

# Cercarial swimming performance and its potential role as a key variable of trematode transmission

## Research Article

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### Abstract

Trematode transmission in aquatic habitats from molluscan intermediate host to vertebrate or invertebrate target host is typically undertaken by a free-living stage known as cercariae. Active locomotion by cercariae is a key aspect of the transmission process with the swimming speed potentially contributing to infection success. Individual cercarial species swim at different speeds but the significance of this to infection potential has not been determined. This study, using data from the scientific literature, investigates the role of swimming speed in relation to cercarial morphology, host-searching strategies and target host species. Larger cercariae swim faster than smaller ones with tail length being the principal factor controlling locomotion rates. Different cercarial morphotypes swim at different speeds, in particular, furcocercariae, with the exception of the schistosomes, being faster swimmers than mono-tailed cercariae. Host-searching behaviour has a significant influence on swimming speeds with ‘active-searching’ strategies swimming slower than those adopting ‘active-waiting’ or ‘prey mimicry’ strategies. Vertebrate-infecting cercariae swim faster than those infecting invertebrates with species targeting fish demonstrating the highest locomotion rates and those targeting arthropods the slowest speeds. The adaptations of individual cercarial swimming speeds to biological variables and their interactions with the physical processes of aquatic habitats are discussed.

### Introduction

Transmission of trematodes from molluscan source hosts to the vertebrate or invertebrate target host is typically undertaken by free-living larval stages known as cercariae. These are lecithotropic larvae dependent on a glycogen store for energy utilisation and morphology that generally comprises an oval body with a tail of variable size and structure. The tail is a characteristic organ of cercariae whose primary function is locomotion, especially within aquatic habitats where both pelagic and demersal species are dependent on its muscular contractions for swimming (Cable, 1965; Galaktionov and Dobrovolskij, 2003).

Active mobility enables cercariae to disperse on emergence from the molluscan host and localize themselves in the ‘host-space’, areas of a habitat where an increased chance of contact with a compatible target host could be expected (Combes *et al.*, 1994; Morley, 2012). In such areas, cercariae need to be capable of maintaining their position whilst under the influence of physical processes such as potentially powerful water currents as well as contact and infect a target host which may be subjected to biological processes such as their own rate of mobility that can affect the transmission process. A key aspect of cercarial locomotion that is necessary to respond to variable biological and physical processes is the swimming speed that is achievable. Cercariae need to be able to achieve an optimal swimming speed that allows them to control their position in the ‘host-space’ in relation to these variables that increases the likelihood of successful transmission.

The tail as the main organ of locomotion is the likely principal factor influencing swimming efficiency and contains both highly developed sets of muscles and the main store of glycogen energy reserves for the cercariae (Galaktionov and Dobrovolskij, 2003). The longitudinal muscles propel the cercariae by contracting against the resistance provided by the hydrostatic skeleton of the tail with fast undulations of this organ in a lateral plane, alternating in phase, provide for movement (Galaktionov and Dobrovolskij, 2003). Swimming cercariae are highly manoeuvrable and able to perform a turn of speed of at least  $70^\circ \text{ s}^{-1}$  at temperatures as low as  $5^\circ \text{C}$  (Chapman and Wilson, 1973). The morphology of the cercarial tail varies between species but at its simplest level can be considered either a single elongated stem organ or one where the stem bifurcates at the distal end forming two branches known as furcae. Species of this latter group are known collectively as furcocercariae and the modifications of the tail in this manner both lead to a more efficient mode of tail-driven locomotion as well as enabling a more protracted floating duration by deploying the furcae in a manner which increases the surface area and reduces the rate of sinking during periods of rest.

