



# Eye fluke (*Tylodelphys clavata*) infection impairs visual ability and hampers foraging success in European perch

Jenny Carolina Vivas Muñoz<sup>1,2</sup> · David Bierbach<sup>1</sup> · Klaus Knopf<sup>1,2</sup>

Received: 19 December 2018 / Accepted: 27 June 2019 / Published online: 8 July 2019  
© Springer-Verlag GmbH Germany, part of Springer Nature 2019

## Abstract

Visual performance and environmental conditions can influence both behavioral patterns and predator-prey interactions of fish. Eye parasites can impair their host's sensory performance with important consequences for the detection of prey, predators, and conspecifics. We used European perch (*Perca fluviatilis*) experimentally infected with the eye fluke *Tylodelphys clavata* and evaluated their feeding behavior and competitive ability under competition with non-infected conspecifics, in groups of four individuals, for two different prey species (*Asellus aquaticus* and *Daphnia magna*). To test whether the effect of *T. clavata* infection differs at different light conditions, we performed the experiments at two light intensities (600 and 6 lx). Foraging efficiency of perch was significantly affected by infection but not by light intensity. The distance at which infected fish attacked both prey species was significantly shorter in comparison to non-infected conspecifics. Additionally, infected fish more often unsuccessfully attacked *A. aquaticus*. Although the outcome of competition depended on prey species, there was a general tendency that non-infected fish consumed more of the available prey under both light intensities. Even though individual prey preferences for either *A. aquaticus* or *D. magna* were observed, we could not detect that infected fish change their prey preference to compensate for a reduced competitive foraging ability. As infection of *T. clavata* impairs foraging efficiency and competitive ability, infected fish would need to spend more time foraging to attain similar food intake as non-infected conspecifics; this presumably increases predation risk and potentially enhances transmission success to the final host.

**Keywords** *Tylodelphys clavata* · Eye fluke · *Perca fluviatilis* · Host-parasite interaction · Foraging behavior · Prey preference · Intraspecific competition

## Introduction

Parasites can have profound effects on host physiology, behavior, and survival (Moore 2002; Poulin 2007). Especially, trophically transmitted parasites can alter the intermediate

hosts' behavior or other phenotypic traits to increase susceptibility to predation by the final host. This strategy to increase transmission success can severely influence host ecology (Moore 2002; Lafferty and Kuris 2012). Several studies have associated parasitic infection with changes in a wide range of fish behavior (Barber et al. 2000; Barber and Wright 2005). However, hitherto, there are only a limited number of experimental studies that can prove the causal relationship between parasite infection and behavioral changes (Barber 2007). The trematode *Tylodelphys clavata* (Nordmann, 1832) has a typical three-host life cycle including aquatic snails and fish as intermediate hosts, and grebes (*Podiceps* spp.) as final hosts. In the fish, *T. clavata* infect the vitreous humor and transmission to the final host is via trophic transmission. By infecting the eyes, *T. clavata* and other diplostomatid trematodes can potentially impair the visual performance (Shariff et al. 1980; Stumbo and Poulin 2016). Consequently, eye flukes provide a suitable model to study host manipulation and behavioral changes.

Section Editor: Astrid Holzer

✉ Jenny Carolina Vivas Muñoz  
jennyvivas@igb-berlin.de

David Bierbach  
bierbach@igb-berlin.de

Klaus Knopf  
klaus.knopf@igb-berlin.de

<sup>1</sup> Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12589 Berlin, Germany

<sup>2</sup> Faculty of Life Sciences, Humboldt University, Invalidenstrasse 42, 10115 Berlin, Germany

Various parts of the fish eye, such as the lens, vitreous humor, and retina are target of *Diplostomum* spp. and *Tylodelphys* spp. In some cases, damage to the sensitive optical tissues as well as cataract formation has been observed in infections with these genera and associated with impaired visual function (Shariff et al. 1980; Padros et al. 2018; Ubels et al. 2018). Behavioral studies have shown that *Diplostomum* spp., invading the eye lenses and causing cataract formation, have important consequences on, among others, foraging efficiency, habitat selection, shoaling, and anti-predator behavior (Crowden and Broom 1980; Owen et al. 1993; Seppälä et al. 2004, 2005a, b, 2008, 2012; Gopko et al. 2017; Flink et al. 2017). These alterations may increase the vulnerability of infected fish to predators, and consequently enhance parasite transmission. Less is known about vitreous humor dwelling eye flukes as they have been considered less pathogenic due to their location and the lack of histopathological information related with these infections (Buchmann et al. 1997). However, a recent study with common bully (*Gobiomorphus cotidianus* (McDowall, 1975)) indicates that *Tylodelphys* sp. metacercariae move in front of the visual field causing retinal obstruction which can potentially reduce visual ability as moving flukes may shift the light transmission over the retina (Stumbo and Poulin 2016). This ocular obstruction seems to be an adaptive manipulation by the parasites since it was significantly higher during day time, when the final host is actively hunting for fish, than at night (Stumbo and Poulin 2016).

Our previous study (Vivas Muñoz et al. 2017) with naturally infected European perch (*Perca fluviatilis* (Linnaeus, 1758)) showed that foraging efficiency declined with increasing infection intensity of *T. clavata* (Nordmann, 1832). Moreover, when two individuals competed for a limited food resource, the more heavily infected fish consumed significantly less of the available food. This indicates that eye fluke infections may have a strong negative effect on the competitive abilities of a visual predatory fish such as perch (Bergman 1988; Diehl 1988) in a foraging context. As a consequence, infected fish would need to spend more time foraging in order to attain similar food intake as less infected conspecifics. This change in time budgets may increase predation risk (Crowden and Broom 1980). Furthermore, infected fish may modify their food preferences to compensate for reduced foraging efficiency and lower competitive ability. Changes in food preferences have been reported in three-spined sticklebacks (*Gasterosteus aculeatus* (Linnaeus, 1758)) infected with pleurocercoids of the cestode *Schistocephalus solidus* (Müller, 1776) which also decrease foraging competitive ability of the host (Milinski 1984; Barber and Huntingford 1995). When competing with non-infected conspecifics for differently sized *Daphnia magna* (Straus, 1820), infected sticklebacks mostly fed on the smaller-sized prey for which the non-infected fish had no preference (Milinski 1984). In the wild,

*S. solidus* infected female sticklebacks fed mostly on benthic invertebrates while non-infected females of the same population fed on planktonic cladocerans (Jakobsen et al. 1988). This might be due to the need to compensate for higher nutritional demands of infected compared to non-infected fish (Pascoe and Matthey 1977) and catching pelagic prey would energetically be more demanding for infected fish as high swimming activity is required (Jakobsen et al. 1988). European perch is one of the most common fish species in northern-temperate lakes (Craig 2000) and considered to be the primary host of *T. clavata* (Kozicka & Niewiadomska 1960). Thus, knowledge about parasite-induced changes in the feeding behavior of perch could significantly contribute to the comprehensive understanding of the role of this parasite in lake food webs. Juvenile perch undergo an ontogenetic dietary shift from zooplankton to benthic invertebrates a couple of months post-hatching (Craig 1978; Guma'a 1978; Persson 1986). However, individual feeding specialization has been observed among juvenile perch which is assumed to reduce intraspecific competition (Svanbäck and Persson 2004; Frankiewicz and Wojtal-Frankiewicz 2012). For instance, some individuals feed primarily on benthic macroinvertebrates, whereas others feed mostly on zooplankton.

