Trematodes modulate aquatic food webs by altering host feeding behaviour

DISSERTATION

zur Erlangung des akademischen Grades

Doctor of Philosophy

(Ph.D.)

eingereicht an der

Lebenswissenschaftlichen Fakultät

der Humboldt-Universität zu Berlin

von

M.Sc. Jenny Carolina Vivas Muñoz

Präsidentin der Humboldt-Universität zu Berlin

Prof. Dr.-Ing. Dr. Sabine Kunst

Dekan der Lebenswissenschaftlichen Fakultät

Prof. Dr. Bernhard Grimm

Gutachterin/Gutachter

1. PD Dr. Klaus Knopf
2. Prof. Dr. Bernd Sures
3. PD Dr. Jasminca Behrmann-Godel

Tag der mündlichen Prüfung: 20. September 2019

This thesis was conducted at the Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin (Germany),

Department of Ecophysiology and Aquaculture

Berlin, 2019

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.

Acknowledgements

The competition of this thesis would not have been possible without all the supportive people around me. First and foremost, I would like to express my deep gratitude and appreciation to my supervisor Dr. Klaus Knopf. Over the last years his guidance and support were essential to help me overcoming problems and progress with this project. Thanks for having always an open door, your valuable advice on multiple matters and the encouraging conversations.

I am grateful to Dr. Sabine Hilt for supporting me during the development of this project. Her valuable and constructive suggestions contributed to the improvement of my work. Further I am indebted to Sabine and Klaus for believing in me and allowing me to be part of the IMPact-Vector graduate school, which apart from funding this study gave me the opportunity to visit Bolivia for the first time.

Without experimental animals, this project would not have been possible. Therefore, I am extremely thankful to Dr. Petr Horák and Mgr. Veronika Siegelová for providing me with snails for my experiments as well as the technical assistance and advice on their maintenance in the lab. Similarly, I would like to thank 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 and being always willing to go fishing for my research. Further many thanks to Amrei Gründer and Janne Ros Irmler for helping me to take care of the animals and also the long hours watching fish videos.

I am also particularly grateful to Dr. Kirsten Pohlmann for her encouragement and support during one of the toughest situations in the last years, as well as for her contribution with my application to IGB's equal opportunity fund, which greatly helped me to finish this thesis.

Sincere thanks to Dr. Milen Nachev and Dr. Alessandro Manfrin for their scientific support with the stable isotopes. I am likewise grateful to Dr. Christian K. Feld for his statistical advice and lessons, which immensely improved my skills in R. Also a

big thank you to Katrin Honka for her hospitality when I went to Essen and all the fun we had making nail art.

I am very fortunate to have friends who always supported and encouraged me even from the distance. Thanks for all your love. I owe a special debt of gratitude to Dr. Andrea Zikova for all the help in the lab, but more importantly, for being a sincere friend and having always open ears and clear thoughts for me. I would also like to express my heartfelt thanks to David Krienelke, who has always been there during all the ups and downs, for your continuous understanding, patience and encouragement. Thank you for believing in me and giving me countless unforgettable memories. I would not have done it without your support.

Last but not least, my biggest debt of gratitude is owed to my parents. Reky, the last years proved to be the hardest of our lives, however, your unwavering faith and confidence on me gave the power to keep going and never give up. Thank you for your strength and patience, I would not have managed to reach this stage without them. Juan, you were the most encouraging person when I started this project. I hope that from heaven you can see that I made it.

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Summary

Parasites are an integral component of ecosystems. There is broad consensus that parasites commonly contribute positively to biodiversity and that they can play important roles structuring communities. Yet, there are still major knowledge gaps about the role that different parasites play in ecosystems. Further research is needed to advance our understanding of the complex relationships between parasites, hosts, communities and ecosystems, and to find a satisfactory way to incorporate parasites into ecological models and food webs. Parasites can influence energy transfer through communities via trophic cascades by inducing alterations on consumer-resource interactions. This study evaluated the role of trematodes on their host's feeding behaviour at two trophic levels. First the impact of infection on grazing activity of freshwater snails (primary consumers) and second the impact of eye fluke infection on feeding behaviour and prey preferences of European perch (*Perca fluviatilis*; secondary consumer).