Emergent cercariae adopt a number of different swimming movement patterns. These may be adapted to minimise energy utilisation for generating propulsion, to reduce the risk of predation, and to promote an effective host-searching strategy (Haas, 1994). Prokofiev and Galaktionov (2009) have grouped cercariae into four basic strategies of host-searching

behaviour that are predominantly based on their differing mechanisms of locomotion and the activity levels of the target hosts. These are (1) 'active searching' whereby cercariae demonstrate continuous swimming activity alongside phototactic and geotactic behaviour that results in this group constantly scanning habitats for potential hosts at a high energy cost. (2) 'Active waiting' for cercariae with intermittent swimming activity. These cercariae demonstrate a two-phase behaviour with an active phase in which the parasite typically undertakes an upward-directed swimming burst alternating with a passive phase of sinking that is extended by increasing the drag through the water by adopting postures and extending structures such as furcae, fin-folds or hair-like appendages (Haas, 1994). Such behaviour reduces the energy cost of maintaining a position in the 'host-space' pelagic zone (Combes *et al.*, 1994; Haas, 1994). (3) 'Passive waiting' includes either cercariae that attach themselves to a substrate and adopt 'ambush' behaviour with relatively poor swimming abilities or those that float passively in the water column for weeks or months with a low energy cost. (4) 'Prey mimicry' where cercariae swim in an active manner that replicates the behaviour of prey favoured by target hosts.

Cercarial swimming speed may be a potentially important controlling variable influencing transmission success in response to the activity of target hosts and different physical conditions of habitats. Individual cercarial species have been recorded to swim at a different speed, although only limited information is available assessing such variable locomotion in relation to biological parameters such as morphology, host-seeking behaviour or designated target hosts, typically by experimental investigations on a small number of species (Prokofiev, 2005; Santos *et al.*, 2007; Selbach and Poulin, 2018). However, comparative examinations of cercarial swimming adaptations that might aid the transmission process have not been evaluated. This study, using data from the scientific literature, investigates the relevance of locomotion to these biological variables and also discusses cercarial speed in relation to the physical dynamics of aquatic habitats.

## Materials and methods

### Source of data

Data on mean cercarial swimming speeds from laboratory studies were obtained from the scientific literature. These were compiled based on searches of the following databases: 'Web of Knowledge', 'Scopus', 'CABI Global Health', 'Helminthological Abstracts', 'PubMed', 'Google Scholar', 'Proquest Dissertations & Theses' and 'Zoological Record' using mainly combinations and variations of the following terms: 'cercariae', 'swimming', 'speed', 'locomotion', 'activity' and 'behaviour'. Searching online databases revealed 66 relevant studies. These were supplemented with unpublished observations on three species undertaken by the author to produce a final dataset of 69 studies. In general, these studies determined speed by measuring the distance travelled by cercariae over a certain time frame. In addition to mean swimming speeds each study was augmented with additional information that included a species geographical region and strain, temperature, if indicated, under which the original study was undertaken, cercarial morphotype, target host and the activity strategy as designated by Prokofiev and Galaktionov (2009). This information is included in Supplementary Table 1. In addition, the influence of cercarial morphology to swimming speeds was determined using measurements of body and tail length for each cercarial species obtained from the scientific literature on morphological studies undertaken, where possible, in the same or adjacent geographical region. An organisms' characteristic length is the conventional measure of locomotion potential

(Peters, 1983). To provide a single geometrically similar measurable parameter of tail length across the different cercarial species a 'functional tail length' was designated using morphological data from the scientific literature (see Supplementary Table 2 for details on the sources of this information for each species). For furcocercariae species, this was determined as the combined length of the three elements that comprise the bifurcated tail (tail stem + furcae + furcae). For the remaining species, this parameter was the actual length of the tail as recorded in morphological studies. The influence of overall cercarial size to swimming speeds was determined by combining functional tail length and body length to provide a total measure of longitudinal size.

### Data analysis

The relationship between cercarial speed and functional tail length or body length was analysed using Pearson's correlation. For further analysis data was grouped according to either cercarial morphotype – furcocercariae (subgrouped as either schistosome, non-schistosome or as a total), echinostome, xiphidiocercariae, parapleurolophocercous cercariae; host searching strategy – 'active waiting', 'active searching', 'passive waiting', 'prey mimicry'; or as a particular target host group – vertebrates, invertebrates, aquatic vertebrates, terrestrial vertebrates, aquatic invertebrates, mammals, birds, amphibians, fish, molluscs, annelids, arthropods. Due to high levels of variability in the recorded swimming speeds of designates within morphotype, host searching and target host groups analysis was undertaken using non-parametric tests (Kruskal–Wallis and Mann–Whitney *U* tests). All data were analysed using the SPSS statistical package.