Considering the negative impact of *T. clavata* infection on perch foraging ability in naturally infected fish (Vivas Muñoz et al. 2017), we used for the first time experimentally infected perch to prove the causal relationship between infection and foraging behavior. Furthermore, we tested whether prey preferences might be influenced by the infection status under intraspecific competition. We used laboratory-reared and experimentally infected juvenile European perch and evaluated their feeding behavior and competitive ability in small groups of four individuals under competition for two different prey species (*Asellus aquaticus* (Linnaeus, 1758) and *D. magna*). Since light intensity can also affect visual performance of fish and influence predator-prey interactions (Sandström 1999), we observed the feeding behavior of perch under competition at two light intensities. We hypothesized that decreasing light intensity should intensify the impact of *T. clavata* on perch's visual ability and predicted that this should lead to an even stronger negative effect of eye fluke infection on foraging efficiency; prey preference; and ultimately, competitive ability of perch under low light conditions.

## Materials and methods

### Experimental animals and maintenance

In order to obtain parasite-free fish, juvenile perch were raised from fertilized egg ribbons collected during the first half of April 2016 from Lake Müggelsee (Berlin, Germany). Egg ribbons were hung in two 45-L glass aquaria (50 × 30 ×

30 cm), and water was supplied by a drip system to the surface in a flow-through system at  $15 \pm 1$  °C. Perch fry hatched within 5 days and were fed ad libitum with live *Artemia salina* (Linnaeus, 1758) nauplii (Micro Artemia Cysts, Ocean Nutrition, Essen, Belgium) once their yolk sack reserve was exhausted.

Approximately 1 month post-hatching fish were transferred into a recirculating system with nine 200 L aquaria ( $100 \times 40 \times 50$  cm). Each of the holding tanks was aerated and illuminated with a 1-m LED strip (eco + LED-strip DAY 5500 K, LEDaquaristik, Hövelhof, Germany) with a 12-h dark-light photoperiod. Water temperature was maintained at room temperature (20–22 °C). Fish were habituated to dry food within 2 weeks. Food size was then progressively increased up to 3 mm (Aller silver 3 mm, Aller aqua, Christiansfeld, Denmark). Additionally, 1 month before the behavioral experiments started, parasite-free live *A. aquaticus* (Sciento, Manchester, UK) and *D. magna* (laboratory bred) were offered together with dry food twice a week to accustom perch to the prey used later in the experiments.

### Experimental infection and tagging

Snails of the genus *Radix*, which are potential hosts for *T. clavata*, were collected from Lake Grimnitzsee (Brandenburg, Germany). In the laboratory, snails were inspected for trematode infections by placing each individual into a plastic test tube with tap water under a light source to induce cercariae shedding. Live, freshly emerged cercariae were observed under a light microscope ( $\times 100$ – $\times 1000$  magnification), and morphological identification of *T. clavata* cercariae was based on the description by Faltýnková et al. (2007) and Mikeš (2001).

Snails with a patent infection of *T. clavata* were kept in the laboratory in a 15-L glass aquarium with aerated copper-free tap water at water temperature of  $21 \pm 1$  °C with a natural photoperiod. Snails were fed ad libitum with fresh lettuce.

Experimental infection was carried out 8 months post-hatching. Twelve hours before the procedure, a snail was removed from the holding tank, placed into a 0.5-L beaker, and cercariae shedding was stimulated with light. The cercariae concentration was estimated from the mean number of cercariae in ten 0.05-ml aliquots. Then, 25 fish were randomly selected from the holding tanks and placed individually in a 5-L bucket with 2 L water and gentle aeration. Each fish was exposed to 300 cercariae for 2 h. After the experimental infection, fish were transferred back to the holding tanks. An additional 20 control fish experienced the same treatment without the exposure to cercariae. Fish were kept in groups of ten individuals depending on their infection status until the behavioral experiments. Four days post-infection, five fish were killed by an overdose of MS-222 (0.5 g/L) (Sigma-Aldrich, Taufkirchen, Germany) and inspected for the number

of established metacercariae using a stereo microscope ( $\times 8$ – $\times 20$  magnification). Identification of *T. clavata* metacercariae was confirmed based on the morphological characteristics described by Kozicka and Niewiadomska (1960). Infection intensity of these five fish varied between 131 and 228 metacercariae per fish (average intensity  $\pm$  SD  $167 \pm 41$ ), which was within the range of previous records in naturally infected juvenile perch (Kennedy 2001; Vivas Muñoz et al. 2017).

Nine months post-infection, infected and non-infected fish were tagged for identification. Fish were anesthetized with MS222 (0.15 g/L) and tagged between the rays of the caudal fin with visible implant elastomer (VIE, Northwest Marine technology, Inc., Shaw Island, WA, USA) following the manufacturer's instructions. Afterwards, fish were returned to the holding tanks.

### Behavioral experiments

Ten months post-infection, the behavioral experiment started. Both infected and non-infected fish used in the experiment appeared healthy to the human eye and alteration in the behavior, such as decreased feeding rates or activity, was not observed during the holding period.

The experiments were carried out in a glass aquarium ( $100 \times 40 \times 50$  cm; water depth 45 cm), illuminated with a rectangular system composed of two 116-cm and two 50-cm LED strips (eco + LED-strip DAY 5500 K, LEDaquaristik, Hövelhof, Germany) placed 65 cm above the aquarium. The experimental set up was covered with a dark curtain in order to exclude extraneous light. The photoperiod was programmed using an automatic light control system (SIMU-LUX, LEDaquaristik, Hövelhof, Germany). During acclimation and the high light intensity experiment, the photoperiod was set on a 12-h day/night cycle with 30 min dim sunrise and sunset simulation; surface light intensity was 600 lx at daytime. For the low light intensity experiment, sunrise simulation stopped at a surface light intensity of 6 lx and was maintained until the end of the experiment. This was the lowest light intensity at which we could clearly identify the small prey (*D. magna*) and the colored tags of the fish on our video recordings. Additionally, a green background containing  $1 \times 1$  cm grid was placed behind the back and under the base of the aquarium.

Fish were tested in ten groups of four, size-matched individuals (two infected and two non-infected) with well distinguishable VIE tags. Even though we size-matched individuals within groups (size difference within one group max. 2 mm), average total length among groups varied between 13 and 16 cm. Fish were observed in groups to create a competitive context and mimic natural conditions as juvenile perch usually live in shoals and the presence of conspecifics seems to reduce stress levels (Strand et al. 2007). Fish were allowed to

acclimatize to the experimental conditions for 1 week and were fed once a day with dry food and live *A. aquaticus* and *D. magna* until 24 h before the experiment began. The acclimatization time was extended long enough in order that all fish show normal feeding behavior.

