

Being successful in the world of narrow opportunities: transmission patterns of the trematode *Ichthyocotylurus pileatus*

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SUMMARY

Parasites with complex life cycles face 2 major challenges for transmission in northern latitudes. They have to cope with the general unpredictability associated with the series of transmission events required for completion of the cycle, and transmission has to be completed within a narrow temporal window because of strong seasonality. Despite this, some parasites show high transmission success, suggesting the operation of effective transmission mechanisms. We explored the transmission of *Ichthyocotylurus pileatus* (Trematoda) from its snail (*Valvata macrostoma*) to fish (*Perca fluviatilis*) hosts by examining some key characteristics in the dynamics of the cercarial emergence from snails. Transmission took place within a few weeks mainly in July, thus verifying the narrow temporal window for transmission. The output of the short-lived cercariae from the snails was low and variable in magnitude, but nevertheless resulted in a rapid and high rate of infection in newly hatched fish. The cercarial emergence showed a strong circadian rhythm with most of the cercariae emerging in early evening and night, which might represent the most likely mechanism underlying the high rate of transmission in this species. We emphasize the importance of holistic approaches combining aspects of multiple host species in studies on transmission of complex life-cycle parasites.

Key words: host-parasite relationships, complex life cycles, community ecology, transmission window, circadian pattern, host exploitation, Digenea, cercarial emergence.

INTRODUCTION

Complex parasite life cycles represent intriguing model systems for studies on the evolutionary ecology of parasite life histories. It is generally proposed that these cycles have evolved from simple 1-host systems by inclusion of additional hosts to increase the probability of transmission (Brown *et al.* 2001; Choisy *et al.* 2003; Cribb *et al.* 2003; Parker *et al.* 2003). Indeed, transmission success is a key determinant of parasite fitness in any host-parasite system, but its significance is emphasized in complex life cycles. First, this is simply because reproduction in the definitive host (determinant of parasite fitness) requires completion of a cascade of unpredictable transmission events. Second, the suitable period for transmission may be temporally limited therefore increasing its unpredictability. This is particularly

evident in northern latitudes, where parasite dynamics are typically driven by strong seasonality, and the unpredictable transmission events between hosts must be completed within a narrow time frame. Yet, some parasite species may have a very high transmission rate resulting in a high number of infections in the next host. Although this may be related to a range of factors, including the structure and dynamics of host populations (e.g. Price, 1990; Bagge *et al.* 2004), it may also be due to parasite adaptations which increase the likelihood of transmission (reviewed by Combes *et al.* 1994, 2002). For example, the temporal emergence of cercariae in many digenae species is not random but synchronized with the chronobiological behaviour of the next host (Combes *et al.* 1994; McCarthy *et al.* 2002). However, studies combining seasonal parasite dynamics in several host species of the life cycle, as well as characteristics of the infective stages, in a single study system, are still surprisingly few but nevertheless required for understanding the mechanisms underlying high transmission success of some parasite species. In this paper, we explored the transmission dynamics of one such species, *Ichthyocotylurus pileatus*, between

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its intermediate hosts, *Valvata macrostoma* and *Perca fluviatilis*.