## Results

The swimming speed of cercariae varies extensively between species and ranges from 0.1 to 25.9 mm s<sup>-1</sup> (Supplementary Table 1). There was no significant difference in the speeds of cercariae between freshwater and marine environments (Mann–Whitney *U* test  $P = 0.884$ ). Similarly, there was no correlation between experimental temperature and swimming speeds (Pearson's correlation 0.040,  $P = 0.772$ ) indicating that these studies were likely undertaken at near-optimal thermal conditions. Larger cercarial species swim at a faster speed than smaller ones (Pearson's correlation 0.286,  $P = 0.017$ ). Furthermore, there is a positive significant correlation for functional tail length and speed of cercariae (Pearson's correlation 0.295,  $P = 0.014$ ) but no relationship occurs between body length and locomotion rates (Pearson's correlation 0.167,  $P = 0.171$ ) indicating the key role of the tail in locomotion.

The majority of species in the dataset infect target hosts at a life stage that are completely aquatic in nature. Only a small number, restricted to Schistosomatidae furcocercariae, infect terrestrial air-breathing vertebrate species, either humans or birds. Compared to furcocercariae that infect aquatic vertebrate hosts, with a mean swimming speed of 6.58 mm s<sup>-1</sup> (s.d. 7.026), these schistosomes swim at significantly slower mean speeds of 1.29 mm s<sup>-1</sup> (s.d. 0.881) (Mann–Whitney *U* test  $P = 0.001$ ). This difference indicates that within this cercarial morphotype schistosomes need to be considered as a separate distinct group who's slower swimming speeds may distort analysis in which they may be included. Subsequent examination of this dataset has consequently omitted the schistosomes from some of the statistical analysis.

Comparisons between the swimming speeds of furcocercariae and mono-tailed cercariae show that the furcocercariae are generally faster swimmers (Table 1). However, statistical analysis indicates that furcocercariae, when including schistosome species, are

**Table 1.** Swimming speeds of cercariae designated according to morphotype

Morphotype	<i>N</i>	Mean speed (mm s <sup>-1</sup> )	s.d.
Furcocercariae			
Non-schistosome	17	4.74	6.128
Schistosome	10	1.29	0.881
Total	27	3.46	5.124
Echinostome	15	2.13	0.999
Parapleurophocercous	9	2.07	1.241
Xiphidiocercariae	8	0.47	0.276
Pleurophocercous	3	2.75	3.765
Gymnocephalous	2	4.69	4.688
Megalurous	2	0.49	0.579
Cotylocercous	1	1.00	–
Trichocercous	1	3.60	–
'Hugh-tailed monostome'	1	3.50	–

not significantly faster (Mann–Whitney *U* test  $P = 0.201$ ) due to the wide variations in cercarial speeds of this diverse group. However, when the slower-swimming schistosomes are omitted from the furcocercariae group the advantages of a bifurcating tail for achieving faster speeds become apparent (Mann–Whitney *U* test  $P = 0.020$ ).

The dataset includes a wide range of different cercarial morphotypes but only four groups (Furcocercariae, Echinostome, Xiphidiocercariae, Parapleurolophous cercariae) have been studied extensively. Comparing the swimming speeds of these four morphotypes indicates that there is a significant difference between them (Kruskal–Wallis test  $P = 0.001$ ). However, comparisons at the individual level found that there is a significant difference only between Xiphidiocercariae and the other morphotypes (Mann–Whitney *U* test  $P < 0.001$  for all comparisons).

The cercarial swimming speeds when designated into the four host-searching behaviour strategies demonstrate different means although the dataset predominantly comprises species with an 'active waiting' or 'active searching' activities (Table 2). There is a significant difference in the swimming speeds of cercariae utilising the different behaviour strategies (Kruskal–Wallis test  $P = 0.008$ , excluding schistosomes). This significant difference is maintained when 'passive waiting', represented by only two examples, is removed from the analysis (Kruskal–Wallis test  $P = 0.011$ , excluding schistosomes). Direct comparisons show that 'active searching' cercariae swim at a significantly slower speed compared to species demonstrating 'active waiting' (Mann–Whitney *U* test  $P = 0.010$ , excluding schistosomes) but not 'prey mimicry' strategies (Mann–Whitney *U* test  $P = 0.066$ ). However, there are no significant differences between 'active waiting' and 'prey mimicry' strategies (Mann–Whitney *U* test  $P = 0.616$ , excluding schistosomes), although this result should be treated with caution due to only three examples of the 'prey mimicry' strategy being available.