The experiments at the two light intensities were carried out on two consecutive days, always in the morning, 30 min after simulated sunrise. On the day of the experiment, an opaque plastic screen was carefully placed in the aquarium and used to confine the fish in the lateral 15 cm of the aquarium. Subsequently, 20 g of black gravel (2–4 mm diameter), 30 live *A. aquaticus* (5–8 mm length, measured from the top of the head to the end of the pleotelson), and 40 live *D. magna* were introduced into the aquarium. The gravel was evenly distributed across the bottom of the tank providing adequate hiding places for the *A. aquaticus* to prevent their accumulation along the aquarium's black silicone seams. After 5 min, when *A. aquaticus* had settled and distributed on the bottom of the tank, the opaque screen was lifted and the feeding behavior of the fish was recorded simultaneously using two cameras (Sony  $\alpha$  7S, Sony, Tokyo, Japan and objective ZEISS Batis 2/25, Carl Zeiss AG, Oberkochen, Germany) for 45 min, obtaining videos from the front and top of the aquarium. Each camera was connected to a monitor-recorder (Shogun inferno, Atomos Global Pty Ltd., Port Melbourne, Australia), which enables control of the camera and the monitoring of the fish from outside the experimental set up. After the experiment, fish were again confined with the opaque plastic screen for 5 min in order to remove the gravel and uneaten prey. After the observations of each group had been completed at both light intensities, the two infected fish were killed by an overdose of MS222 (0.5 g/L). The eyes were dissected, and the number of *T. clavata* metacercariae was determined as described above.

## Video and data analysis

### Feeding behavior of perch

Reaction distance was used as a parameter of the visual ability of the fish according to Vinyard and O'Brien (1976). It was measured, as the distance between the fish snout and the prey at the moment it first orientated, or accelerated towards the prey. The two videos (front and top views) per experiment were analyzed simultaneously allowing the calculation of the reaction distance using Pythagoras' theorem and correcting for the perspective distortion. The first 20 attacks a fish made to each prey species were used to calculate the mean reaction distances per individual, which were subsequently used in the analysis.

To compare the reaction distances between infected and non-infected individuals at both light intensities, a linear mixed model (LMM) with Gaussian error distribution and linear link function was used. Mean reaction distance to *A. aquaticus* and, separately, to *D. magna* were the dependent variables. As fixed effect of interest, we include light intensity (high vs. low) and infection status (infected vs. non-infected), as well as their interaction term "light by infection." However, this interaction term had no significant effect in either model (*A. aquaticus*:  $F_{1, 27.9} = 2.33$ ;  $P = 0.14$ ; *D. magna*:  $F_{1, 16.8} = 0.001$ ;  $P = 0.98$ ) and was thus removed from the final models. Although body size of fish within each tested group was matched, the ten groups differed slightly in average body size. Therefore, each individual's body size (TL) was included as a covariate in the model. To account for the repeated testing of the same individuals (in high and low light intensity) and the group-wise test design, "group ID" as well as "individual ID (nested within group)" were included as random factors.

To evaluate how successful attacks were, the fraction of attacks when the fish successfully captured the prey was calculated. This success rate (arcsin-sqrt transformed to match a Gaussian distribution of data points) per prey species was then used in an LMM with the above-described fixed and random factors. In the final model for *A. aquaticus*, the interaction term between light intensity and infection status was removed as it was not significant ( $F_{1, 29.6} = 0.43$ ,  $P = 0.51$ ).

To test for differences in the number of consumed prey between infection status and light intensity, two separate general LMMs (Poisson error distribution, Log link function) were run with the same fixed/random effects structure as described above. For *A. aquaticus* consumption, the interaction (light by infection) term was retained, but it was removed from the model analyzing *D. magna* consumption ( $F_{1, 75} = 2.64$ ;  $P = 0.11$ ).

In order to assess if fish had a preference for one of the two prey species, the fraction of consumed *A. aquaticus* towards the total number of consumed items (*A. aquaticus* and *D. magna*) was calculated per fish at each light intensity and compared using a Kruskal–Wallis test.

Considering that some fish did not feed during the observation period, we evaluated the influence of infection status (infected vs non-infected) on the tendency to feed by categorizing the fish that fed and the ones that did not (yes vs. no) using Pearson's chi-square test per each light intensity.

### Activity level of prey organisms

To observe if the light intensity had an influence on the activity level of *A. aquaticus*, we used the top view video to enumerate the number of gridlines that a prey individual crossed within 1 min. Activity levels of 50 *A. aquaticus* (5 per video) at each light intensity were compared using a Mann–Whitney

*U* test. We did not succeed in achieving a comparable method of determining the activity of *D. magna*.

For all analyses, significance was accepted when  $P \leq 0.05$ . All statistical analyses were performed in SPSS 25 (IBM, New York, USA).

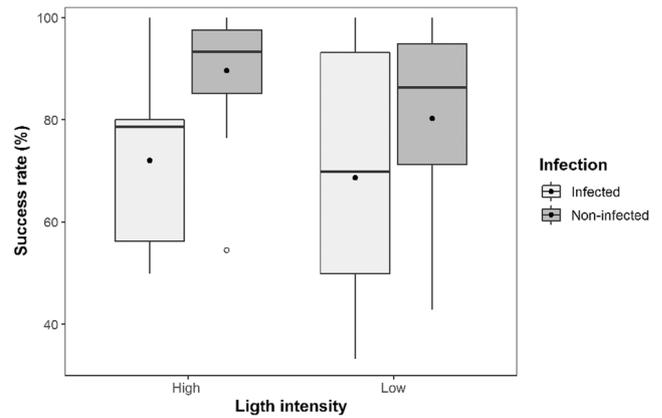
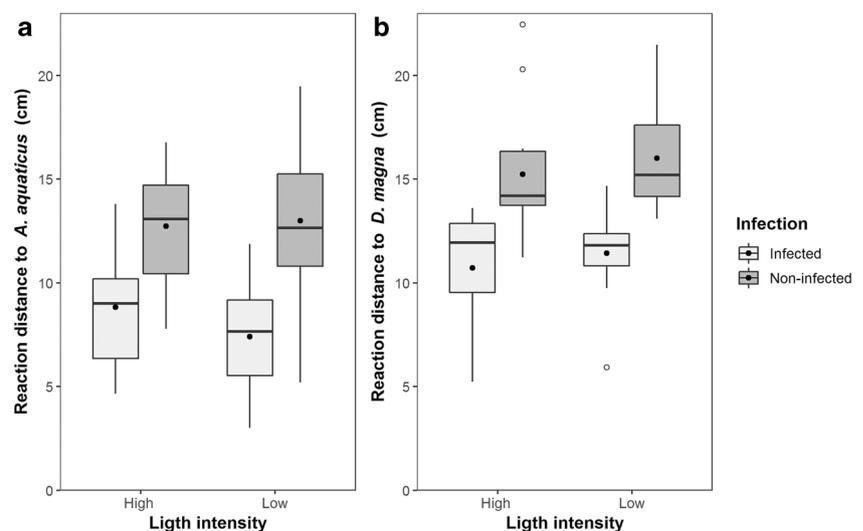
## Results

The infection intensity of experimentally infected fish ranged from 114 to 236 metacercariae per fish (mean  $\pm$  SD  $168 \pm 31$ ). During the feeding experiments, a total of eight individuals (20% of all fish tested) did not feed under both light intensities, six of which were infected (infection intensity ranged from 148 to 225 metacercariae per fish). An additional non-infected fish did not consume any prey item during the low light intensity observation. Even though the majority of fish that did not feed were infected, infection status did not significantly affect the tendency to feed at both light intensities (Pearson's chi-square test: high light intensity:  $\chi^2_1 = 1.41$ ;  $P = 0.235$ ; low light intensity:  $\chi^2_1 = 0.57$ ;  $P = 0.449$ ).

