HELMINTHOLOGY - SHORT COMMUNICATION

Temperature does not influence functional response of amphipods consuming different trematode prey

Ana Born-Torrijos[1] · Rachel A. Paterson[2,3] · Gabrielle S. van Beest[1,4] · Jessica Schwelm[5] · Tereza Vyhlídalová[6] · Eirik H. Henriksen[7] · Rune Knudsen[7] · Roar Kristoffersen[7] · Per-Arne Amundsen[7] · Miroslava Soldánová[1]

Abstract

Direct consumption on free-living cercariae stages of trematodes by non-host organisms interferes with trematode transmission and leads to reduced infections in the next suitable hosts. Consumer functional responses provide a useful tool to examine relationships between consumption rates and ecologically relevant prey densities, whilst also accounting for abiotic factors that likely influence consumption rates. We investigated how temperature influences the consumer functional response of the amphipod *Gammarus lacustris* towards the cercariae of three freshwater trematodes (*Diplostomum*, *Apatemon* and *Trichobilharzia*). Amphipods displayed different functional responses towards the parasites, with Type II responses for *Diplostomum* and Type I responses for *Apatemon* prey. Temperature did not alter the consumption rate of the amphipod predator. *Trichobilharzia* was likely consumed at similar proportions as *Diplostomum*; however, this could not be fully evaluated due to low replication. Whilst Type II responses of invertebrate predators are common to various invertebrate prey types, this is the first time a non-filter feeding predator has been shown to exhibit Type I response towards cercarial prey. The prey-specific consumption patterns of amphipods were related to cercarial distribution in the water column rather than to the size of cercariae or temperature influence. The substantial energy flow into food webs by non-host consumer organisms highlights the importance of understanding the mechanisms that modulate functional responses and direct predation in the context of parasitic organisms.

Keywords Predator-prey · Cercariae · Transmission interference · *Gammarus lacustris*

Introduction

Trematodes are highly abundant parasitic organisms in aquatic ecosystems, with the biomass of their free-living life stages often equivalent to the most abundant insect orders (Preston et al. 2013). The immense mass of trematodes is largely attributed to the asexual production and daily release of thousands of free-living infective cercariae (larvae) from their first

---

✉ Miroslava Soldánová
soldanova@paru.cas.cz

1 Institute of Parasitology, Biology Centre, Czech Academy of Sciences, 37005 České Budějovice, Czech Republic

2 School of Biosciences, Cardiff University, Cardiff CF10 3AX, UK

3 The Norwegian Institute for Nature Research, P. O. Box 5685 Torgarden, NO-7485 Trondheim, Norway

4 Cavanilles Institute for Biodiversity and Evolutionary Biology, Science Park, University of Valencia, P. O. Box 22085, 46071 Valencia, Spain

5 Aquatic Ecology and Centre for Water and Environmental Research, University of Duisburg-Essen, Universitätsstraße 5, D-45141 Essen, Germany

6 Faculty of Science, University of South Bohemia in České Budějovice, Branišovská 31, 37005 České Budějovice, Czech Republic

7 Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, N9037 Tromsø, Norway

intermediate molluscan hosts (Preston et al. 2013; Soldánová et al. 2016). Whilst successful transmission of cercariae is essential to complete the trematode's life cycle, direct consumption of cercariae by non-host organisms can lead to reduced transmission to their next suitable host (Johnson et al. 2010). The loss of cercariae by consumption from different organisms has been reported (e.g. rotifers, molluscs, insect larvae, fishes; Orlofske et al. 2015; Welsh et al. 2017), but its importance appears to be largely overlooked despite the significant contribution parasites may have to energy flow through food webs when being consumed by non-host organisms (Thieltges et al. 2008; Johnson et al. 2010). Cercarial consumption may also be context dependent, influenced by environmental conditions such as temperature or habitat complexity, in addition to the impact of the size and behaviour of the parasite and the predator (e.g. Orlofske et al. 2015; Selbach et al. 2019).