Cercarial swimming speed varied according to the type of target host, with cercariae infecting arthropods having the slowest swimming speeds whilst those targeting fish achieving the fastest rates of locomotion (Table 3). There is a significant difference in the swimming speeds of cercariae infecting the seven main host groups (humans, birds, amphibians, fish, molluscs, arthropods and annelids) in the dataset (Kruskal–Wallis test  $P < 0.001$ ). More specifically, cercariae infecting vertebrates swim at significantly faster speeds than those infecting invertebrates (Mann–

**Table 2.** Swimming speeds of cercariae designated according to host-searching behaviour

Host-searching behaviour	<i>N</i>	Mean speed (mm s <sup>-1</sup> )	s.d.
Active searching	33	1.78	1.569
Active waiting	31	3.29	4.827
Prey mimicry	3	4.17	2.566
Passive waiting	2	0.54	0.651

Host-searching strategies grouped according to Prokofiev and Galaktionov (2009).

**Table 3.** Swimming speeds of cercariae grouped according to known target hosts

Target host	<i>N</i>	Mean speed (mm s <sup>-1</sup> )	s.d.
Vertebrates	42	3.10	4.236
Terrestrial vertebrates	10	1.29	0.881
Humans	8	1.07	0.535
Birds	2	2.15	1.77
Aquatic vertebrates	32	3.67	4.703
Fish	23	4.03	5.265
Amphibians (tadpoles)	9	2.73	2.848
Invertebrates (aquatic)	31	1.47	1.021
Molluscs	19	1.79	0.967
Annelids	4	1.20	0.297
Arthropods	7	0.47	0.258

Whitney *U* test  $P = 0.018$ ) which is more pronounced when comparing only the speeds of cercariae infecting aquatic vertebrates compared to aquatic invertebrates (Mann–Whitney *U* test  $P = 0.002$ ). Cercariae targeting arthropods swim at the slowest speeds, significantly different from those infecting annelids (Mann–Whitney *U* test  $P = 0.012$ ), molluscs (Mann–Whitney *U* test  $P < 0.001$ ), fish (Mann–Whitney *U* test  $P < 0.001$ ), amphibians (Mann–Whitney *U* test  $P < 0.001$ , and humans (Mann–Whitney *U* test  $P = 0.006$ ). Cercariae infecting molluscs swam significantly faster than those infecting humans (Mann–Whitney *U* test  $P = 0.045$ ), but showed no difference compared to species infecting annelids (Mann–Whitney *U* test  $P = 0.324$ ), fish (Mann–Whitney *U* test  $P = 0.050$ ), or amphibians (Mann–Whitney *U* test  $P = 0.498$ ).

In general, due to high levels of variability, differences between cercarial speeds of other target host groupings were not significant. In particular, fish-infecting cercariae demonstrated the widest range of swimming speeds varying between 0.48 and 25.9 mm s<sup>-1</sup>, with a majority of species capable of swimming in excess of 2 mm s<sup>-1</sup> (Supplementary Table 1). The wide variability in speeds of this group resulted in no significantly different locomotion from any other group except for humans (Mann–Whitney *U* test  $P = 0.010$ ). This difference was replicated by amphibians which were also significantly faster than human-infecting cercariae (Mann–Whitney *U* test  $P = 0.036$ ).

## Discussion

Cercarial swimming proficiency is a potential key trait for the behavioural control of free-living parasite transport. Locomotion plays an important role in determining dispersal from the molluscan intermediate host, maintenance in the 'host-space', avoidance

of predators or unfavourable conditions, and the location and penetration of target hosts.