Infected fish attacked both *A. aquaticus* and *D. magna* at shorter distances compared to non-infected fish (LMM: *A. aquaticus*:  $F_{1, 23.6} = 32.24$ ;  $P < 0.001$ ; *D. magna*:  $F_{1, 12.66} = 23.77$ ;  $P < 0.001$ ; Fig. 1). This difference between infected and non-infected fish was independent of light intensity (LMM: *A. aquaticus*:  $F_{1, 28.8} = 0.42$ ;  $P = 0.523$ ; *D. magna*:  $F_{1, 17.61} = 1.00$ ;  $P = 0.33$ ).

Attacks towards *D. magna* were almost always successful, regardless of whether the fish were infected or not ( $99\% \pm 2\%$  SD). Attacks on *A. aquaticus* showed a differentiated picture: infected fish had significantly lower success rates compared to non-infected fish (LMM:  $F_{1, 30.9} = 5.90$ ;  $P = 0.021$ ), and this was independent of light intensity (LMM:  $F_{1, 30.3} = 1.68$ ;  $P = 0.21$ ; Fig. 2). Infected fish failed more frequently to make

**Fig. 1** Reaction distance of non-infected and *Tylodelphys clavata*-infected juvenile European perch (*Perca fluviatilis*) under competition attacking **a** *Asellus aquaticus* and **b** *Daphnia magna* at two light treatments: high light intensity (600 lx) and low light intensity (6 lx). Box plots show medians (horizontal thicker lines), means (black circles), first and third quartiles (box limits), ranges (whiskers), and extreme values (open circles)

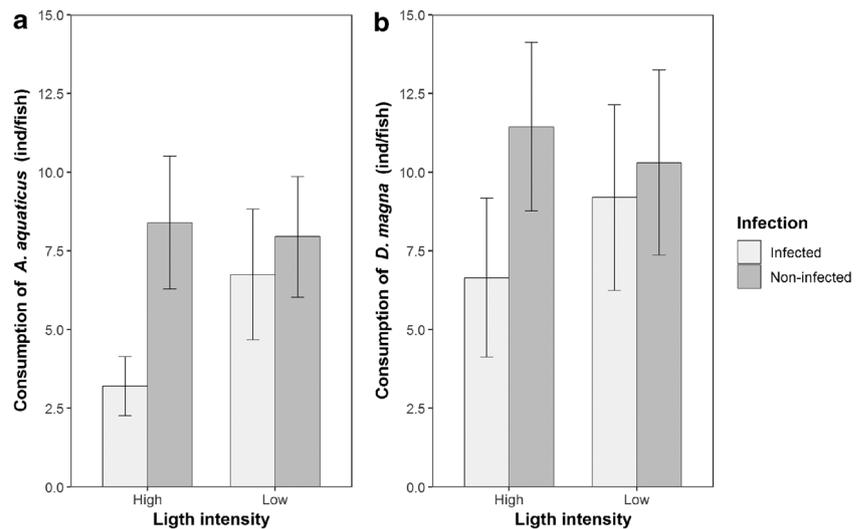


**Fig. 2** Percentage of successful attacks by non-infected and *Tylodelphys clavata*-infected juvenile European perch (*Perca fluviatilis*) under competition when attacking *Asellus aquaticus* under two light treatments: high light intensity (600 lx) and low light intensity (6 lx). Box plots show medians (horizontal thicker lines), means (black circles), first and third quartiles (box limits), ranges (whiskers), and extreme values (open circles)

contact with the prey by snapping at it before the prey was within range or getting a stone or gravel instead of an *A. aquaticus* which was next to it.

In general, infected fish consumed less of the available prey than the non-infected fish (Fig. 3). Regarding the consumption of *A. aquaticus*, we found non-infected fish to consume similar amounts of prey items at both light intensities while infected fish increased the consumption of *A. aquaticus* at low light intensity (Fig. 3; LMM: sig. effect of interaction term between light intensity and infection status:  $F_{1, 75} = 9.99$ ;  $P = 0.002$ ; main factors: light intensity:  $F_{1, 75} = 7.43$ ;  $P = 0.008$ ; infection status:  $F_{1, 75} = 1.70$ ;  $P = 0.197$ ). The consumption of *D. magna* by perch showed a similar trend, but there was no significant effect of the light intensity (LMM:  $F_{1, 76} = 0.29$ ;  $P = 0.59$ ) or infection status

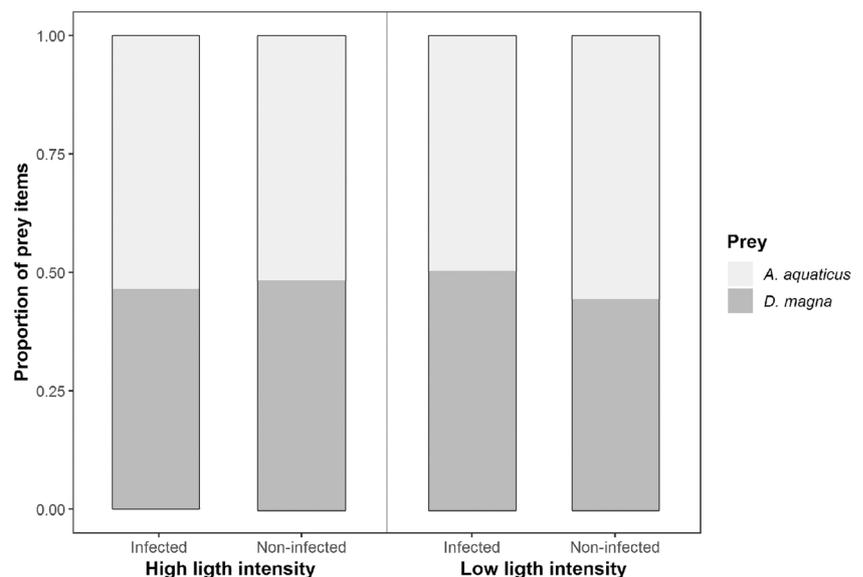
**Fig. 3** Consumption of **a** *Asellus aquaticus* and **b** *Daphnia magna* by non-infected and *Tylodelphys clavata*-infected juvenile European perch (*Perca fluviatilis*) under competition at two light treatments: high light intensity (600 lx) and low light intensity (6 lx). Bars indicate mean value  $\pm$  standard error



(LMM:  $F_{1, 76} = 0.90$ ;  $P = 0.35$ ). In all analyses, body size of the experimental fish had no significant effect (results not shown).

Individual feeding preference of perch for either *D. magna* or *A. aquaticus* was observed. Considering only the individuals which fed, at low light intensity, one third of the fish consumed predominantly *A. aquaticus* (> 80% of all consumed prey items) and another third of the individuals consumed predominantly *D. magna* (> 80% of all consumed prey items). A similar pattern was observed at high light intensity whereby 70% of fish showed the same prey preference as in the experiment at low light intensity. However, prey preference of the fish was not influenced by infection status. The mean fraction of *A. aquaticus* from the total consumed prey items was similar between infected and non-infected individuals at both light intensities (Kruskal–Wallis test:  $\chi^2 = 0.228$ ,  $df = 3$ ,  $P = 0.97$ ; Fig. 4).

