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

Neil J. Morley

School of Biological Sciences, Royal Holloway, University of London, Egham, Surrey, TW20 0EX, UK.

Email: n.morley@rhul.ac.uk

Tel.: +44 (0)1784 443186

Fax: +44 (0)1784414224

Running title:

Cercarial swimming speed and trematode transmission

**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 a 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. The present 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 mimcry’ strategies. Vertebrate-infecting cercariae swim faster than those infecting invertebrates with fish targeting fish demonstrating the highest locomotion rates and those targeting arthropods the slowest speeds. The adaptions of individual cercarial swimming speeds to biological variables and their interactions with the physical processes of aquatic habitats are discussed.

**Key words:**

Cercariae, swimming, locomotion, behaviour, speed, transmission

**Key findings**

Cercarial swimming speeds are related to tail morphology

Swimming speeds are linked with host-searching strategies and target host species

Schistosome furcocercariae swim slower than other vertebrate-infecting furcocercariae

Swimming speeds are insufficient for chasing actively-moving target hosts

Swimming speeds may maintain a vertical but not a horizontal position in aquatic flows

**Introduction**

Transmission of trematodes from molluscan source hosts to the vertebrate or invertebrate target host is typically undertaken by a free-living larval stage known as a cercariae. These are lecithotropic larvae dependent on a glycogen store for energy utilisation and a 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 Dobrovolski, 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 in order 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 principle 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 Dobrovolski, 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 Dobrovolski, 2003). Swimming cercariae are highly manoeuvrable and able to perform a turn of speed of at least 70º/sec at temperatures as low as 5ºC (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 increasing the surface area and reduced the rate of sinking during periods of rest.

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 search’- 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 2-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 maintain 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 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 and. 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, more large scale examinations of cercarial swimming adaptations that might aid the transmission process have not been evaluated. The present 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 was 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’, ‘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 addition to mean swimming speeds each study was augmented with additional information that included 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). In order 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 Pearsons correlation. For the purposes of further analysis data was grouped according to either cercarial morphotype- furcocercariae (subgrouped as either schistosome, non-schistosome, or as a total), echinostome, xiphidiocercariae, pleurolophocerous 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, fish, molluscs, annelids, arthropods. The cercarial speed of designates within morphotype, host searching, and target host groups were analysed using one-way ANOVA. All data was analysed using SPSS statistical package.

**Results**

The swimming speed of cercariae varies extensively between species and ranges from 0.1 to 25.9 mm/sec (Supplementary table 1). Larger cercarial species swim at a faster speed than smaller ones (Pearson correlation 0.286, *P*= 0.017). Furthermore, there is a positive significant correlation for functional tail length and speed of cercariae (Pearson correlation 0.295, *P*= 0.014) but no relationship occurs between body length and locomotion rates (Pearson correlation 0.167, *P*= 0.171) indicating the key role of the tail in locomotion.

The majority of species in the database 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/sec (SD 7.026), these schistosomes swim at significantly slower mean speeds of 1.29 mm/sec (SD 0.881) (one-way ANOVA *P*= 0.029, F= 5.562). 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 not significantly faster (one-way ANOVA *P*= 0.078, F= 3.201) 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 becomes apparent (one-way ANOVA *P*= 0.008, F= 7.511).

The dataset includes a wide range of different cercarial morphotypes but only four groups (Furcocercariae, Echinostome, Xiphidiocercairae, Pleurolophous cercariae) have been studied extensively. Comparing the swimming speeds of these four morphotypes indicates that there is a slight significant difference between them (one-way ANOVA *P*= 0.049, F= 2.836; schistosomes excluded from furcocercariae group).

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 slight significant difference in the swimming speeds of cercariae utilising the different behaviour strategies (one-way ANOVA *P=* 0.050, F= 2.793, excluding schistosomes). This difference becomes more highly significant when ‘passive waiting’, represented by only two examples, is removed from the analysis (one-way ANOVA *P=* 0.031, F= 3.734, excluding schistosomes). Direct comparisons show that ‘active searching’ cercariae swim at a significantly slower speed compared to species demonstrating both ‘active waiting’ (one-way ANOVA *P*= 0.011, F= 6.927, excluding schistosomes) and ‘prey mimicry’ strategies (one-way ANOVA *P*= 0.022, F= 5.792). However, there are no significant differences between ‘active waiting’ and ‘prey mimicry’ strategies (one-way ANOVA *P*= 0.878, F= 0.024, excluding schistosomes).