Temperature, in particular, is recognised as a major driver of both predator-prey and parasite transmission dynamics as it simultaneously influences both consumption rates (e.g. Goedknegt et al. 2015; Laverty et al. 2017) and the production of free-living parasite stages (Poulin 2006). In order to understand how temperature may affect parasite transmission through its influence on parasite consumption by non-hosts, it is essential to examine potential predator-prey interactions. Consumer functional responses (hereafter FR) provide a useful tool to examine relationships between consumption rates and ecologically relevant prey densities (e.g. Holling 1959; Jeschke et al. 2004), and thus increasing our understanding of the impact predators have on prey populations (e.g. Bovy et al. 2015; Paterson et al. 2015). Here, we address the potential consumption of trematode cercariae by the omnivorous amphipod *Gammarus lacustris* G.O. Sars, 1863 (Malacostraca, Gammaridae), one of the most common macroinvertebrates in European subarctic lakes. This amphipod co-occurs in the nearshore benthic habitat with the lymnaeid snail *Radix balthica* L. (Gastropoda, Pulmonata), which release dense aggregations of larval trematodes, including *Diplostomum* Poirier, 1886 (Diplostomidae), *Apatemon* Szidat, 1928 (Strigeidae) and *Trichobilharzia* Skrjabin and Zakharow, 1920 (Schistosomatidae) (Soldánová et al. 2017). We utilised a FR approach to investigate whether the consumption of these three trematode prey taxa by *G. lacustris* was altered by temperature variation.

Materials and methods

Study organisms and maintenance

All study organisms were obtained from Takvatn, a subarctic lake in northern Norway (69° 07′ N, 19° 05′ E), during August and October 2017 and 2018. *Gammarus lacustris* amphipods

($n = 340$ males; length [pereon + pleosome] mean ± SD: 11.9 ± 1.7 mm) were collected from the lake substrate (4–10-m depth) by dredge net with a rectangular metal frame (20 × 35-cm opening, 1-mm mesh), whereas *R. balthica* snails were hand-picked from the littoral zone (< 1-m depth). Amphipod sex was confirmed under the microscope. Study organisms were acclimatised for 3–10 days in a climatic chamber, with light:dark (20:4, 10:14 h) and temperature (13, 6 °C) conditions reflecting measures taken in August and October, respectively (data loggers Onset HOBO UA-002-64 Pendant 64K, MA, USA). Amphipods were maintained in 6-L aquaria with aerated lake water (replaced every 72 h) and provided ad libitum with natural prey (e.g., copepods, cladocerans), whereas snails were individually maintained in 40-mL beakers with lake water (replaced daily) and provided with lettuce (*Lactuca sativa* L.).

Snails were screened for trematode infections by placing each beaker under a light source for 24 h to stimulate cercarial emergence, with taxa identified in vivo (Soldánová et al. 2017). Three trematode genera that do not infect amphipods were selected for the experimental assays, i.e. *Trichobilharzia*, *Apatemon* and *Diplostomum*. *Trichobilharzia franki* haplotype "peregra" (hereafter *Trichobilharzia*) has a two-host life cycle with birds as definitive hosts, whereas *Apatemon* and *Diplostomum* have a three-host life cycle, with fish and piscivorous birds as second intermediate and definitive hosts, respectively (Soldánová et al. 2017). The three trematodes display intermittent swimming periods, with *Diplostomum* and *Trichobilharzia* tending to accumulate close to the water surface in relation to the light intensity and *Apatemon* continuously swimming with only short pauses. However, *Apatemon* exhibits nocturnal emergence, whereas *Diplostomum* and *Trichobilharzia* exhibit diurnal emergence (Bell 1996; Karvonen et al. 2004; Haas et al. 2008; Soldánová et al. 2016). Cercarial size also differed between these trematodes (*Apatemon* ∼ 530 μm, *Diplostomum* ∼ 690 μm, *Trichobilharzia* ∼ 940 μm; total length, $n = 33$, 31 and 23 live cercariae specimens, respectively).

To obtain cercarial prey for the experiment, snails were individually incubated in 40 mL of filtered lake water under a light source (*Trichobilharzia*, *Diplostomum*) or covered with aluminium foil to mimic night-time (*Apatemon*). Host-induced variability in cercariae (e.g. maturity or size) was accounted for by preparing a pool of freshly emitted cercariae from multiple infected snails for each trematode genus. Thereafter, cercariae were individually pipetted into a plastic beaker with a small volume of filtered lake water (10 mL) in densities required for the FR experiment. All cercariae were the same age (< 4 h), alive and active when offered to the predator.

Experimental design

A randomised, fully factorial design was used to test the effect of temperatures relevant to the studied system (13, 6 °C, average water temperatures in August and October, respectively) on cercarial prey consumption. Each amphipod was supplied with one of eight prey densities (2, 4, 6, 10, 20, 50, 70 or 100 cercariae) from one trematode genus. Each treatment combination was replicated six times with the exception of *Trichobilharzia*, which was replicated twice due to the low availability of *Trichobilharzia*-infected snails.