Cercarial speed is directly related to the functional tail length with longer or bifurcate tails capable of providing greater rates of locomotion, confirming that this is the principal role of this organ. However, although furcocercariae are potentially capable of swimming at higher speeds than cercariae with a single tail length it is apparent that within this morphotype that the schistosomes swim at a significantly slower speed. The reasons for this are likely to be associated with adaptive behaviour patterns of locating air-breathing terrestrial hosts in aquatic environments. Nevertheless, furcocercariae targeting aquatic hosts do conform to the expectation of greater speed indicating the advantages of this morphological adaptation.

The swimming speed is highly variable, whether compared across morphotypes, related target hosts or even the same strain of species. Some of the intraspecific variations may be accounted for by differences in experimental protocols and conditions between different studies. Thus, individual swimming speeds derived from experimental sources should not be interpreted in absolute terms. However, pronounced variations may still remain, even within studies undertaken using the same experimental conditions, e.g. studies undertaken on *Cryptocotyle lingua* from Northern Ireland (Rea and Irwin, 1992, 1995, 2001; Cross *et al.*, 2001, 2005).

Large differences in swimming speeds found between studies conducted on the same cercarial species may be a result of genetic variability. For marine invertebrate larvae, it is known that there is a large inter-individual variability in swimming performances amongst clutches and even among siblings of a single clutch (Nanninga and Berumen, 2014), such that up to a third of the variation may be genetic in origin (Hiblish *et al.*, 1999). Populations of cercariae are also known to demonstrate wide genetic variations (Semyenova *et al.*, 2007) and this is known to affect cercarial biology (Lu *et al.*, 2009; Berkhout *et al.*, 2014) as well as be influenced by environmental conditions, particularly genotype-by-temperature interactions (Berkhout *et al.*, 2014). Nevertheless, the significance of these differences in swimming speeds has to be considered within the context of the activity of the target host and the physical dynamics of their aquatic habitats which generally involve animal speeds and water movements of a far higher magnitude.

Correlation of swimming speed with host-searching behaviour suggests that locomotion predominantly plays a role mainly in distinguishing between 'active searching' and other strategies. 'Active searching' cercariae swim at significantly slower speeds which may be a means of conserving energy utilisation for these continuously moving species. In contrast, there are no differences between 'active waiting' and 'prey mimicry' strategies which may be because the majority of species in these two datasets infect fish, which may require comparable levels of locomotion ability, although this result should be treated with caution due to the relatively few examples available from this latter group. Nevertheless, some 'active searching' cercariae appear to be able to regulate their swimming speed over the duration of their free-living existence. Echinostome and Plagiorchid cercariae may decrease their swimming speed in close proximity to molluscan and arthropod hosts, thereby increasing the amount of time spent in the vicinity of their targets and facilitating infections (Cable, 1965; Dixon, 1984).

The swimming speed of individual cercarial species appears to be related not only to their host-location strategies but also the activity of their target hosts. Cercariae that adopt an 'active waiting' strategy generally infect vertebrate target hosts with fish or humans predominating in the dataset. Cercariae infecting these two very different target hosts swim at different speeds, with fish-infecting species generally swimming at higher velocities. The

fastest recorded cercariae is *Transversotrema patialense* with a speed of  $25.9 \text{ mm s}^{-1}$ , an unusual species with an 'active waiting' strategy, of which the adults are ectoparasitic on the skin surface of tropical freshwater fish (Anderson and Whitfield, 1975) and this aspect may be an important contributory factor determining its locomotion.

Target host groups, therefore, appear to influence the speed of cercariae, although there is often a large degree of variability between species within each group. Broadly speaking the slowest swimming cercarial species would appear to infect invertebrate target hosts that are either sedentary or often inactive, whilst faster swimming cercariae target active vertebrate hosts like fish or amphibian tadpoles. However, sustaining cruising speeds of fish are typically in excess of  $50 \text{ mm s}^{-1}$  and can reach  $5000 \text{ mm s}^{-1}$  (Beamish, 1978), far beyond the speeds attainable by all fish-infecting cercarial species, indicating that parasite infection strategies are unlikely to involve any prolonged or successful periods of 'chasing'. The exceptions to such generalizations would appear to be the relatively slow-swimming schistosome species that target terrestrial mammal hosts which, although possessing the capacity to move swiftly through the water when fording or swimming, largely spend the majority of water-contact time in more static activities such as for humans bathing or washing clothes (Upatham, 1974a).