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). Cercariae infecting vertebrates swim at significantly faster speeds than those infecting invertebrates (one-way ANOVA *P=* 0.040, F= 4.363) which is more pronounced when comparing only the speeds of cercariae infecting aquatic vertebrates compared to aquatic invertebrates (one-way ANOVA *P=* 0.014, F= 6.438). Cercariae targeting arthropods swim at the slowest speeds, significantly different from those infecting annelids (one-way ANOVA *P*= 0.002, F= 18.037) and molluscs (one-way ANOVA *P*= 0.002, F= 12.424). However there are no significant differences between the speeds of those species targeting molluscs and annelids (one-way ANOVA *P*= 0.243, F= 1.446).

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/sec, with a majority of species capable of swimming in excess of 2 mm/sec (Supplementary table 1). However, the wide variability in speeds of this group resulted in no significantly different locomotion from any other group.

**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.

The speeds that cercariae are capable of attaining is directly related to the functional tail length with longer or bifurcate tails capable of providing greater rates of locomotion. This is unsurprising and adds further confirmatory evidence that locomotion is the principle role of the cercarial tail as indicated previously e.g. Galaktionov and Dobrovolski (2003). 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 than other furcocercariae. 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 of cercariae is highly variable, whether compared across morphotypes, related target hosts, or even the same strain of species. Some of the intraspecies variations may be accounted for by differences in experimental protocols and conditions, particularly light intensity and temperature, 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).

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 are large inter-individual variability in swimming performances amongst clutches and even among siblings of a single clutch (Nanninga and Berumen, 2014). Indeed, Hiblish *et al.* (1999) calculated about a third of the variation in swimming speeds of mollusc veliger larvae may be genetic in origin. Populations of cercariae are also known to demonstrate wide genetic variations, the extent of which being dependent on the species and the origins of their production, sporocyst or redia, in the molluscan host (Semyenova *et al.* 2007). Such variation is known to effect cercarial biology (Lu *et al.* 2009, Berkhout *et al.* 2014) and can be influenced by environmental conditions particularly genotype-by-temperature interactions (Berkhout *et al.* 2014). Nevertheless, the significance of these differences in swimming speeds have 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 speed 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.

Nevertheless, some ‘active searching’ cercariae appear to be able to regulate their swimming speed over the duration of their free-living existence. Dixon (1984) found that cercariae of *Echinoparyphium recurvatum* and *Plagiorchis elegans*, which infect molluscs and insect larvae respectively, change their swimming speeds in close proximity to target hosts. *Echinoparyphium recurvatum* cercariae decrease their speed and increase their rate of turning as they approach a snail beginning at a distance of 5 mm thereby increasing the amount of time spent in the vicinity of the target host. In contrast, *P. elegans* cercariae adopt a two-phase change in swimming speed, slowing down between 5 and 10 mm from an insect larval host then increasing as the distance reduces to 5 mm or less. This slowing down would appear to initially allow for a greater time within the vicinity of the host before a burst of speed and increased rate of turning closer to the host either in response to or to overcome turbulence caused by its movements and thereby increase the probability of making contact with the host surface. Cable (1965) indicates that other plagiorchid cercariae that infect aquatic arthropods may also regulate their swimming speeds, slowing down in response to host respiratory currents that then allows the parasite to be carried to the gills where penetration occurs.

The swimming speed that individual cercarial species are able to attain 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 terrestrial vertebrates (Humans) predominating in the data set. It is apparent that cercariae infecting these two very different target hosts swim at different speeds. Human-infecting cercariae, which in the data set is restricted to *S. mansoni*, attain speeds ranging from 0.46-2.1 mm/sec whilst fish-infecting cercariae generally appear to be able to reach higher swimming velocities ranging from 0.48-25.9 mm/sec, with many species capable of speeds between 2 and 9 mm/sec. Aquatic birds are the other target host that cercariae utilise an ‘active waiting’ strategy although only two species, *Bilharzia polonica* (0.9 mm/sec) and *Trichobilharzia ocellata* (3.4 mm/sec) occur in the data set which despite having widely different speeds appear more comparable to speeds attained by human-infecting cercariae than fish-infecting ones. In contrast, the fastest recorded cercariae is *Transversotrema patialense* with a speed of 25.9 mm/sec, but this is an unusual species 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 such levels of locomotion.