Prior to each assay, amphipods were held without food for 48 h to standardise satiation levels preceding exposure to cercarial prey. Each amphipod was randomly assigned to an individual experimental arena (diameter 55 mm) containing 60 mL of filtered lake water, which was placed on a black surface to mimic the amphipod's natural habitat. Amphipods were provided with a given density of cercariae prey from the prepared beakers, which were rinsed twice with filtered lake water. Consumed cercariae were not replaced during the assay (non-replacement design), with amphipods removed after 30 min. Unconsumed cercariae were counted by filtering the water from each arena through a 12-μm-pore filter membrane (Whatman, Nuclepore Track-Etch Membrane, Sigma-Aldrich), which was then fixed and stained in a 70% ethanol and carmine solution prior to counting cercariae under a stereomicroscope. Control replicates ($n = 6$ *Apatemon* and *Diplostomum*, $n = 2$ *Trichobilharzia*) in the absence of amphipods were run for each prey density to assess the potential loss of cercariae due to the filtration procedure (0–13 *Apatemon*, 0–21 *Diplostomum*, 0–22 *Trichobilharzia* cercariae lost, Supplementary Table S1), with the number of prey consumed by each amphipod adjusted by the mean loss of prey specific to each trematode genus and cercariae density. Prey survival (in terms of vital/mobile cercariae) in the absence of predators was 100%.

All amphipods were maintained for 48 h post assay in individual arenas under the same conditions. Amphipods which died or moulted prior to, during or post assay were replaced with another randomly selected amphipod, as moulting may influence the feeding behaviour of *Gammarus* (Bovy et al. 2015). Amphipods were then euthanised by immersion in carbonated water.

Statistical analysis

All statistical analyses were completed in R (R Core Team 2017, version 3.6.1). The presence of outliers and/or differences in prey consumption rates resulting from the experimental timeframe was determined by visual inspection of raw data plots, with one outlier detected in the *Diplostomum* dataset at the 10-prey density (Supplementary Fig. S1a).

To determine which FR model type (I, II or III) best described the relationship between cercariae density and the number of cercariae consumed, logistic regressions were fitted to each amphipod-trematode combination using frair::frair_test (version 0.5.100; Pritchard et al. 2017). Type I FRs assume a linear relationship between cercariae density and the number of cercariae consumed. Type II FRs (decreasing proportional consumption with increasing prey density) are indicated by a significant negative first-order term, whereas Type III FRs are indicated by significant positive first-order term, then a significant negative second-order term (initial increase then decrease in proportional consumption; Juliano 2001; Pritchard et al. 2017). Whilst parameters *a* (capture/attack rate), *h* (handling time, i.e. time spent subjugating, ingesting and digesting each prey item) and *T* (experimental time) describe a Type II response, Type I response show negligible *h*, being thus characterised by *a* and *T* only. The fixed parameter *T* was set to 0.5/24 (30 min), and after starting estimates had been provided, FR models were fitted using maximum likelihood estimation (MLE) by using frair::frair_fit (Pritchard et al. 2017). Due to the low number of replicates in *Trichobilharzia* prey, FR analyses could not be run for this prey and results are presented as a plot in Supplementary Fig. S1c. A single model was fitted for each trematode-amphipod dataset, including data at 6 and 13 °C, to test for differences in cercariae consumption between temperatures. Amphipods displayed different FR types towards each prey genus, and therefore, model parameters between these types could not be compared. A Type II FR was detected with *Diplostomum*, whereas in the analyses involving *Apatemon*, frair_test did not show any evidence of Type II or III FRs. Raw data comparing consumed prey or proportion of consumed prey across densities were plotted to check the fitting of the *Apatemon* data to a Type I FR. To visualise the uncertainty around the fitted FRs, bootstrapping ($n = 1500$) was used to construct 95% confidence intervals.

Results and discussion

Amphipods showed different consumption rates when preying on *Diplostomum* and *Apatemon*, with higher proportion of cercariae consumed at low prey densities (< 10 prey densities) and a slight decrease in consumption at 70- and 100-*Diplostomum* prey density. However, the proportion of consumed cercariae is similar between temperatures within the same prey genera. Raw data suggests that amphipods consumed *Trichobilharzia* cercariae at similar proportions to *Diplostomum*; however, this could not be fully evaluated for *Trichobilharzia* due to low replication. Raw data and percentage of consumed cercariae at each amphipod-prey combination are summarised in Supplementary Table S2.