However, such anomalies may also have implications for other cercarial species, potentially indicating that many infections predominantly occur only when target hosts are behaving in an active manner that facilitates infections at particular slow rates of swimming efficiency. For example, fish may potentially be preferentially infected during periods of rest. Nevertheless, as no cercarial species can match the speeds achievable by their active target host unless they are infecting slow-moving or sedentary species, the different performance speeds adopted by those targeting specific host groups may, therefore, have an as yet unknown relevance beyond swimming in the open water of aquatic habitats. For example, many fish are infected by accidental contact with cercariae in the water column when they are brought passively to the host gills due to the flow of water through this organ for ventilation (Mikheev *et al.*, 2014). The high speeds of fish-infecting species may, therefore, be preferentially intended for a 'burst' response to a chance encounter with the gill surface to achieve and maintain contact before initiating penetration.

Although cercarial swimming speeds may be related to host-searching behaviour and target host species these biological factors are themselves influenced and interconnected by the physical factors which characterise aquatic habitats. Thus, the speed that cercariae can achieve is also important for determining if they are capable of actively maintaining their position in the 'host space', especially within flowing water conditions, or whether they are simply passively dispersed. Mileikovsky (1973), whilst evaluating the swimming speeds of marine invertebrate larvae, considered that only those capable of speeds in excess of  $1 \text{ cm min}^{-1}$  ( $0.17 \text{ mm s}^{-1}$ ) would be able to perform active vertical movements irrespective of the strength of the local tidal currents which may attain horizontal speeds of  $80 \text{ cm s}^{-1}$  but only vertical speeds of  $0.1 \text{ mm s}^{-1}$ . Similarly, vertical currents are negligible in flowing freshwater habitats which are characterised by unidirectional horizontal currents of variable velocities (Maitland, 1990). Nevertheless, vertical currents can reach a maximum of  $0.6 \text{ mm s}^{-1}$  in still freshwater conditions found in lakes (Verber, 1967).

As most cercariae in this study were capable of speeds in excess of  $0.1$  or  $0.6 \text{ mm s}^{-1}$  it suggests that they would also be able to retain their vertical position in the pelagic zone of most kinds of still or flowing water conditions. However, similar to marine invertebrate larvae, they would be unable to maintain any kind of horizontal position in even the weakest form of marine or freshwater flowing water habitat. Certainly, vertical migrations

by cercariae are well known (Fingerut *et al.*, 2003; Fitzpatrick *et al.*, 2016) and even though it is likely that they lack a strong enough swimming ability to directly control their horizontal dispersal it does not completely preclude cercarial-induced movements in this plane. In marine environments horizontal flow velocities vary with depth, current reversals in different layers can occur in some flow regimes whilst flow will slow closer to the sea bed due to friction. Marine invertebrate larvae are thought to exploit behaviourally this layered vertical structure of marine flows by vertically swimming and maintaining position in horizontal layers that are flowing in a preferred direction (Pineda and Reys, 2018). Similar horizontal layering with differing flow regimes also occur on freshwater lakes which are exploited by zooplankton during diel vertical migrations (Horne and Goldman, 1994). It is possible that cercariae may also utilise this physical characteristic of aquatic environments to enable horizontal dispersal or stability in a similar manner.

Nevertheless, the relatively low swimming speed of most cercariae in relation to horizontal water movements suggests that they are predominantly adapted not to physical variables but rather biological ones associated with their target hosts. It therefore seems likely that greater levels of successful transmission take place in habitats where horizontal water movements are largely absent. Static, shallow, water bodies such as ephemeral, semi-permanent or permanent pools, small ponds, marshes, irrigation canals, flood zones, and coastal pools and bays would appear to offer ideal conditions for cercarial transmission (Styczynska-Jurewicz, 1966). The increased prevalence of trematode infections in freshwater molluscs found in small ponds compared to lakes (Zdárská, 1964; Styczynska-Jurewicz, 1966; Faltýnková, 2005) would suggest that these environments may facilitate parasite transmission with free-living stages, although other factors, such as colonization potential and competition, may complicate this pattern (Soldánová *et al.*, 2011). Such elevated prevalences are not only associated with their static nature but also often due to the greater density of potential hosts and the increased likelihood of more frequent contacts in a small area of limited surfaces (Styczynska-Jurewicz, 1966). Many small static water bodies occur close to larger bodies of water such as lakes, rivers or the open sea and may act as a source and sink of infection for these bigger biotopes using animals, particularly vertebrates, that are capable of making frequent movements between the two kinds of aquatic habitats (Styczynska-Jurewicz, 1966).