Thus, cercariae that infect particular target host groups swim at different speeds, 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 mm/sec and can reach 5000 mm/sec (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 schistosome cercarial species, with relatively modest or slow swimming speeds that target terrestrial mammal hosts such as humans, and these vertebrates, although possessing the capacity to move swiftly through 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, it is possible that 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 is able to 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 in order 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 are able to achieve is also important for determining if these free-living parasites 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 1cm/min (0.17 mm/sec) would be able to perform active vertical movements irrespective of the strength of the local tidal currents which may attain horizontal speeds of 80 cm/sec but only vertical speeds of 0.1 mm/sec. Similarly, vertical currents are negligible in flowing freshwater habitats which are characterised by unidirectional horizontal currents of variable velocities dependent on the nature of the gradient and surface of the bed (Maitland, 1990). Nevertheless, vertical currents can reach a maximum of 0.6 mm/sec in still freshwater conditions found in lakes (Verber, 1967).

As most cercariae in the present study were capable of speeds in excess of 0.1 or 0.6 mm/sec 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 studied and commonly accepted (Fingerut *et al.* 2003; Fitzpatrick *et al.* 2016) and even though it is likely that these parasite stages 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 velocities 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 Reyns, 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 to marine and freshwater zooplankton.

Nevertheless, the relatively low swimming speed of most cercariae in relation to the horizontal water movements found in many environments suggests that these larval parasites are predominantly adapted not to physical variables but rather biological ones associated with their target hosts behaviour. 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 (Stycznyka-Jurewicz, 1966). The increased prevalence of trematode infections in freshwater molluscs found in small ponds compared to lakes (Zdarska, 1964; Stycznyka-Jurewicz, 1966, Faltýnková, 2005) would suggest that these environments may facilitate parasite transmission with free-living stages, although other factors 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 (Stycznka-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 (Stycznka-Jurewicz, 1966).

Nevertheless, studies undertaken with slow-swimming schistosomes in flowing water environments indicate peak infections within flowing water occur at mean velocities of 30 to 40 cm s-1 with slower velocities reducing the likelihood of contact with a target host and higher velocities dispersing the cercariae and interfering with their ability to penetrate (Jewsbury, 1985). Extreme turbulence, such as found associated with waterfalls or rivers with high velocity and flow volumes causes extensive damage to cercariae resulting in few successful infections (Upatham, 1973, 1974b). These velocities exceed the swimming speeds of schistosome cercariae by several magnitudes suggesting that they are unable to regulate their positions in such flowing-water environments, encountering hosts only by chance and that it is probably only after contacting and attaching to the host that the magnitude of flowing water velocities described by Jewsbury (1985) are able to influence infections.

Nevertheless, infection rates and worm burdens 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). The importance of static aquatic environments for parasite transmission, where the influence of physical processes are reduced, has been emphasised by Styczyaska-Jurewicz (1966). 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, although the rate of this drop appears to vary from one species to another (Rea and Irwin, 2001; Prokofiev, 2005). A declining rate of swimming speed as the cercariae age will affect its ability to maintain its position in the ‘host-space’ under the influence of water currents as well as contact and infect a target host. This may be an additional unappreciated factor in the reduced infectivity success of older cercariae (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), whilst assessing the swimming speeds of marine invertebrate larvae, considered thermal effects 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 10ºC change in temperature due to altered water viscosity. Changes in temperature and water viscosity have also been found to affect the swimming movements of *S. 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 was acquired from studies undertaken at a range of temperatures, typically between 15 and 25ºC. 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 individual 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 10ºC increases, which are normal thermal responses for ectothermic animals and have been previously determined to follow this pattern for trematode egg and cercarial development rates (Morley & Lewis, 2013, 2017). However, such changes in cercarial speed over different temperatures are unlikely to be sufficient to significantly influence host contact and penetration whilst under the influence of physical and biological variables which are typically occurring at velocities of far higher magnitudes in aquatic habitats.

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.