In the current study, amphipods, namely *G. lacustris*, for the first time have been shown to efficiently consume trematode cercariae, potentially constituting an additional foraging resource for this abundant and widespread freshwater crustacean. The amphipods displayed Type II FRs towards *Diplostomum* at both temperatures (logistic regressions; Fig. 1a; Supplementary Table S3), which are commonly observed in gammarids and other invertebrates consuming various invertebrate prey types (e.g. Jeschke et al. 2004; Bovy et al. 2015; Wasserman et al. 2016; Iltis et al. 2018). In contrast, the consumption of *Apatemon* prey at both temperatures could best be described by a Type I FR, as the proportion of prey consumed was not modified by increasing prey density (Fig. 1b; Supplementary Fig. S2). Type I FRs assume a linear relationship between prey density and consumption and are usually restricted to filter feeding species (Jeschke et al. 2004). Predators showing Type II and Type III FRs typically exhibit long handling time h of their prey, whilst those displaying a Type I FR show negligible handling time h and fulfil the satiation condition. This means unless their gut is completely filled, consumers should search for food at a maximal rate with maximal effort, thus likely spending longer time foraging (Jeschke et al. 2004). Even if non-filter feeders would neither fulfil the handling nor the satiation condition described for Type I FRs, our data show for the first time that a non-filter feeding predator may also exhibit a Type I FR towards specific cercarial prey. Future experiments should include higher *Apatemon* prey densities to determine when the saturation point is reached.

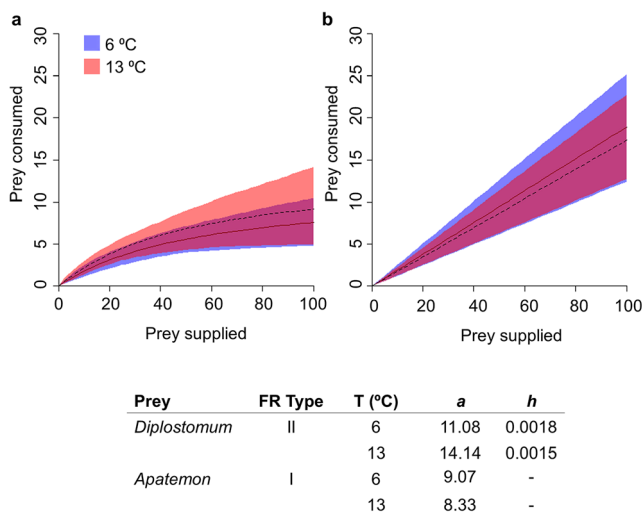Differences in FR type depending on the cercarial prey genera consumed by *G. lacustris* suggest that prey-related traits could be affecting their predation risk (e.g. size or behaviour, Orlofske et al. 2015; Selbach et al. 2019). Jeschke et al. (2004) showed that in addition to the low handling time and satiation conditions typically associated with Type I FRs, invertebrate consumers must also be relatively large compared to their food. The size difference between *Diplostomum* and *Apatemon* is roughly 160 μm and should not have a major effect on the handling time displayed by amphipods. However, even if the relative predator/prey size of *G. lacustris* - *Apatemon* would set the limit to justify a Type I response according to the size condition shown by Jeschke et al. (2004), other factors linked to *Apatemon*'s cercarial behaviour or distribution in the water column might enable *G. lacustris* to continuously feed on them. *Gammarus lacustris* remains on or close to the bottom substrate during the day, swimming throughout the water column at night, mostly feeding on zooplankton (Wilhelm and Schindler 1999). Whilst both *Apatemon* and *Diplostomum* perform similar swimming behaviour, *Diplostomum* tends to occupy a position in the upper water column (Haas et al. 2008), and *Apatemon* likely swims faster (Santos et al. 2007; Selbach and Poulin 2018) and rests for shorter periods (Bell 1996) closer to intermediate positions of the water column (pers. obs.). The continuous movement and shorter distance to *Apatemon* prey may likely facilitate a constant consumption by benthic dwelling *G. lacustris* visual predators.

The overlapping 95% confidence intervals indicated that temperature did not alter FRs of amphipods towards any of the trematode prey (Fig. 1), even though FR attack rate a differed significantly between temperatures for amphipods preying on *Diplostomum* (Supplementary Table S4). Our results thus indicate a low impact of temperature on the consumption of cercarial prey, similar to previously reported for other invertebrate predator-prey systems (e.g. Paterson et al. 2015; Wasserman et al. 2016), but contrasting what was observed in gammarids by Laverty et al. (2017). Laverty et al. (2017) showed an increased prey consumption at increased temperatures, but their higher temperature range (11 and 20 °C vs current study 6 and 13 °C) may have triggered this change in consumption rate. Furthermore, the larger prey sizes used in their experiment (0.4–0.8 cm) may have altered the temperature impact on the predator's FR.