Trematodes of the genus *Ichthyocotylurus* are ubiquitous parasites of freshwater fish (Faulkner *et al.* 1989) and have a 3-host life cycle with snail first intermediate hosts (genus *Valvata*), fish second intermediate hosts, and avian definitive hosts (Niewiadomska and Kozicka, 1970; Niewiadomska, 2003; Harrod and Griffiths, 2005; Faltýnková *et al.* 2007, 2008). *Ichthyocotylurus* species are among the most successful parasites of freshwater fish in Northern Europe interpreted indirectly from the intensities of infection in fish second intermediate hosts. For example, prevalence of *Ichthyocotylurus erraticus* in economically significant coregonid fishes is typically close to 100% and the intensity can reach hundreds or even thousands of parasites in an individual fish (e.g. Karvonen and Valtonen, 2004; Harrod and Griffiths, 2005). Similar intensities of *Ichthyocotylurus* spp. infection have also been recorded in percid fishes (Faulkner *et al.* 1989; Balling and Pfeiffer, 1997; Karvonen *et al.* 2005). These numbers are exceptionally high compared to most freshwater parasite species in similar systems (e.g. Valtonen *et al.* 1997, 2003; Karvonen and Valtonen, 2004; Karvonen *et al.* 2005). In general, the intensity of *Ichthyocotylurus* spp. infection in fish may depend on the population size and infection prevalence in *Valvata* snail intermediate hosts. Both of these are known to be highly variable between and within systems (Swennen *et al.* 1979; Heitkamp, 1982; Krieger, 1985; van den Berg *et al.* 1997; Grigorovich *et al.* 2005; Harrod and Griffiths, 2005; Mouthon and Daufresne, 2006; Faltýnková *et al.* 2008), suggesting that the risk of infection is likely to be spatially heterogeneous. On the other hand, dynamics of the infective stages such as the magnitude of cercarial output from the snail population, and its variation within days and season, could also underlie the high infection success. However, as previous studies have focused mainly on spatio-temporal patterns of transmission (Harrod and Griffiths, 2005; Karvonen *et al.* 2005), or details of cercarial output in laboratory host colonies (Bell *et al.* 1999), comprehensive understanding of these aspects in natural systems is limited.

In this paper, we conducted a temporally structured study on the transmission dynamics of *Ichthyocotylurus pileatus*. In the first part of the study, we recorded seasonality of infection in the *V. macrostoma* population and subsequently determined the precise temporal pattern of cercarial output. Secondly, using infected snails collected from the wild, we investigated the details of cercarial emergence which might underlie high infection rates in fish. These included the rate of cercarial output from the snails, circadian rhythm of cercarial emergence, and cercarial life-span under standardized laboratory conditions. Thirdly, we sampled a

recently hatched cohort of wild perch (*Perca fluviatilis*) repeatedly throughout the season and determined the rate of transmission in relation to temporal pattern of infection in the snails. We discuss the results while comparing life-history traits of other trematode parasites in similar systems.

MATERIALS AND METHODS

Sampling and processing of snails

Sampling of *Valvata (Tropidina) macrostoma* Mörch, 1864 was carried out in Lake Konnevesi (62°N 26°E), a large oligotrophic lake (area 113 km², mean depth 13 m, maximum depth 56 m) in Central Finland. Snails were collected monthly (May–October 2007) by taking grab sediment samples from a site located ca. 70–100 m offshore (depth 5–6 m) with a bottom substrate of mud and small rocks. Parallel samples were taken also from a shallow site close to shore (see Faltýnková *et al.* 2008), but because of low prevalence of *Ichthyocotylurus* at that site (0.4%), this study used data only from the deeper site. Each time, snails were put separately into well-plates with 15 ml of lake water to allow emergence of cercariae overnight. Snails were then examined for infection and measured for shell length. Cercariae were identified according to the protocols of Combes (1980), Odening *et al.* (1970), Odening and Bockhardt (1971), Swennen *et al.* (1979) and Faltýnková *et al.* (2007). The species affiliation of *Ichthyocotylurus pileatus* was verified experimentally by exposing young *Stizostedion lucioperca* to the parasite cercariae and studying morphology of the metacercariae. Snails which did not shed cercariae were dissected to detect pre-patent infections. Snails with patent infections were put separately into containers with 300 ml of lake water, which was changed every second day. All snails were fed *ad libitum* with algae growing on submerged parts of *Equisetum fluviatile* taken from the lake.

