward second intermediate host snails immediately after their emergence from the first intermediate host. Cercarial infectivity then rises to a peak approximately 2 h post-emergence. This initial period of sub-maximal infectivity is thought to be a dispersal phase preventing metacercarial super-infection of first intermediate hosts emitting cercariae. Such dispersal phases of sub-maximal infectivity have been demonstrated for the cercariae of *Echinoparyphium recurvatum* by Evans & Gordon (1983) and McCarthy (1989), and for *Echinostoma liei* (= *Echinostoma caproni*) by Evans (1985). In a recent study Haas *et al.* (1995) observed that the cercariae of *Hypoderaeum conoideum* showed no

chemotactic orientation towards the snail host within 1 h of being shed, and they suggested that this may assist the cercariae to leave the immediate area of their first intermediate host snail (*Lymnaea stagnalis*) and to disperse.

Although it is known that an initial sub-maximal infectivity dispersal phase, followed by a maximal infectivity host-location phase, occurs in the life of some echinostome cercariae, very little is known about the behavioural responses of the cercariae to potentially important environmental stimuli such as light and gravity during these phases. However, Haas *et al.* (1995) have reported that the cercariae of three species of echinostome investigated by them (*Pseudechinoparyphium echinatum*, *Echinostoma revolutum* and *Hypoderaeum conoideum*) show phases of converted orientation towards light and gravity in their immediate post-shedding period, and then seem to search the microhabitats of their second intermediate hosts hours later. The present study (first reported in unpublished form by McCarthy (1989)) set out to examine the phototactic responses of the

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cercariae of the echinostome *Echinoparyphium recurvatum* during their sub-maximal dispersal phase and also during their period of maximal infectivity to the second intermediate host *Lymnaea peregra*.

### Materials and methods

The apparatus used to investigate the phototactic behaviour of *E. recurvatum* cercariae was a simple light/dark choice chamber constructed from a small clear circular polystyrene petri dish (5 cm in diameter and 1 cm in depth) half of which was blacked out using light-proof black PVC tape. The choice chamber was situated in a dark room in which the temperature was a constant 18–20°C. It was illuminated directly from above using a fibre-optic cold light source. The choice chamber was filled with 20 ml of synthetic hard water medium (HMSO, 1969) at a temperature of 18–20°C. Cercariae of *E. recurvatum* were collected within 10 min of their emergence from a pool of naturally infected *Lymnaea peregra* snails obtained from Harting Pond, Sussex, England. An investigation of the transmission dynamics of cercariae from this source using *L. peregra* as experimental second intermediate hosts (McCarthy, 1989) had shown that the cercariae showed an initial post-emergence phase of low infectivity over the temperature range 10–25°C with infectivity becoming maximal approximately 2–2.5 h post-emergence. Twenty cercariae were introduced via a Pasteur pipette into the centre of the choice chamber and the lid was replaced. The cercariae were then allowed to distribute for a period of 20 min after which time the lid was removed and the numbers of cercariae on each side of the chamber were counted. The lid was then replaced and the cercariae were allowed to distribute for 2 h after which the numbers of cercariae on each side of the choice chamber were again determined. The phototactic responses were thus determined for cercariae at 0.5 h post-emergence and 2.5 h post-emergence. The entire experiment was repeated 20 times, each time starting with freshly emitted cercariae.

### Results

The results of this study are shown in table 1. They clearly indicate that 0.5 h after their emergence from *L. peregra*, *E. recurvatum* cercariae show a markedly positive phototaxis. A t-test on cercarial counts transformed by log (x+1) showed that at 0.5 h post-emergence the mean number of cercariae in the light half of the choice chamber was significantly greater than that on the dark side,

Table 1. Phototactic responses of *Echinoparyphium recurvatum* cercariae of different post-emergence ages.

Post-emergence age of cercariae	Infectivity of cercariae	Mean ( $\pm$ SE) no. of cercariae on each side of the choice chamber	
		Light	Dark
0.5 h	sub-maximal	17.1 ( $\pm$ 0.6)	2.9 ( $\pm$ 0.3)
2.5 h	maximal	1.8 ( $\pm$ 0.5)	18.2 ( $\pm$ 0.5)

$P < 0.01$ . At 2.5 h post-emission, the phototactic response of the cercariae appeared to have been reversed to a markedly negative phototaxis. At 2.5 h post-emergence, the mean number of cercariae in the dark half of the chamber was significantly greater than that on the light side,  $P < 0.01$ . Over the period examined the cercariae showed a 'phototactic switch' from positive to negative phototaxis.

### Discussion

The initial post-emergence positive phototaxis of *E. recurvatum* cercariae observed in the present study is similar to that observed for echinostome cercariae by Cort (1922). This author did in fact suggest that this positive reaction to light was responsible for the emergence of the cercariae from first intermediate host snails predominantly under conditions of illumination. The results of the present study have revealed an interesting age-related change in the phototactic behaviour of the cercariae of *E. recurvatum*, a phototactic switch, which parallels the change in infectivity of the parasite over the same period. The initial positive phototaxis of cercariae is coincident with the initial sub-maximal infectivity phase demonstrated by Evans & Gordon (1983) and McCarthy (1989). The marked negative phototaxis of cercariae 2.5 h post-emergence is coincident with the maximal infectivity of cercariae that is attained at this time (see Evans & Gordon, 1983; McCarthy, 1989). This pattern of behaviour would seem to suggest that *E. recurvatum* cercariae have an initially positively phototactic, low infectivity, dispersal phase followed by a negatively phototactic, maximally infective, host location and infection phase. The negatively phototactic phase could be expected to enhance the probability of contact with benthic second intermediate host snails.

Although to date, to the author's knowledge, no named example of a positive phototactic dispersal phase followed by a negatively phototactic infection phase has been clearly demonstrated for a named digenean cercaria, Cable (1972) noted that in certain cercariae, 'sometimes phototaxis is initially positive and changes later, usually a short time after emerging from the first intermediate host'. The phenomenon is much better documented in the case of monogenean oncomiracidia. The authors Boret (1967) and Paling (1969) demonstrated that in oncomiracidia of *Diplozoon paradoxicum* and *Discotyle sagittata* respectively there is an initial positive phototactic dispersal phase followed by a negatively phototactic host-location and infection phase. The phototactic responses of *E. recurvatum* cercariae observed in the present study raises the question as to how the cercariae perceive differences in light intensity. Although no ultrastructural studies have been carried out on cercariae of *E. recurvatum*, studies by Fournier (1984) revealed rhabdomeric photoreceptors in cercariae of another echinostome, *Echinostoma togoensis* (= *Echinostoma caproni*). It is possible that similar structures may exist in the cercaria of *E. recurvatum*.

The present study has examined the response of *E. recurvatum* cercariae to light during a low infectivity dispersal phase and a high infectivity host location phase. However, nothing is yet known about the response of

these cercariae to the potentially important factor of gravity during these different phases. Lowenberger and Rau (1994) have demonstrated interesting changes in the vertical distribution of *Plagiorchis elegans* cercariae after their emergence from the snail host. An investigation of the response of *E. recurvatum* cercariae to gravity at various times post-emergence will be the subject of a future study.

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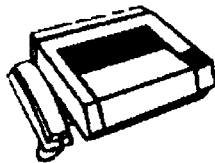
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