Cercarial emergence patterns, as well as activity and survival rates, can be species-specific and/or temperature-dependent (Poulin 2006). Therefore, the absence of the ambient temperature influences on cercariae consumption may demonstrate the ability for amphipods to exploit the different emergence and active swimming periods intrinsic to *Diplostomum* and *Apatemon* throughout the year (Bell 1996; Karvonen et al. 2004). Nevertheless, the most profound impact could be expected on the *Diplostomum* population, as Type II FRs are considered to have larger implications for prey populations, potentially resulting in local prey extinction

Prey	FR Type	T (ºC)	a	h
Diplostomum	II	6	11.08	0.0018
		13	14.14	0.0015
Apatemon	I	6	9.07	-
		13	8.33	-

Fig. 1 The effects of temperature (6 and 13 °C) on the consumer functional response of *Gammarus lacustris* amphipods towards **a** *Diplostomum* (Type II) and **b** *Apatemon* (Type I) cercariae prey. Lines indicate mean functional response, and coloured bars are 95% confidence intervals (blue, 6 °C; pink, 13 °C). Attack rate a and handling time h are shown by cercarial prey and temperature (T)

because high proportions of prey are consumed at low densities (Hassell 1978).

For the first time, a Type I FR has been revealed for a non-filter feeder species. The likely constant consumption of *Apatemon* by amphipods represents a continuous energetic source for this non-host organism, even when different prey densities are available. Therefore, the increased consumption rate and thus energy profit per unit time that amphipods gain when preying on intermediate and high abundances of *Apatemon*, in contrast to the lower predation on *Diplostomum*, might likely impact the energy transfer through the food web, making *Apatemon* a more profitable prey for amphipods. Further FR experiments on large-bodied cercariae such as *Trichobilharzia* might help to understand the role of cercarial size for FR types. Investigating the mechanisms that mediate changes in FRs and direct predation has important implications for trematode population and disease dynamics, as well as for ecosystem energetics.

Compliance with ethical standards

Competing interests The authors declare that they have no competing interests.

References

Bell AS (1996) Studies on the biosystematics and biology of strigeids (Digenea) parasitic in freshwater fish. PhD Dissertation, University of Stirling

Born-Torrijos A, Paterson RA, van Beest GS, Schwelm J, Vyhlídalová T, Henriksen EH, Knudsen R, Kristoffersen R, Amundsen PA, Soldánová M (2020) FR_GammarusPredation, Data from: Temperature does not influence functional response of amphipods consuming different trematode prey. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.pzgmsbcj4

Bovy HC, Barrios-O'Neill D, Emmerson MC, Aldridge DC, Dick JT (2015) Predicting the predatory impacts of the "demon shrimp" *Dikerogammarus haemobaphes*, on native and previously introduced species. Biol Invasions 17:597–607. https://doi.org/10.1007/s10530-014-0751-9

Goedknegt MA, Welsh JE, Drent J, Thieltges DW (2015) Climate change and parasite transmission: how temperature affects parasite infectivity via predation on infective stages. Ecosphere 6:96. https://doi.org/10.1890/ES15-00016.1

Haas W, Beran B, Loy C (2008) Selection of the hosts' habitat by cercariae: from laboratory to the field. J Parasitol 94:1233–1238. https://doi.org/10.1645/GE-1192.1

Hassell MP (1978) A basic model. In: Hassell M (ed) The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton, pp 12–27

Holling CS (1959) Some characteristics of simple types of predation and parasitism. Can Entomol 91:385–398. https://doi.org/10.4039/Ent91385-7

Iltis C, Spataro T, Wattier R, Médoc V (2018) Parasitism may alter functional response comparisons: a case study on the killer shrimp *Dikerogammarus villosus* and two non-invasive gammarids. Biol Invasions 20:619–632. https://doi.org/10.1007/s10530-017-1563-5

Jeschke JM, Kopp M, Tollrian R (2004) Consumer food systems: why type I functional responses are exclusive to filter feeders. Biol Rev 79:337–349. https://doi.org/10.1017/s1464793103006286