Ecological traits of cercariae

Three traits were measured including daily cercarial output from the snails, circadian rhythm of the shedding and cercarial longevity. First, to determine the daily cercarial output, a total of 15 infected snails were followed until the death of the snails. Snails were kept separately in containers with 250 ml of lake water under standard laboratory conditions with constant temperature (20 °C) and natural light regime (sunrise 4.30 sunset 22.00; i.e. 17.30 h light/6.30 h dark). Each day, the water was changed and 24 subsamples of 2.5 ml (total 60 ml) were taken from the cercarial suspension to estimate the total number. Snails were fed *ad libitum* with algae on *E. fluviatile* during the study. Secondly, the circadian rhythm of cercarial shedding was followed in August 2007

under natural light regime. A total of 13 infected snails were placed into well-plates, each well with 15 ml of lake water, and the number of emerged cercariae was determined every 2 h for 24 h. To determine the longevity of the cercariae, 17 infected snails were placed individually in 15 ml of water and 20 freshly emerged cercariae (maximum age 3 h) were taken from each snail (308 cercariae in total; 3 snails shed fewer than 20 cercariae). Cercariae were placed in well-plates with 10 ml of lake water so that each well contained 4 cercariae. The experiment was initiated when the maximum age of the cercariae was 4 h after which their status (alive/dead) was checked every 4 h. Dead cercariae changed colour from opalesque to milky whitish, did not respond to mechanical stimuli, and commonly had unnatural shapes and/or tail part separated from the body.

Sampling and processing of fish

A total of 218 juvenile perch (*Perca fluviatilis*) from a cohort hatched in the same spring were sampled monthly (July–October 2007) from the lake. Note that all fish were uninfected in the beginning because of their young age so that the results were not confounded by previous infections. Fish were captured with nets (in July) and fish traps from a location next to the snail sampling site (see above) once a month, except in July and September when samples were taken every 2 weeks. Each time, the fish were measured and weighed, and the internal organs of each fish were examined for metacercariae of *I. pileatus* by compressing the organs between 2 glass plates under a stereomicroscope.

Data analysis

For the analysis of the circadian rhythm in cercarial output, proportional cercarial numbers were calculated for each snail individual and time-point. A repeated-measures ANOVA on arcsine transformed data was then used to analyse differences between the time-points. Non-parametric Kruskal-Wallis test was used in analysing differences in parasite abundance in fish between the sampling times as the data did not meet the assumptions of the parametric tests even after transformations.

RESULTS

Prevalence and patency of infection in snails

A total of 41 of 266 snails (15.4%) were infected with *Ichthyocotylurus pileatus* during the sampling period in May–October. The prevalence of infection changed significantly during the season with a peak in July (36.8%), intermediate prevalence in May and June, and low prevalence in September–October (Fig. 1). Prevalence of patent infections followed a

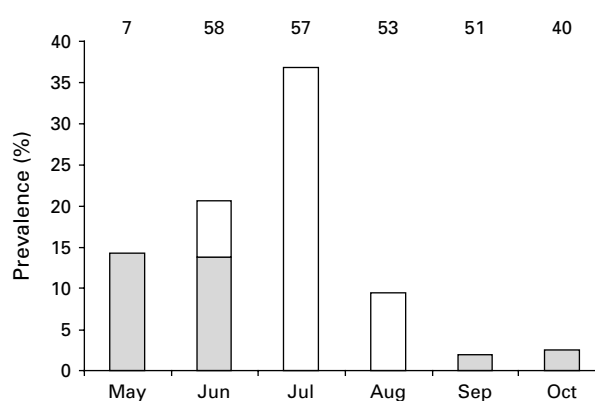


Fig. 1. Monthly (May–October 2007) prevalence of *Ichthyocotylurus pileatus* in *Valvata macrostoma* sampled from Lake Konnevesi, Central Finland. White bars indicate patent infections (spontaneous cercarial emergence) and grey bars indicate pre-patent infections (no cercarial emergence). Numbers on top of columns indicate sample size for each month.

similar pattern (Fig. 1). There were no patent infections in May, but sporocysts with developing cercariae were found. We assumed that these were *I. pileatus*, which is reasonable as it was the only trematode species with sporocysts found in these snails (Faltýnková *et al.* 2008). In June, a few snails harboured mature cercariae of *I. pileatus* (spontaneous cercarial emergence in some of the cases) whereas in July–August cercariae emerged from all infected snails. Developing new infections (mother sporocysts) were observed in September and October (Fig. 1).