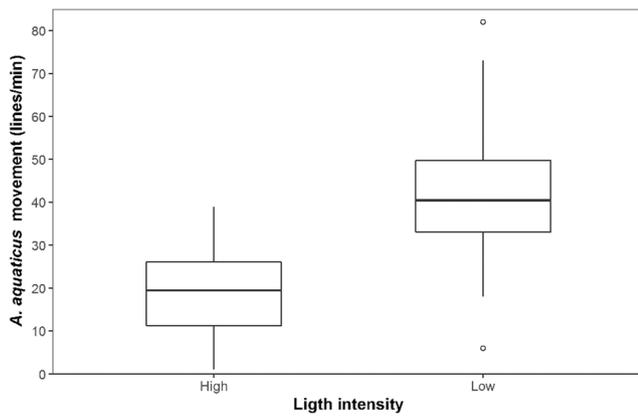
**Fig. 4** Proportion of *Asellus aquaticus* and *Daphnia magna* ingested by non-infected and *Tylodelphys clavata*-infected juvenile European perch (*Perca fluviatilis*) under competition at two light treatments: high light intensity (600 lx) and low light intensity (6 lx)



The activity of *A. aquaticus* was significantly affected by the light intensity. The animals were more than twice as active at the low light intensity as at the high light intensity (Mann–Whitney  $U$  test:  $W = 1$ ;  $n_1 = n_2 = 10$ ;  $P < 0.001$ ; Fig. 5).

## Discussion

It is widely accepted that parasites can have strong effects on fish behavior (Barber et al. 2000; Barber and Wright 2005; Barber et al. 2017). Infection of sensory organs may impair their performance and consequently affect the fish' perception of the environment, which in turn may result in a modified behavior. A previous study with naturally infected perch has already shown a correlation between *T. clavata* intensity and reaction distance as well as impaired competitive ability of their host (Vivas Muñoz et al. 2017). However, in the latter



**Fig. 5** Activity level of *Asellus aquaticus*, measured as lines crossed per minute, at high light intensity (600 lx;  $n = 50$ ) and low light intensity (6 lx;  $n = 50$ ). Box plots show medians (horizontal thicker lines), first and third quartiles (box limits), ranges (whiskers), and extreme values (open circles)

study, it remained unclear whether the observed behavioral alterations are cause or consequence of infection (Poulin 1995). For instance, weaker competitors might be intrinsically prone to infection, rather than infection being responsible for reduced competitive ability. The present experiments, with parasite-free laboratory-reared and experimentally infected perch, now provide evidence for the causal relationship between the infection of *T. clavata* and the negative effects derived therefrom on the foraging efficiency and competitive ability of their host.

*Tylodelphys clavata* metacercariae inhabit the vitreous humor preferring the suspensory ligaments, which are important for focus adjustment (Kennedy 2001; Khorramshahi et al. 2008). Moreover, there is evidence that *Tylodelphys* sp. metacercariae cause retinal obstruction in common bully (*G. cotidianus*). As flukes move in the visual field, they may shift the light intensity over the retina, thus impairing visual ability (Stumbo and Poulin 2016). These alterations can impose vital constraints in a visual predator such as European perch (Bergman 1988; Diehl 1988). The reaction distance is a common behavioral measure of visual ability (Vinyard and O'Brien 1976). In addition to the impact of *Tylodelphys* spp. on the visual performance of the fish host as suggested by Stumbo and Poulin (2016) and Vivas Muñoz et al. (2017), eye flukes also affect the host's energy budget (Voutilainen et al. 2008). However, the energy requirement for the maintenance of the small, full-grown metacercariae is presumably low and the effects of infection on the reaction distance can hardly be explained by the energy debt caused by the parasite. Additionally, histological sections of common bully's eyes did not reveal damage to the optical tissues caused by the presence of *Tylodelphys* sp. metacercariae (Stumbo and Poulin 2016). Thus, the effect on visual ability is considered as the main impact of *T. clavata*. In this study, we found that the distances at which infected perch attack both *A. aquaticus* and

*D. magna* were shorter in comparison to non-infected conspecifics. The reaction distances of the experimentally infected perch are comparable to those of naturally infected perch (Vivas Muñoz et al. 2017).

We observed that non-infected fish had higher success rates when preying on *A. aquaticus* than infected ones. This was not only due to successful escapes of the prey, but also due to attacks when infected fish failed to make contact with the prey. Crowden and Broom (1980) reported similar results for dace (*Leuciscus leuciscus* (Linnaeus, 1758)), where the reaction distances decreased as the infection intensity of the eye fluke *Diplostomum spathaceum* (Rudolphi, 1819) increased. Simultaneously, the number of unsuccessful attacks and attacks towards inedible objects increased. Furthermore, heavily infected dace spent more time feeding. The present study shows that impaired sensory performance is not only caused by eye flukes invading the lens such as *Diplostomum* spp. but also by vitreous humor-dwelling eye flukes.

Since foraging efficiency is affected by *T. clavata*, as a compensatory mechanism fish would have to increase the amount of time spent foraging. This would presumably come at the expense of other activities, such as anti-predator behavior. Risk-taking behavior during foraging of fish infected with eye flukes has not yet been analyzed. However, it is known that dace infected with *D. spathaceum* spend more time near the water surface while foraging, which may increase their vulnerability to predators (Crowden and Broom 1980). Furthermore, several studies with *Diplostomum* spp. invading the eye lenses have shown that infection can impact various behavioral patterns (e.g., impaired crypsis, reduced escape response, and activity latency after a simulated avian predator attack) which may increase predation risk and consequently transmission success to the final host (Seppälä et al. 2005a, b; Gopko et al. 2017; Flink et al. 2017). Despite the lack of information on the influence of vitreous humor-dwelling eye flukes on their hosts' anti-predatory behavior, the detrimental effect caused by *Tylodelphys* sp. seems to be an adaptive manipulation, as retinal obstruction significantly increases during day time, when the final host is active (Stumbo and Poulin 2016).

Perch is visually adapted to day light conditions and foraging is nearly totally absent during the night (Ali et al. 1977; Bergman 1988; Diehl 1988; Guma'a 1978). Besides being diurnally active, high foraging activity also occurs during dusk and dawn (Craig 1977; Persson 1983; Huusko et al. 1996). We initially hypothesized that decreasing light intensity would intensify the impact of *T. clavata* on the visual ability. However, in our experiments, light intensity did not significantly affect the reaction distance or success rate of perch. Commonly, the reaction distance of visual predators decreases when light intensity falls below a certain threshold level (Vinyard and O'Brien 1976). It has been shown that the attack success of European perch decreases to 60% at 0.02 lx

(Bergman 1988), and the reaction distance of the closely related yellow perch (*Perca flavescens* (Mitchill, 1814)) greatly decreases when light intensity falls below 2 lx (Richmond et al. 2004). Consequently, our low illumination level of 6 lx may not have been low enough to detect a significant extra effect of the eye flukes on the reaction distance or success rate of perch. Another variable that can negatively affect the feeding efficiency of visual predators by reducing their reaction distance is turbidity (Vinyard and O'Brien 1976; Utne 1997). Accordingly, feeding rate of European perch decreases with increasing turbidity levels (Nurminen et al. 2010; Pekcan-Hekim et al. 2013). Thus, both light intensity and turbidity should be considered in further studies evaluating the impact of eye fluke infection under different environmental conditions.