**Financial support**

This research received no specific grant from any funding agency, commercial or not-for-profit sectors.

**Conflicts of interest**

None

**Ethical standards**

Not applicable

**References**

**Anderson, RM, and Whitfield, PJ** (1975). Survival characteristics of the free-living cercarial population of the ectoparasitic digenean *Transversotrema patialensis* (Soparker, 1924). *Parasitology* **70**, 295-310. doi: 0.1017/S0031182000052082

**Beamish, FWH** (1978). Swimming capacity. InHoar, W.S., & Randall, D.J. (eds.) *Fish Physiology* Volume 7. London, UK: Academic Press, pp 101-187.

**Berkhout, BW, Lloyd, MM, Poulin, R, and Studer, A** (2014). Variation among genotypes in response to increasing temperature in a marine parasite: Evolutionary potential in the face of global warming? *International Journal for Parasitology* **44**, 1019-1027. doi: 10.1016/j.ijpara.2014.07.002

**Cable, RM** (1965). “Thereby hangs a tail”. *Journal of Parasitology* **51**, 3-12. doi: 10.2307/3275635

**Chapman, HD, and Wilson, RA** (1973). The propulsion of the cercariae of *Himasthla secunda* (Nicoll) and *Cryptocotyle lingua. Parasitology* **67**, 1-15. doi: 10.1017/S0031182000046242

**Combes, C, Fournier, A, Mone, H, and Theron, A** (1994). Behaviours in trematode cercariae that enhance parasite transmission: patterns and processes. *Parasitology* **109**, S3-S13. doi.org/10.1017/S0031182000085048

**Dixon, MD** (1984). *Strategies of host location employed by larval trematodes*. PhD thesis, University of York, York, UK.

**Faltýnková, A** (2005). Larval trematodes (Digenea) in molluscs from small water bodies near České Budějovice, Czech Republic. *Acta Parasitologica* **50**, 49-55.

**Fingerut, JT, Zimmer, CA, and Zimmer, RK** (2003). Larval swimming overpowers turbulent mixing and facilitates transmission of a marine parasite. *Ecology* **84**, 2502-2515. doi.org/10.1890/02-4035

**Fitzpatrick, KB, Smith, NF, and Cohen, JH** (2016). Swimming behavior of marine cercariae: Effects of gravity and hydrostatic pressure. *Journal of Experimental Marine Biology & Ecology* **476**, 8-14. doi.org/10.1016/j.jembe.2015.12.002

**Galaktionov, K, and Dobrovolskij, A** (2003). *The Biology and evolution of trematodes: An essay on the biology, morphology, life cycles, transmissions, and evolution of digenetic trematodes.* Dordrecht, Holland: Kluwer.

**Haas, W** (1969). Reizphysiologische Untersuchungen an cercarien von *Diplostomum spathaceum. Zeitschrift fur Vergleichende Physiologie* **64**, 254-287. doi.org/10.1007/BF00340546

**Haas, W** (1994). Physiological analyses of host-finding behaviour in trematode cercariae: Adaptations for transmission success. *Parasitology* **109**, S15-S29. doi.org/10.1017/S003118200008505X

**Hiblish, TJ, Sasada, K, Eyster, LS, and Pechenik, JA** (1999). Relationship between rates of swimming and growth in veliger larvae: genetic variance and covariance. *Journal of Experimental Marine Biology & Ecology* **239**, 183-193. doi.org/10.1016/S0022-0981(99)00009-X

**Horne, AJ, and Goldman, CR** (1994). *Limnology.* 2nd Edn. New York USA: McGra-Hill, Inc.

**Jewsbury, JM** (1985). Effects of water velocity on snails and cercariae. *Parasitology Today* **1**, 116-117. doi.org/10.1016/0169-4758(85)90009-2

**Lu, D-B, Wang, T-P, Rudge, JW, Donnelly, C.A, Fang, G-R, and Webster, JP** (2009). Evolution in a multi-host parasite: Chronobiological circadian rhythm and population genetics of *Schistosoma japonicum* cercariae indicates contrasting definitive host reservoirs by habitat. *International Journal for Parasitology* **39**, 1581-1588. doi.org/10.1016/j.ijpara.2009.06.003