Cercarial output and survival

Thirteen of the 15 snails had died on day 48 of the experiment. However, 2 snails were still alive on day 63 but the cercarial output from these snails was relatively low (26.9% of the mean output during the preceding 48 days). Thus, we included data only from the 48 days in the analysis. The mean daily output of cercariae from the snails ranged between 8.9 ± 4.6 and 315.3 ± 74.2 (average = 166.6 ± 12.8 ; all figures indicate mean \pm S.E.) cercariae per day so that the average cercarial output decreased towards the host death (Fig. 2). Data were best described by a linear model ($R^2=0.90$). The coefficient of variation in cercarial output (measuring daily variance in cercarial output among snail individuals) was highest within 10–20 days to host death, whereas it was low in the previous snail life (Fig. 3). In other words, cercarial output was roughly similar between the individual snails in the beginning but the variation increased thereafter. However, when the death of the host approached, cercarial output was very low from all snails.

The cercarial emergence showed a distinct nocturnal rhythm so that the highest numbers were

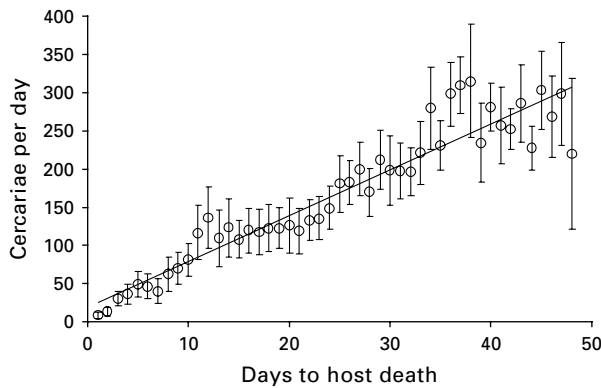


Fig. 2. Mean cercarial output (\pm s.e.) of *Ichthyocotylurus pileatus* from *Valvata macrostoma* ($n=15$) during a period of 48 days before death of the hosts under laboratory conditions. The fitted line represents linear regression ($R^2=0.90$).

released from 21.00–01.00 h ($71.2 \pm 0.1\%$ of the total output) with a peak in 21.00–23.00 h ($30.0 \pm 0.1\%$ of the total output) (repeated-measures ANOVA on arcsine transformed data: $F_{11}=11.7$, $P<0.001$). In other words, shedding of the cercariae was highest in early evening and night. During daytime, the emergence of cercariae was low and reached the minimum from 11.00–17.00 h ($1.7 \pm 0.01\%$ of the total output) (Fig. 4).

Mortality of the cercariae was low for the first 8 h, but increased steeply thereafter so that $52.9 \pm 0.1\%$ of the cercariae were alive after 20 h and $17.9 \pm 0.03\%$ after 40 h. After that, the mortality rate levelled off and the last cercaria died after 76 h (Fig. 5). An exponential model provided a good fit to the data ($R^2=0.96$).

Pattern of infection in perch

The prevalence of *I. pileatus* infection in perch was low in July but increased steeply in August reaching 100% at the beginning of September (Fig. 6). The abundance of infection also changed significantly during the study period (Kruskal-Wallis: $\chi^2=179.02$, D.F. = 5, $P<0.001$) and followed a similar pattern as the prevalence. The maximum mean abundance, 33.9 ± 6.5 parasites per fish, was recorded at the end of the study period in October (Fig. 6). The maximum intensity of infection in an individual fish was 139 parasites. Average fish length increased from 27.22 ± 0.51 mm to 70.68 ± 1.18 mm between July and October.