The outcome of competition for limited resources is strongly influenced by the competitor's abilities, the environmental conditions, and social dominance (e.g. Eiane et al. 1997; Winfield 1986; Metcalfe 1986; Westerberg et al. 2004). A previous study showed that infection with *T. clavata* correlates significantly with the host foraging success in competition between two individuals (Vivas Muñoz et al. 2017). Similarly, in the present study with groups of four individuals, infected fish consumed less of the available *A. aquaticus* than the non-infected conspecifics under high light intensity. However, when light intensity decreased, infected fish increased the consumption of *A. aquaticus* and no difference was detected between infected and non-infected individuals. The obvious compensation of the impaired competitive ability caused by the infection with *T. clavata* can be explained with light-dependent behavioral changes of the prey. From a field study, Andrikovics (1981) described an approximate threefold increase of *A. aquaticus* nocturnal activity compared to the day time, and during the experiments, *A. aquaticus* were twice as active at low light intensity as at high light intensity. The increased activity of *A. aquaticus* may result in an increase in the prey encounter rate. This should equally benefit infected and non-infected fish. However, the easier detectability of the crawling prey may reduce the restriction caused by impaired vision ability closing the competitiveness gap between infected and non-infected fish. The diurnal behavior of the metacercariae, as shown for a *Tylodelphys* species in New Zealand, where retinal obstruction caused by the presence of the parasites decreased at night time (Stumbo and Poulin 2016), might also affect the competitiveness of infected fish at different light conditions. However, this does not seem to apply to *T. clavata* at the light intensities used in our experiment, since light intensity had no effect on the reaction distance or visual performance of infected fish.

Furthermore, infected fish may to some extent compensate their reduced visual ability by social information from non-infected conspecifics. One of the benefits of being part of a group is an increase in detection of food sources, even when

subject to competition by members of the group (Pitcher and Parrish 1993). European perch have a higher capture and growth rate in groups than solitary individuals (Eklöv 1992). Thus, it is possible that visually impaired infected fish use information from other members of the group for prey location. This strategy would be most profitable when prey is clustered together as more prey would enter the reduced visual range of infected fish. In our experiment, this was the case with *D. magna*, which was patchily distributed in comparison to *A. aquaticus*, and this might be a reason why consumption of *D. magna* did not significantly differ between infected and uninfected fish.

In our experiments, a total of eight individuals did not feed at both light intensities, six of which were infected. This might be related to the social position of these fish within the group. For rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)), it has been shown that some individuals can directly suppress the foraging rate of others through aggressive behavior (Metcalfe 1986; Brännåas et al. 2001). On the other hand, within groups of young perch, overt aggressive behavior as interference competition for food resources is still unclear. Westerberg et al. (2004) observed that in some cases, individuals with the highest prey attack rate performed aggressive acts against other members of the group. Contrarily, no aggressive behavior was observed during feeding experiments by Staffan et al. (2002). Although we did not observe aggressive interactions between the experimental fish, and did not find significant evidence that the absence of foraging was related to the infection status, it cannot be ruled out that social dominance or interaction may have influenced the foraging behavior of these individuals.

Parasite-induced impaired visual ability can also affect the performance of a fish within a shoal, as it depends on an adequate response to various sensory stimuli, especially visual stimuli from shoal mates (Partridge and Pitcher 1980). Observations on the shoaling behavior of rainbow trout showed that individuals infected with *D. spathaceum* formed smaller shoals, more often divided into separate groups, and after a simulated avian predator attack, shoal cohesiveness did not increase in comparison to non-infected shoals. These alterations may increase predation risk and consequently enhance transmission success to the final bird host (Seppälä et al. 2008). It has also been detected that non-infected three-spined sticklebacks prefer to join mixed shoals with both *Diplostomum pseudospathaceum* (Niewiadomska, 1984) infected and non-infected members over non-infected shoals, while infected individuals did not show any preference (Rahn et al. 2018). In this case, non-infected fish could benefit when competing for food resources with weak competitors. However, increased predation risk might be the price of that benefit as infected fish may be less alert or behave differently making the group more vulnerable to predators. The influence of *T. clavata* on shoaling behavior of its fish hosts has yet not

been studied, but considering its impact on visual ability, it is feasible that similar effects as described for *Diplostomum* spp. could be observed.

There is evidence of individual feeding specializations among perch juveniles, which has been considered to be a strategy to reduce intraspecific competition (Svanbäck and Persson 2004; Frankiewicz and Wojtal-Frankiewicz 2012). In a long time study, individual feeding specialization fluctuated with population density in response to resources levels (Svanbäck and Persson 2004). Considering the impact of *T. clavata* infection on visual ability, we initially hypothesized that infected fish may change their food preferences as a compensatory mechanism for reduced foraging competitive ability. For instance, infected fish would prefer to feed on a prey for which there is less competition as it has been observed in three-spined sticklebacks infected with *S. solidus* (Milinski 1984). Even though we observed a clear individual prey preference among the experimental individuals, which was consistent in the two consecutive observations under the two different light intensities, we found no evidence that the infection status affected the prey preference.

The fact that fish infected with *T. clavata* would need to spend more time foraging to attain similar food intake as non-infected conspecifics presumably increases their predation risk. Furthermore, our results showed that prey species and behavior can also influence the outcome of competition. Within a small group, infected fish performed better competing for a prey clustered together in an area (*D. magna*) than for a prey spatially more dispersed (*A. aquaticus*). However, an interesting question for further studies is whether infected fish may modify their risk-taking behavior as a compensatory mechanism for reduced foraging competitive ability; for instance, by being more willing to feed in areas with higher predation risk or being less alert and resume feeding faster after an unsuccessful predatory attack. A modification on the risk-taking behavior during foraging may increase predation risk and potentially enhance transmission success of *T. clavata* to the final bird host.

**Acknowledgments** We are grateful to Dr. Jasminca Behrmann-Godel for her valuable advice on raising perch in the lab and Mathias Kunow for his support in collecting fertilized eggs of perch. Further, we would like to thank Janne Ros Irmeler and Amrei Gründer for their support with the videos and Dr. Sabine Hilt for her valuable comments on an earlier draft of the manuscript.

**Funding information** This research was supported by the Graduate School IMPact-Vector funded by the Senate Competition Committee grant (SAW-2014-SGN-3) of the Leibniz-Association. Research of D.B. is currently supported by the DFG (BI 1828/2-1).

## Compliance with ethical standards

**Conflict of interest** The authors declare that there is no conflict of interest.

**Ethical approval** Tagging of the fish, experimental infection, and behavioral experiments were performed in accordance with the German Animal Welfare Act and were approved by the Berlin State Office for Health and Social Affairs (LaGeSo, reference number G0243/16).