Johnson PTJ, Dobson A, Lafferty KD, Marcogliese D, Memmott J, Orlofske SA, Poulin R, Thieltges DW (2010) When parasites become prey: ecological and epidemiological significance of eating parasites. Trends Ecol Evol 25:362–371. https://doi.org/10.1016/j.tree.2010.01.005

Juliano SA (2001) Non-linear curve fitting: predation and functional response curves. In: Scheiner SM, Gurevitch J (eds) Design and analysis of ecological experiments. Oxford University Press, Oxford, pp 178–196

Karvonen A, Kirsi S, Hudson PJ, Valtonen ET (2004) Patterns of cercarial production from *Diplostomum spathaceum*: terminal investment or bet hedging? Parasitology 129:87–92. https://doi.org/10.1017/S0031182004005281

Laverty C, Brenner D, McIlwaine C, Lennon JJ, Dick JTA, Lucy FE, Christian KA (2017) Temperature rise and parasitic infection interact to increase the impact of an invasive species. Int J Parasitol 47:291–296. https://doi.org/10.1016/j.ijpara.2016.12.004

Orlofske SA, Jadin RC, Johnson PTJ (2015) It's a predator-eat-parasite world: how characteristics of predator, parasite and environment affect consumption. Oecologia 178:537–547. https://doi.org/10.1007/s00442-015-3243-4

Paterson RA, Dick JTA, Pritchard DW, Ennis M, Hatcher MJ, Dunn AM (2015) Predicting invasive species impacts: a community module functional response approach reveals context dependencies. J Anim Ecol 84:453–463. https://doi.org/10.1111/1365-2656.12292

Poulin R (2006) Global warming and temperature-mediated increases in cercarial emergence in trematode parasites. Parasitology 132:143–151. https://doi.org/10.1017/S0031182005008693

Preston DL, Orlofske SA, Lambden JP, Johnson PTJ (2013) Biomass and productivity of trematode parasites in pond ecosystems. J Anim Ecol 82:509–517. https://doi.org/10.1111/1365-2656.12030

Pritchard DW, Paterson RA, Bovy HC, Barrios-O'Neill D (2017) frair: an R package for fitting and comparing consumer functional responses. Methods Ecol Evol 8:1528–1534. https://doi.org/10.1111/2041-210X.12784

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Santos MJ, Karvonen A, Pedrot JC, Faltýnková A, Seppälä O, Valtonen ET (2007) Qualitative and quantitative behavioral traits in a

community of furcocercariae trematodes: tools for species separation? J Parasitol 93:1319–1323. https://doi.org/10.1645/GE-1225.1

Selbach C, 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. https://doi.org/10.1017/S0031182018000288

Selbach C, Rosenkranz M, Poulin R (2019) Cercarial behavior determines risk of predation. J Parasitol 105:330–333. https://doi.org/10.1645/18-165

Soldánová M, Selbach C, Sures B (2016) The early worm catches the bird? Productivity and patterns of *Trichobilharzia szidati* cercarial emission from *Lymnaea stagnalis*. PLoS One 11:e0149678. https://doi.org/10.1371/journal.pone.0149678

Soldánová M, Georgieva S, Roháčová J, Knudsen R, Kuhn JA, Henriksen EH, Siwertsson A, Shaw JC, Kuris AM, Amundsen P-A, Scholz T, Lafferty KD, Kostadinova A (2017) Molecular analyses reveal high species diversity of trematodes in a sub-Arctic lake. Int J Parasitol 47:327–345. https://doi.org/10.1016/j.ijpara.2016.12.008

Thieltges DW, Jensen KT, Poulin R (2008) The role biotic factors in the transmission of free-living endohelminth stages. Parasitology 135: 407–426. https://doi.org/10.1017/S0031182007000248

Wasserman RJ, Alexander MR, Weyl OLF, Barrios-O'Neill D, Froneman PW, Dalu T (2016) Emergent effects of structural complexity and temperature on predator–prey interactions. Ecosphere 7: e01239. https://doi.org/10.1002/ecs2.1239

Welsh JE, Liddell C, van der Meer J, Thieltges DW (2017) Parasites as prey: the effect of cercarial density and alternative prey on consumption of cercariae by four non-host species. Parasitology 144:1775–1782. https://doi.org/10.1017/S003182017001056

Wilhelm FM, Schindler DW (1999) Effects of *Gammarus lacustris* (Crustacea: Amphipoda) on plankton community structure in an alpine lake. Can J Fish Aquat Sci 56:1401–1408. https://doi.org/10.1139/f99-067