DISCUSSION

In northern latitudes, parasites with complex life cycles have to cope with the general unpredictability of transmission through multiple hosts as well as the narrow time frame for transmission emerging from seasonality. In this paper, we investigated the

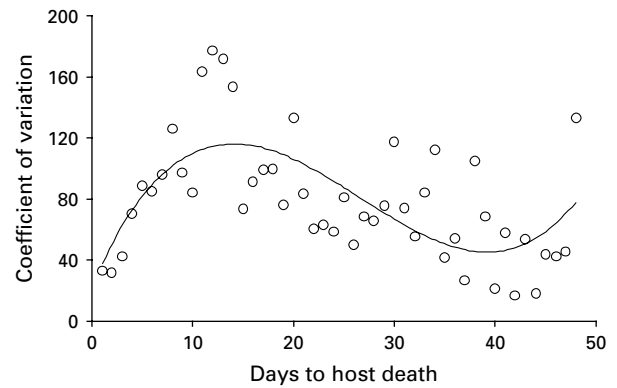


Fig. 3. Coefficient of variation in cercarial output of *Ichthyocotylurus pileatus* from *Valvata macrostoma* ($n=15$) during the period of 48 days before death of the hosts under laboratory conditions. The fitted line is $y = a_1x^3 + a_2x^2 + a_3x + b$, where $a_1=0.009$, $a_2=-0.7217$, $a_3=14.979$ and $b=23.279$ ($R^2=0.42$).

transmission patterns of *Ichthyocotylurus pileatus*, which is, along with other species in the same genus, one of the most successful parasites of freshwater fish, despite the apparent challenges in transmission (Faulkner *et al.* 1989; Karvonen and Valtonen, 2004; Harrod and Griffiths, 2005; Karvonen *et al.* 2005). Essentially, we were interested in temporal patterns of cercarial output from snails which could at least partly explain the high rate of transmission. Secondly, we quantified the transmission rate in detail by repeatedly sampling a newly hatched cohort of wild perch.

Our results indicated that the cercarial output from *Valvata macrostoma* was limited to a few weeks mainly in July, which verifies the narrow temporal window for transmission in *I. pileatus*. In our previous study, we showed that the population of *V. macrostoma* undergoes a rapid turnover in July–August so that the larger, more frequently infected snails disappear from the population and are replaced by a new cohort of young snails (Faltýnková *et al.* 2008). This coincides with the observed decrease in cercarial output and may be due to higher mortality rate among the infected snails (Jokela *et al.* 1999, 2005; Karvonen *et al.* 2004). Nevertheless, the cercarial output resulted in 100% infection in the population of juvenile perch with a mean abundance of 33.9 (maximum 139) parasites per individual fish. It is important to note, however, that *Ichthyocotylurus* parasites accumulate in fish with age and therefore infection intensities observed in the juvenile fish continue to increase and may reach several hundreds in older fish. An earlier study has shown that this is true also in the present system (Karvonen *et al.* 2005), although in that study *I. pileatus* metacercariae were identified as *I. variegatus* because of uncertainties in species composition at that time. The pattern of infection in fish also followed the cercarial emergence from the snail population with

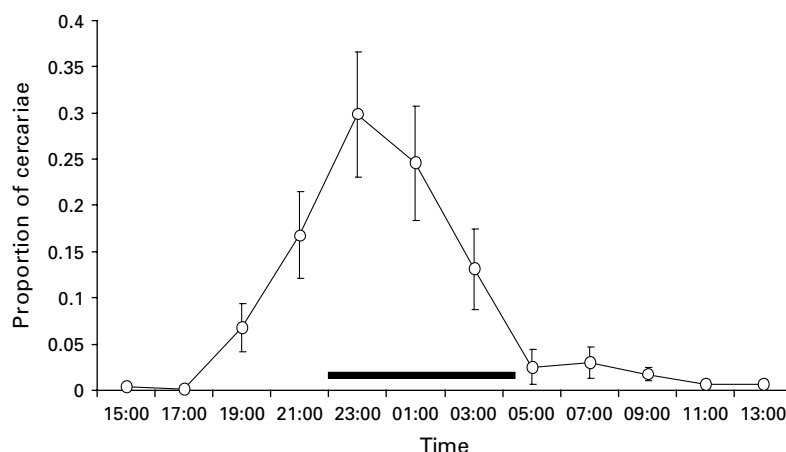


Fig. 4. Circadian rhythm of the cercarial output of *Ichthyocotylurus pileatus* from *Valvata macrostoma* under natural light rhythm in the laboratory. Dots represent mean proportional output (\pm s.e.) of the cercariae from 13 snails. Black bar indicates the time between sunset and sunrise, 22.00–04.30.