## References

- Ali MA, Ryder RA, Anctil M (1977) Photoreceptors and visual pigments as related to behavioral responses and preferred habitats of perch (*Perca* spp.) and pikeperches (*Stizostedion* spp.). *J Fish Res Board Can* 34:1475–1480. <https://doi.org/10.1139/f77-212>
- Andrikovics S (1981) Further data to daily migration of the larvae of aquatic insect. *Opusc Zool* 17–18:49–55
- Barber I (2007) Parasites, behaviour and welfare in fish. *Appl Anim Behav Sci* 104:251–264. <https://doi.org/10.1016/j.applanim.2006.09.005>
- Barber I, Huntingford FA (1995) The effect of *Schistocephalus solidus* (Cestoda: Pseudophyllidea) on the foraging and shoaling behaviour of three-spined sticklebacks, *Gasterosteus aculeatus*. *Behaviour* 132:1223–1240. <https://doi.org/10.1163/156853995X00540>
- Barber I, Wright HA (2005) Effects of parasites on fish behaviour: interactions with host physiology. In: Katherine RWW, Sloman A, Sigal B (eds) *Fish physiology*. Academic Press, San Diego, pp 109–149. [https://doi.org/10.1016/S1546-5098\(05\)24004-9](https://doi.org/10.1016/S1546-5098(05)24004-9)
- Barber I, Hoare D, Krause J (2000) Effects of parasites on fish behaviour: an evolutionary perspective and review. *Rev Fish Biol Fish* 10:131–165. <https://doi.org/10.1023/A:1016658224470>
- Barber I, Mora AB, Payne EM, Weinersmith KL, Sih A (2017) Parasitism, personality and cognition in fish. *Behav Process* 141: 205–219. <https://doi.org/10.1016/j.beproc.2016.11.012>
- Bergman E (1988) Foraging abilities and niche breadths of two percid, *Perca fluviatilis* and *Gymnocephalus cernua*, under different environmental conditions. *J Anim Ecol* 57:443–453. <https://doi.org/10.2307/4916>
- Brännäs E, Alanärä A, Magnhagen C (2001) The social behaviour of fish. In: Keeling LJ, Gonyou HW (eds) *Social behaviour in farm animals*. CABI publishing, New York, pp 275–304
- Buchmann K, Moller SH, Uldal A, Bresciani J (1997) Different seasonal infection dynamics of two species of eye-flukes (*Diplostomum spathaceum* and *Tylodelphys clavata*) in rainbow trout (*Oncorhynchus mykiss*). *Bull Eur Assoc Fish Pathol* 17:165–170
- Craig JF (1977) Seasonal changes in the day and night activity of adult perch, *Perca fluviatilis* L. *J Fish Biol* 11:161–166. [https://doi.org/10.1111/j.1095-8649.1977.tb04109.x](https://doi.org/10.1111/j.1111/j.1095-8649.1977.tb04109.x)
- Craig JF (1978) A study of the food and feeding of perch, *Perca fluviatilis* L., in Windermere. *Freshw Biol* 8:59–68. <https://doi.org/10.1111/j.1365-2427.1978.tb01426.x>
- Craig JF (2000) Percid fishes: systematics, ecology and exploitation. Blackwell Science, Oxford
- Crowden AE, Broom DM (1980) Effects of the eye-fluke, *Diplostomum spathaceum*, on the behaviour of dace (*Leuciscus leuciscus*). *Anim Behav* 28:287–294. [https://doi.org/10.1016/S0003-3472\(80\)80031-5](https://doi.org/10.1016/S0003-3472(80)80031-5)
- Diehl S (1988) Foraging efficiency of three freshwater fishes: effects of structural complexity and light. *Oikos* 53:207–214. <https://doi.org/10.2307/3566064>
- Eiane K, Aksnes DL, Giske J (1997) The significance of optical properties in competition among visual and tactile planktivores: a theoretical study. *Ecol Model* 98:123–136. [https://doi.org/10.1016/S0304-3800\(96\)01909-6](https://doi.org/10.1016/S0304-3800(96)01909-6)
- Eklöv P (1992) Group foraging versus solitary foraging efficiency in piscivorous predators: the perch, *Perca fluviatilis*, and pike, *Esox lucius*, patterns. *Anim Behav* 44:313–326. [https://doi.org/10.1016/0003-3472\(92\)90037-A](https://doi.org/10.1016/0003-3472(92)90037-A)