**Maitland, P** (1990). *Biology of fresh waters.* 2nd edition. Glasgow, UK: Blackie & son Ltd.

**Mikheev, VN, Pasternak, AF, Valtonen, ET, and Taskinen, J** (2014). Increased ventilation by fish leads to a higher risk of parasitism. *Parasites & Vectors* **7**, 281. doi.org/10.1186/1756-3305-7-281

**Mileikovsky, SA** (1973). Speed of active movement of pelagic larvae of marine invertebrates and their ability to regulate their vertical position. *Marine Biology* **23**, 11-17. doi.org/10.1007/BF00394107

**Morley, NJ** (2012). Cercariae (Platyhelminthes: Trematoda) as neglected components of zooplankton communities in freshwater habitats. *Hydrobiologia* **691**, 7-19. doi.org/10.1007/s10750-012-1029-9

**Morley, NJ and Lewis, JW** (2013). Thermodynamics of cercarial development and emergence in trematodes. *Parasitology* **140**, 1211-1224. doi.org/10.1017/S0031182012001783

**Morley, NJ, and Lewis, JW** (2017). Thermodynamics of egg production, development and hatching in trematodes. *Journal of Helminthology* **91**, 284-294. doi.org/10.1017/S0022149X16000249

**De Montaudouin, X, Wgeberg, AM, Jensen, KT, and Sauriau, PG** (1998). Infection characteristics of *Himasthla elongata* cercariae in cockles as a function of water current. *Diseases of Aquatic Organisms* **34**, 63-70. doi:10.3354/dao034063

**Nanninga, GB, and Berumen, ML** (2014). The role of individual variation in marine larval dispersal. *Frontiers in Marine Science* **1**, 71. doi.org/10.3389/fmars.2014.00071

**Nguyen, KH, Gemmell, BJ, & Rohr, JR** (2020). Effects of temperature and viscosity on miracidial and cercarial movement of *Schistosoma mansoni*: ramifications for disease transmission. *International Journal for Parasitology* **50**, 153-159. doi.org/10.1016/j.ijpara.2019.12.003

**Pechenik, JA, and Fried, B** (1995). Effect of temperature on survival and infectivity of *Echinostoma trivolvis* cercariae: a test of the energy limitation hypothesis. *Parasitology* **111**, 373-378. doi.org/10.1017/S0031182000081920

**Peters, RH** (1983). *The ecological implications of body size.* Cambridge, UK: Cambridge University Press.

**Pineda, J, and Reyns, N** (2018). Larval transport in the coastal zone: Biological and physical processes. In Carrier, T.J., Reitzel, A.M., & Heyland, A. (eds.) *Evolutionary ecology of marine invertebrate larvae*. Oxford UK: Oxford University Press,pp. 145-163.

**Prokofiev, VV** (2005). Patterns of swimming of cercariae in some Trematode species. *Parazitologiya* **39**, 204-220. [In Russian]

**Prokofiev, VV, and Galaktionov, KV** (2009). Strategies of search behaviour in trematode cercariae. *Proceedings of the Zoological Institute of the Russian Academy of Sciences* **313**, 308-318. [In Russian]

**Rea, JG, and Irwin, SWB** (1992). The effects of age, temperature, light quality and wavelength on the swimming behaviour of the cercariae of *Cryptocotyle lingua* (Digenea: Heterophyidae). *Parasitology* **105**, 131-137. doi.org/10.1017/S0031182000073789

**Rea, JG, and Irwin, SWB** (1995). The effects of age, temperature and shadow stimuli on activity patterns of the cercariae of *Cryptocotyle lingua* (Digenea: Heterophyidae). *Parasitology* **111**, 95-101. doi.org/10.1017/S0031182000064647

**Rea, JG, and Irwin, SWB** (2001). Fun with flukes: the use of ICT in the study of larval trematode behaviour. *Journal of Biological Education* **36**, 35-41. doi.org/10.1080/00219266.2001.9655793

**Santos, MJ, Karvonen, A, Pedro, JC, Faltynkova, A, Seppala, O, and Valtonen, ET** (2007). Qualitative and quantitative behavioural traits in a community of furcocercariae trematodes: Tools for species separation? *Journal of Parasitology* **93**, 1319-1323. doi.org/10.1645/GE-1225.1