In freshwater ecosystems, snails can significantly influence the competition between primary producers through grazing of periphyton. This activity can potentially be modified by trematodes, which mostly use molluscs as a first intermediate host. In this study, four different freshwater snail–trematode systems were used to test whether a general pattern can be detected for the impact of trematode infections on snail periphyton grazing activity. In the examined systems, mass-specific periphyton grazing rates of infected snails were higher, lower, or similar to rates of non-infected conspecifics, showing that no general pattern exists. The variation across studied snail–trematode systems may result from differences on how the parasites use the resources of the snail and thus affect its energy budget. Trematode infections can significantly alter the grazing rate of snails, where, depending on the system, the mass-specific grazing rate can double or halve. This result underlines both, the high ecological relevance of trematodes and the need for comprehensive studies at the species level to allow an integration of these host–parasite interactions into aquatic food web concepts

Visual performance as well as environmental conditions can influence both behavioral patterns and consumer-resource interactions of fish. Eye parasites can impair their host's sensory performance with important consequences for the detection of prey, predators and conspecifics. European perch experimentally infected with the eye fluke *Tylodelphys clavata* were used to evaluate their feeding behaviour 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, the experiment was performed 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 had more unsuccessful attacks on *A. aquaticus*. Although the outcome of competition depended on prey species presumably driven by prey distribution and behaviour patterns, there was a general tendency that non-infected fish consumed more of the available prey under both light intensities. 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; under natural conditions this presumably increases predation risk and potentially enhances transmission success of the parasite to the final host. Moreover, such alterations on predator-prey interactions may also modulate energy flow from lower to upper trophic levels.

Intraspecific diet specialization, usually driven by resources availability, competition and predation, is common in natural populations. However, the role of parasites on diet specialization of their hosts has rarely been studied. To evaluate whether perch alter their prey preference as a compensatory mechanism for reduced foraging efficiency and competitive ability caused by *T. clavata* infection, young-of-the-year (YOY) perch from Lake Müggelsee were sampled and their diet was evaluated using both stomach content and stable isotope analyses. The diet of the fish was dominated by zooplankton and benthic macroinvertebrates. Both methods in agreement indicated that with increasing infection intensity fish had a more selective diet, feeding mainly on *Dikerogammarus villosus*, while less intensively infected fish appeared to be generalist feeders showing no preference for any particular prey type.

Thus, infection with eye flukes can indirectly affect not only the energy flow to higher trophic levels, by increasing host's predation risk, but also the interaction of the host with lower trophic levels by altering the prey preference.

The results from this study confirm that trematodes can play a relevant role within food webs by altering their hosts' feeding behaviour. Furthermore, in this way trematodes can affect the interaction strengths of their hosts with other species at various trophic levels. The key to understanding how populations and community dynamics are influenced by the interaction of individual species, is by having a solid understanding of the diversity of interactions between all species involved. The thorough study of the interactions in individual host-parasite systems and their ramification on other members of the food web is a prerequisite for the creation of realistic food web models in which parasites are adequately included.

Keywords: Trematodes, host-parasite interaction, feeding behaviour, freshwater snails, *Tylodelphys clavata*, eye fluke, *Perca fluviatilis*, intraspecific competition, intraspecific diet specialization

Zusammenfassung

Parasiten sind ein integraler Bestandteil von Ökosystemen. Es besteht weitgehend Einigkeit darüber, dass Parasiten im Allgemeinen die Biodiversität erhöhen, und dass sie eine wichtige Rolle bei der Strukturierung von Lebensgemeinschaften spielen können. Es bestehen jedoch noch immer noch große Wissenslücken dazu, welche Rolle verschiede Parasiten im Ökosystem spielen. Weitere Forschung ist notwendig, um unser Verständnis der komplexen Zusammenhänge zwischen Parasiten, Wirten, Lebensgemeinschaften und Ökosystemen zu verbessern, und einen zufriedenstellenden Weg zu finden, Parasiten in ökologische Modelle und Nahrungsnetze zu integrieren. Parasiten können den Energietransfer in Lebensgemeinschaften über trophische Kaskaden beeinflussen, indem sie Änderungen in den Konsumenten-Ressourcen-Interaktionen induzieren. In der vorliegenden Arbeit wurde die Rolle von Trematoden auf das Fraßverhalten ihrer Wirte auf zwei trophischen Ebenen untersucht. Dies war zum einen die Auswirkung einer Infektion auf die Grazingaktivität von Süßwasserschnecken (Primärkonsumenten) und zum zweiten die Auswirkungen einer Infektion mit Metazerkarien in den Augen auf das Fraßverhalten und Beutepräferenz beim Flussbarsch (*Perca fluviatilis*; Sekundärkonsument).