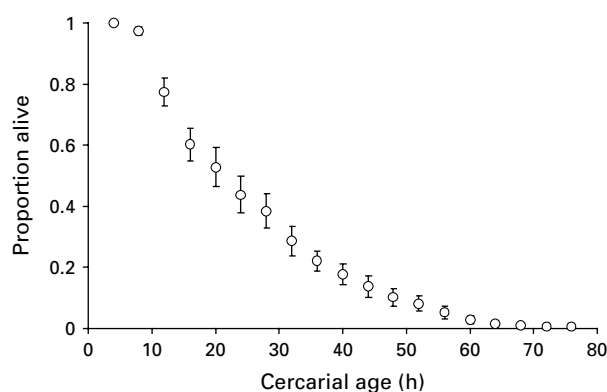


Fig. 5. Survival (\pm s.e.) of *Ichthyocotylurus pileatus* cercariae as a function of cercarial age under standardized laboratory conditions. Data show the mean survival (\pm s.e.) for the cercariae extracted from 17 *Valvata macrostoma* snails (approximately 20 cercariae snail⁻¹, 308 cercariae in total).

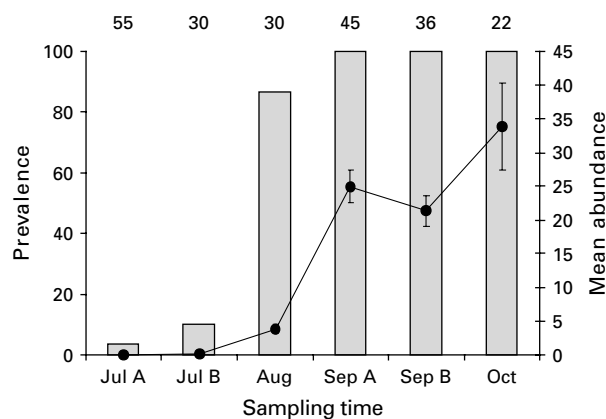


Fig. 6. Prevalence (columns) and mean abundance (dots \pm s.e.) of *Ichthyocotylurus pileatus* in 0+ perch sampled from Lake Konnevesi. Note that the fish were sampled twice per month in July and September. Numbers on top of columns indicate sample size.

a time lag of a couple of weeks, which was the time required for the infection to become detectable in fish. In general, the timing of the patent infections in snails corresponded to the seasonality of infection in other trematode species in similar systems. For example, the peak of cercarial emergence in *Diplostomum spathaceum* is in July–August, although the overall period of transmission is slightly longer than in *I. pileatus* (Karvonen *et al.* 2004). Similarly, cercariae of *Rhipidocotyle feminea* emerge from the clam *Anodonta piscinalis* mainly during a few weeks in August (Taskinen *et al.* 1994; Taskinen, 1998). Infection intensities of these parasites in fish are nevertheless different than those of *I. pileatus* (Valtonen *et al.* 1997, 2003). Although this represents a quite rough comparison between the trematode species because the data come from different systems at different times, it nevertheless suggests that seasonality of transmission *per se* is unlikely to

provide a comprehensive explanation for the relative high abundances of *I. pileatus* in fish. We also recorded the magnitude and rhythm of the cercarial emergence of *I. pileatus* and found that the cercarial output was decreasing linearly as the death of the host approached. Moreover, the cercarial emergence followed a very strong circadian rhythm with most of the cercariae shed in early evening and night. The mean number of *I. pileatus* cercariae emerged from an individual snail in a day (166.6) corresponded roughly to that recorded earlier in the related species *Ichthyocotylurus erraticus* (mean 100; 154) and *I. variegatus* (mean 127) in the laboratory (Swennen *et al.* 1979; Bell *et al.* 1999). However, there was considerable variation among individual snails and the degree of variation also changed with the progression of the cercarial emergence. On the other hand, average numbers of cercariae were significantly lower compared to many other trematode

species. For example, *D. spathaceum* may release tens of thousands of cercariae from an individual *Lymnaea stagnalis* in a day (mean up to 37 000; Karvonen *et al.* 2004) and the corresponding numbers in *R. fennica* may also exceed 10 000 cercariae (Taskinen, 1998). This difference is probably related to the small size of *Valvata* and corresponding physical space for the parasite sporocysts. For example, a large part of the differences in cercarial output of 2 *Diplostomum* species has been shown to be related to the size difference of their snail hosts (Karvonen *et al.* 2006).