- Faltýnková A, Našincová V, Kablásková L (2007) Larval trematodes (Digenea) of the great pond snail, *Lymnaea stagnalis* (L.), (Gastropoda, Pulmonata) in Central Europe: a survey of species and key to their identification. *Parasite* 14:39–51. <https://doi.org/10.1051/parasite/2007141039>
- Flink H, Behrens JW, Svensson PA (2017) Consequences of eye fluke infection on anti-predator behaviours in invasive round gobies in Kalmar sound. *Parasitol Res* 116:1653–1663. <https://doi.org/10.1007/s00436-017-5439-5>
- Frankiewicz P, Wojtal-Frankiewicz A (2012) Two different feeding tactics of young-of-the-year perch, *Perca fluviatilis* L., inhabiting the littoral zone of the lowland Sulejow Reservoir (Central Poland). *Ecohydrol Hydrobiol* 12:35–41. <https://doi.org/10.2478/v10104-012-0001-7>
- Gopko M, Mikheev VN, Taskinen J (2017) Deterioration of basic components of the anti-predator behavior in fish harboring eye fluke larvae. *Behav Ecol Sociobiol* 71:68. <https://doi.org/10.1007/s00265-017-2300-x>
- Guma'a SA (1978) The food and feeding habits of young perch, *Perca fluviatilis*, in Windermere. *Freshw Biol* 8:177–187. <https://doi.org/10.1111/j.1365-2427.1978.tb01439.x>
- Huusko A, Vuorimies O, Sutela T (1996) Temperature- and light-mediated predation by perch on vendace larvae. *J Fish Biol* 49:441–457. <https://doi.org/10.1111/j.1095-8649.1996.tb00040.x>
- Jakobsen PJ, Johnsen GH, Larsson P (1988) Effects of predation risk and parasitism on the feeding ecology, habitat use, and abundance of lacustrine threespine stickleback (*Gasterosteus aculeatus*). *Can J Fish Aquat Sci* 45:426–431. <https://doi.org/10.1139/f88-051>
- Kennedy CR (2001) Interspecific interactions between larval digeneans in the eyes of perch, *Perca fluviatilis*. *Parasitology* 122:S13–S22. <https://doi.org/10.1017/S0031182000016851>
- Khorranshahi O, Schartau JM, Kröger RHH (2008) A complex system of ligaments and a muscle keep the crystalline lens in place in the eyes of bony fishes (teleosts). *Vis Res* 48:1503–1508. <https://doi.org/10.1016/j.visres.2008.03.017>
- Kozicka J, Niewiadomska K (1960) Studies on the biology and taxonomy of trematodes of the genus *Tylodelphys* Diesing, 1850 (Diplostomatidae). *Acta Parasitol Pol* 8:379–400
- Lafferty KD, Kuris AM (2012) Ecological consequences of manipulative parasites. In: Hughes DP, Brodeur J, Thomas F (eds) *Host manipulation by parasites*. Oxford university press, Oxford, pp 158–171
- Metcalf NB (1986) Intraspecific variation in competitive ability and food intake in salmonids: consequences for energy budgets and growth rates. *J Fish Biol* 28:525–532. <https://doi.org/10.1111/j.1095-8649.1986.tb05190.x>
- Mikeš L (2001) Simplified determination key, Cercariae. 1st workshop on bird schistosomes and cercarial dermatitis. Dolní Věstonice, Czech Republic
- Milinski M (1984) Parasites determine a predator's optimal feeding strategy. *Behav Ecol Sociobiol* 15:35–37. <https://doi.org/10.1007/BF00310212>
- Moore J (2002) *Parasites and behaviour of animals*. Oxford series in ecology and evolution. Oxford University Press, New York, p 315
- Nurminen L, Pekcan-Hekim Z, Horppila J (2010) Feeding efficiency of planktivorous perch *Perca fluviatilis* and roach *Rutilus rutilus* in varying turbidity: an individual-based approach. *J Fish Biol* 76:1848–1855. <https://doi.org/10.1111/j.1095-8649.2010.02600.x>
- Owen SF, Barber I, Hart PJB (1993) Low level infection by eye fluke, *Diplostomum* spp., affects the vision of three-spined sticklebacks, *Gasterosteus aculeatus*. *J Fish Biol* 42:803–806. <https://doi.org/10.1111/j.1095-8649.1993.tb00387.x>
- Padros F, Knudsen R, Blasco-Costa I (2018) Histopathological characterisation of retinal lesions associated to *Diplostomum* species (Platyhelminthes: Trematoda) infection in polymorphic Arctic charr *Salvelinus alpinus*. *Int J Parasitol* 7:68–74. <https://doi.org/10.1016/j.ijppaw.2018.01.007>
- Partridge BL, Pitcher TJ (1980) The sensory basis of fish schools: relative roles of lateral line and vision. *J Comp Physiol* 135(4):315–325. <https://doi.org/10.1007/BF00657647>
- Pascoe D, Matthey D (1977) Dietary Stress in Parasitized and Non-parasitized *Gasterosteus aculeatus* L. *Z Parasitenkd* 51:179–186. <https://doi.org/10.1007/BF00500957>
- Pekcan-Hekim Z, Joensuu L, Horppila J (2013) Predation by visual planktivore perch (*Perca fluviatilis*) in a turbulent and turbid environment. *Can J Fish Aquat Sci* 70:854–859. <https://doi.org/10.1139/cjfas-2012-0466>
- Persson L (1983) Food consumption and competition between age classes in a perch *Perca fluviatilis* population in a shallow eutrophic lake. *Oikos* 40:197–207. <https://doi.org/10.2307/3544583>
- Persson L (1986) Effects of reduced interspecific competition on resource utilization in perch (*Perca fluviatilis*). *Ecology* 67:355–364. <https://doi.org/10.2307/1938578>
- Pitcher TJ, Parrish JK (1993) Functions of shoaling behaviour in teleosts. In: Pitcher TJ (ed) *Behaviour of teleost fish*. Chapman & Hall, London, pp 363–439
- Poulin R (1995) “Adaptive” changes in the behaviour of parasitized animals: a critical review. *Int J Parasitol* 25:1371–1383. [https://doi.org/10.1016/0020-7519\(95\)00100-X](https://doi.org/10.1016/0020-7519(95)00100-X)
- Poulin R (2007) *Evolutionary ecology of parasites* 2nd edn. Princeton University Press, Princeton
- Rahn AK, Vitt S, Drolshagen L, Scharsack JP, Rick IP, Bakker TCM (2018) Parasitic infection of the eye lens affects shoaling preferences in three-spined stickleback. *Biol J Linn Soc* 123(2):377–387. <https://doi.org/10.1093/biolinnean/blx155>
- Richmond HE, Hrabik TR, Mensinger AF (2004) Light intensity, prey detection and foraging mechanisms of age 0 year yellow perch. *J Fish Biol* 65:195–205. <https://doi.org/10.1111/j.0022-1112.2004.00444.x>
- Sandström A (1999) Visual ecology of fish – a review with special reference to percids. *Natl Bd Fish Pub Fiskeriverket Rapp* 2:45–80
- Seppälä O, Karvonen A, Valtonen ET (2004) Parasite-induced change in host behaviour and susceptibility to predation in an eye fluke-fish interaction. *Anim Behav* 68:257–263. <https://doi.org/10.1016/j.anbehav.2003.10.021>
- Seppälä O, Karvonen A, Valtonen ET (2005a) Impaired crypsis of fish infected with a trophically transmitted parasite. *Anim Behav* 70:895–900. <https://doi.org/10.1016/j.anbehav.2005.01.021>
- Seppälä O, Karvonen A, Valtonen ET (2005b) Manipulation of fish host by eye flukes in relation to cataract formation and parasite infectivity. *Anim Behav* 70:889–894. <https://doi.org/10.1016/j.anbehav.2005.01.020>
- Seppälä O, Karvonen A, Valtonen ET (2008) Shoaling behaviour of fish under parasitism and predation risk. *Anim Behav* 75:145–150. <https://doi.org/10.1016/j.anbehav.2007.04.022>
- Seppälä O, Karvonen A, Valtonen ET (2012) Variation in food intake underlying ‘specific’ host manipulation by a trophically transmitted parasite. *Evol Ecol Res* 14:73–81
- Shariff M, Richards RH, Sommerville C (1980) The histopathology of acute and chronic infections of rainbow trout *Salmo gairdneri* Richardson with eye flukes, *Diplostomum* spp. *J Fish Dis* 3:455–465. <https://doi.org/10.1111/j.1365-2761.1980.tb00432.x>
- Staffan F, Magnhagen C, Alanära A (2002) Variation in food intake within groups of juvenile perch. *J Fish Biol* 60:771–774. <https://doi.org/10.1111/j.1095-8649.2002.tb01702.x>
- Strand Å, Alanära A, Magnhagen C (2007) Effect of group size on feed intake, growth and feed efficiency of juvenile perch. *J Fish Biol* 71:615–619. <https://doi.org/10.1111/j.1095-8649.2007.01497.x>
- Stumbo AD, Poulin R (2016) Possible mechanism of host manipulation resulting from a diel behaviour pattern of eye-dwelling parasites? *Parasitology* 143:1261–1267. <https://doi.org/10.1017/S0031182016000810>

- Svanbäck R, Persson L (2004) Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms. *J Anim Ecol* 73:973–982. <https://doi.org/10.1111/j.0021-8790.2004.00868.x>
- Ubels JL, DeJong RJ, Hoolsema B, Wurzberger A, Nguyen T, Blankespoor HD, Blankespoor CL (2018) Impairment of retinal function in yellow perch (*Perca flavescens*) by *Diplostomum baeri* metacercariae. *Int J Parasitol Parasites Wildl* 7:171–179. <https://doi.org/10.1016/j.ijppaw.2018.05.001>
- Utne ACW (1997) The effect of turbidity and illumination on the reaction distance and search time of the marine planktivore *Gobiusculus flavescens*. *J Fish Biol* 50:926–938. <https://doi.org/10.1111/j.1095-8649.1997.tb01619.x>
- Vinyard GL, O'Brien J (1976) Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). *J Fish Res Board Can* 33(12):2845–2849. <https://doi.org/10.1139/f76-342>
- Vivas Muñoz JC, Staaks G, Knopf K (2017) The eye fluke *Tylodelphys clavata* affects prey detection and intraspecific competition of European perch (*Perca fluviatilis*). *Parasitol Res* 116:2561–2567. <https://doi.org/10.1007/s00436-017-5564-1>
- Voutilainen A, Figueiredo K, Huuskonen H (2008) Effects of the eye fluke *Diplostomum spathaceum* on the energetics and feeding of Arctic charr *Salvelinus alpinus*. *J Fish Biol* 73:2228–2237. <https://doi.org/10.1111/j.1095-8649.2008.02050.x>
- Westerberg M, Staffan F, Magnhagen C (2004) Influence of predation risk on individual competitive ability and growth in Eurasian perch, *Perca fluviatilis*. *Anim Behav* 67:273–279. <https://doi.org/10.1016/j.anbehav.2003.06.003>
- Winfield IJ (1986) The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, *Rutilus rutilus*, rudd, *Scardinius erythrophthalmus*, and perch, *Perca fluviatilis*. *I J Fish Biol* 29:37–48. <https://doi.org/10.1111/j.1095-8649.1986.tb04997.x>

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.