**Selbach, C, and Poulin, R** (2018). Parasites in space and time: a novel method to assess and illustrate host-searching behaviour of trematode cercariae. *Parasitology* **145**, 1469-1474. doi.org/10.1017/S0031182018000288

**Semyenova, SK, Khrisanfova, GG, Korsunenko, AV, Voronin, MV, Beer, SV, Vodvanitskaya, SV, Serbina, EA, and Yurlova, NI** (2007). Multilocus variation in cercariae, parthenogenetic progeny of different species of the class Trematoda. *Doklady Biological Sciences* **414**, 235-238. doi.org/10.1134/S0012496607030192

**Soldánová, M, Faltýnková, A, Scholtz, T, and Kostadinova, A** (2011). Parasites in a man-made landscape: contrasting patterns of trematode flow in a fishpond area in central Europe. *Parasitology* **138**, 789-807. doi.org/10.1017/S0031182011000291

**Stables, JN, and Chappell, LH** (1986). *Diplostomum spathaceum* (Rud. 1819): effects of physical factors on the infection of rainbow trout (*Salmo gairdneri*) by cercariae. *Parasitology* **93**, 71-79. doi.org/10.1017/S0031182000049830

**Styczyska-Jurewicz, E** (1966). Astatic-water bodies as characteristic habitat of some parasites of man and animals. *Verhandlungen des Internationalen Vereinigung fur theoretische und angewandte Limnologie* **16**, 604-611. doi.org/10.1080/03680770.1965.11895737

**Upatham, ES** (1973). Effect of a waterfall on the infectivity of St. Lucian *Schistosoma mansoni. Transactions of the Royal Society of Tropical Medicine & Hygiene* **67**, 884-885. doi.org/10.1016/0035-9203(73)90022-9

**Upatham, ES** (1974a). Studies on the effects of cercarial concentration and length of exposure on the infection of mice by St Lucian *Schistosoma mansoni* cercariae in a natural running-water habitat. *Parasitology* **68**, 155-159. doi.org/10.1017/S0031182000045698

**Upatham, ES** (1974b). Dispersion of St Lucian *Schistosoma mansoni* cercariae in natural standing and running waters determined by cercaia counts and mouse exposure. *Annals of Tropical Medicine & Parasitology* **68**, 343-352. doi.org/10.1080/00034983.1974.11686957

**Verber, JL** (1967). *Lake currents*. *Technical Report of the Federal Water Pollution Control Administration*. Chicago, USA: Federal Water Pollution Control Administration.

**Whyte, SK, Secombes, C.J, and Chappell, LH** (1991). Studies on the infectivity of *Diplostomum spathaceum* in rainbow trout (*Oncorhynchus mykiss*). *Journal of Helminthology* **65**, 169-178. doi.org/10.1017/S0022149X0001066X

**Young, CM** (1995). Behavior and locomotion during the dispersal phase of larval life. In McEdward, L. (ed.), *Ecology of Marine Invertebrate larvae*. Boca Raton, USA: CRC Press, pp. 249-277.

**Zdárská, Z** (1964). The influence of the biotope on the extensity of invasion of freshwater snails by the larval stages of trematodes in conditions of Czechoslovakia. In Ergens, R., and Rysavy, B. (eds.) *Parasitic worms and aquatic conditions*. Prague, Czech Republic: Czechoslovak Academy of Sciences, pp. 69-72.

|  |  |  |  |
| --- | --- | --- | --- |
| Morphotype | N | Mean speed (mm/sec) | SD |
| 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 |
| Philophthalmidea | 2 | 0.49 | 0.579 |
| Cotylocercous | 1 | 1.00 | - |
| Trichocercous | 1 | 3.60 | - |
| ‘Large-tailed monostome’ | 1 | 3.50 | - |

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

|  |  |  |  |
| --- | --- | --- | --- |
| Host-searching behaviour | N | Mean speed (mm/sec) | SD |
| 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 |

Table 2. Swimming speeds of cercariae designated according to host-searching behaviour. Host-searching strategies grouped according to Prokofiev & Galaktionov (2009).

|  |  |  |  |
| --- | --- | --- | --- |
| Target host | N | Mean speed (mm/sec) | SD |
| Vertebrates |  | 35 | 3.39 | 4.583 |
|  | 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 |

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