However, slow-swimming schistosomes in flowing water environments achieve peak infections at mean velocities of 30–40 cm s<sup>-1</sup> with slower velocities reducing the likelihood of contact with a target host and higher velocities, often accompanied by extreme turbulence, dispersing or damaging cercariae resulting in only chance encounters with hosts and few successful infections (Upatham, 1973, 1974b; Jewsbury, 1985). These studies suggest certain flow rates facilitate infections in terrestrial mammals, possibly associated with the behaviour of target hosts and their interactions with other elements of these habitats.

Nevertheless, infection rates in terrestrial mammals are still lower in flowing water rather than static water environments. This may be due to the opportunity for multiple penetration attempt of immobile or slow-moving hosts by cercariae in static environments whereas cercariae that fail to successfully penetrate on their first attempt are immediately carried away in the surface flow (Upatham, 1974a). Studies with species that infect aquatic hosts show similar responses in flowing water. At low flow regimes there is a trend for transmission success to be similar to static water conditions (De Montaudouin *et al.*, 1998; Fingerut *et al.*, 2003), however, as flow rates increase infections decline until water currents are too fast to enable any transmission to occur (Stables and Chappell, 1986; Fingerut *et al.*, 2003).

Cercarial swimming speed declines with age (Rea and Irwin, 2001; Prokofiev, 2005), affecting the ability of older cercariae to maintain their position in the 'host-space' as well as contact and infect a target. This may be an additional unappreciated factor in the reduced cercarial infectivity with age (Anderson and Whitfield, 1975; Whyte *et al.*, 1991; Pechenik and Fried, 1995). Similarly, swimming speeds also change as a function of temperature, being always positively thermokinetic. Young (1995) considered thermal effects on marine invertebrate larval locomotion were only partly physiological, due to an increase in biochemical reaction rates, but also attributable to changes in water viscosity that occur with temperature fluctuations. As much as 40% of changes in swimming speed may occur over a 10°C change in temperature due to altered water viscosity. Changes in temperature and water viscosity have also been found to affect the swimming movements of *Schistosoma mansoni* cercariae, which has been suggested may potentially lead to differing levels of transmission success during seasonal changes in water temperature (Nguyen *et al.*, 2020). In the same way, water viscosity differences may ensure larvae living in cold water environments require less drag to stay afloat than larvae from tropical latitudes (Young, 1995). In the present investigation, data were acquired from studies undertaken at a range of experimental temperatures, typically between 15 and 25°C. These temperatures appear to have been chosen as those most accurately reflecting conditions in natural habitats in which the cercariae occur and are therefore likely to reflect optimum thermal conditions for determining swimming performance for each study. Cercarial swimming speeds have only rarely been studied over different temperatures, e.g. Haas (1969, 1994), Fingerut *et al.* (2003), Nguyen *et al.* (2020); and this limited information would indicate that speed increases as a function of temperature, typically doubling or tripling over 10°C increases, a normal thermal response for ectothermic animals and previously demonstrated for trematode development rates (Morley and Lewis, 2013, 2017). However, such thermal changes in cercarial speed are unlikely to significantly influence infectivity where physical and biological movements are typically occurring at velocities of far higher magnitudes.

The speed of cercarial swimming studied under laboratory conditions is highly variable between species and different strains of the same species. Nevertheless, it is apparent that host searching strategies and target host groups broadly influence the speeds that cercariae can achieve. Locomotion is, therefore, an important variable determining infection success. Understanding cercarial swimming under more natural conditions would greatly enhance our understanding of the process of transmission and would be a subject worthy of further investigations.

**Supplementary material.** The supplementary material for this article can be found at <https://doi.org/10.1017/S0031182020001171>.

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