Several trematode species are known to match the timing of cercarial emergence with the activity of the next host (reviewed by Combes *et al.* 1994; McCarthy *et al.* 2002). Indeed, the most likely mechanism of cercarial output underlying the high transmission rate in *I. pileatus* would be the strong nocturnal pattern where most of the cercariae emerge in early evening and night, and very few during the day. In general, perch, the next hosts for *I. pileatus*, are active mainly during daytime with the highest activity at dawn and dusk, and lowest during night. Moreover, the fish spend more time in the littoral zone during night, whereas at daytime, they are mainly in open water (Huusko *et al.* 1996; Zamora and Moreno-Amich, 2002; Lorke *et al.* 2008). It is possible that the fish seek shelter near the bottom during the early evening and night and subsequently become exposed to the cercariae. Interestingly, however, Bell *et al.* (1999) found that cercariae of the related species, *I. variegatus*, which also uses percid fishes as the second intermediate hosts, emerged mainly during the day. While these results are contradictory, it should be noted that the timing of the cercarial emergence in *I. variegatus* (Bell *et al.* 1999) showed higher variation compared to *I. pileatus* in this study. Moreover, the parasites may use different percid fish species as primary intermediate hosts. We explored the longevity of *I. pileatus* cercariae and found that some cercariae survived up to 76 h, but the majority died within 48 h. Although this time is somewhat longer compared, for example, to the survival time of *D. spathaceum* cercariae under similar conditions (Karvonen *et al.* 2003), the pattern of mortality was quite typical for infective stages with limited energy reserves. Indeed, trematode cercariae rely on finite glycogen reserves (Tielens, 1997) and once these are depleted, the cercariae die. Interestingly, because of this energy allocation, cercariae tend to lose their infectivity first (Karvonen *et al.* 2003), which suggests that the infectious period of *I. pileatus* cercariae is probably significantly shorter than their survival time.

In addition to the cercarial characteristics studied in the present paper, high transmission efficiency to fish could be a result of very high cercarial infectivity. However, our uncontrolled preliminary infection trials with *I. pileatus* cercariae and pike

perch suggest that this would not be the case (Faltýnková, Karvonen and Valtonen, unpublished observations). High transmission rate could also be a result of high density of infected snails in a lake when cercarial numbers could result in a high total output from the snail population. Previous workers have shown that densities of *Valvata* spp. can be very high (from hundreds to thousands per m²), but also highly variable between and within populations (Heitkamp, 1982; Krieger, 1985; van den Berg *et al.* 1997; Grigorovich *et al.* 2005; Harrod and Griffiths, 2005; Mouthon and Daufresne, 2006). Although we did not quantify the density of *V. macrostoma* in detail, our sampling protocol suggests that densities were not that high as several relatively large sediment hauls were required for the sample sizes obtained in this study. To conclude, we showed that despite the narrow temporal window, transmission of *I. pileatus* from snail hosts resulted in 100% infection in juvenile perch. Infection intensities in these fish were comparable or higher than those of most other parasite species in adult perch (Valtonen *et al.* 1997; Karvonen *et al.* 2006), supporting the numerical dominance of this species in parasite communities of perch. Numbers of cercariae emerged from individual snails were relatively low, but the strong circadian pattern of cercarial release could at least partly account for the high infection rate in fish. More investigations on the dynamics of different species of *Ichthyocotylurus* combining the dynamics of host populations, as well as those of cercarial emergence and infectivity, are needed to unravel the mechanisms underlying the high infection intensities observed among the species of this genus.

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