In Süßwasserökosystemen können Schnecken den Wettbewerb zwischen Primärproduzenten durch Beweidung von Periphyton erheblich beeinflussen. Diese Aktivität kann möglicherweise durch Trematoden, die meist Mollusken als ersten Zwischenwirt nutzen, modifiziert werden. In dieser Studie wurden vier verschiedene Süßwasserschnecken-Trematoden-Systeme verwendet, um zu testen, ob ein allgemeines Muster für die Auswirkung von Trematodeninfektionen auf die Grazingaktivität von Schnecken auf das Periphyton nachgewiesen werden kann. Bei den untersuchten Systemen waren die massenspezifischen Grazingraten auf Periphyton bei infizierten Schnecken entweder höher, niedriger oder ähnlich denen derjenigen von nicht infizierten Artgenossen, was zeigt, dass kein allgemeines Muster existiert. Die Unterschiede zwischen den untersuchten Schnecken-Trematoden-Systemen können darauf zurückzuführen sein, wie unterschiedlich die Parasiten die Ressourcen der Schnecke nutzen und damit deren Energiebudget

beeinflussen. Die Infektion mit Trematoden kann die Grazingrate von Schnecken erheblich verändern, wobei sich die massespezifische Grazingrate je nach System verdoppeln oder halbieren kann. Dieses Ergebnis unterstreicht sowohl die hohe ökologische Relevanz von Trematoden als auch die Notwendigkeit umfassender Untersuchungen auf Artniveau, um diese Wirt-Parasit-Wechselwirkungen in Konzepte aquatischer Nahrungsnetze integrieren zu können.

Sowohl die Sehkraft als auch Umgebungsbedingungen können Verhaltensmuster und Konsumenten-Ressourcen-Interaktionen von Fischen beeinflussen. Augenparasiten können die sensorische Leistungsfähigkeit ihres Wirtes beeinträchtigen, was entscheidende Auswirkungen auf das Erkennen von Beutetieren, Raubtieren und Artgenossen hat. Mit dem Augenparasiten *Tylodelphys clavata* experimentell infizierte Flussbarsche wurden in Gruppen von vier Individuen und mit zwei verschiedenen Beutetierarten (*Asellus aquaticus* und *Daphnia magna*) eingesetzt, um deren Fraßverhalten und Wettbewerbsfähigkeit in Konkurrenz mit nicht infizierten Artgenossen zu untersuchen. Um zu testen, ob sich die Auswirkung einer Infektion mit *T. clavata* bei verschiedenen Lichtbedingungen unterscheidet, wurde das Experiment bei zwei Lichtintensitäten (600 Lux und 6 Lux) durchgeführt. Die Effizienz der Nahrungssuche der Flussbarsche wurde signifikant durch die Infektion, aber nicht durch die Lichtintensität beeinflusst. Die Entfernung, aus der infizierte Fische die beiden Beutetierarten attackierten, war im Vergleich zu nicht infizierten Artgenossen signifikant kürzer. Außerdem attackierten infizierte Fische *A. aquaticus* öfters erfolglos. Obwohl das Ergebnis des Wettbewerbs von der Beutetierart abhing, was vermutlich durch deren Verteilung und Verhaltensmuster bedingt war, bestand allgemein die Tendenz, dass nicht infizierte Fische bei beiden Lichtintensitäten mehr von den verfügbaren Beutetieren verzehrten. Da die Infektion mit *T. clavata* die Effizienz der Nahrungssuche und die Wettbewerbsfähigkeit beeinträchtigt, müssten infizierte Fische mehr Zeit mit der Nahrungssuche verbringen, um eine ähnliche Nahrungsaufnahme zu erreichen wie nicht infizierte Artgenossen. Unter natürlichen Bedingungen erhöht dies vermutlich das Prädationsrisiko und damit potentiell auch die erfolgreiche Übertragung des Parasiten zum Endwirt. Darüber hinaus können solche Änderungen von Räuber-Beute-Interaktionen auch den Energiefluss von unteren zu oberen trophischen Ebenen modulieren.

Intraspezifische Spezialisierung auf eine bestimmte Ernährung, was in der Regel von deren Verfügbarkeit, Wettbewerb und Prädation verursacht wird, findet sich häufig in natürlichen Populationen. Die Rolle von Parasiten auf die Ernährungsspezialisierung ihrer Wirte wurde jedoch nur selten untersucht. Um zu prüfen, ob der Flussbarsch als Kompensation für die durch die Infektion mit *T. clavata* verursachte verringerte Effizienz der Nahrungssuche und Wettbewerbsfähigkeit seine Beutepräferenz verändert, wurde die Beutezusammensetzung von young-of-the-year (YOY) Flussbarschen aus dem Müggelsees mittels Mageninhaltsanalysen und Stabilisotopenanalysen untersucht. Die Nahrung der Fische war von Zooplankton und benthischen Makroinvertebraten dominiert. Beide Methoden ergaben übereinstimmend, dass sich die Fische mit zunehmender Intensität der Infektion selektiver und hauptsächlich von *Dikerogammarus villosus* ernährten, während sich geringer infizierte Fische Generalisten herausstellten, die keinen besonderen Beutetyp bevorzugten. Somit kann eine Infektion der Augen mit Metazerkarien auf indirekte Weise nicht nur den Energiefluss zu höheren trophischen Ebenen durch ein erhöhtes Prädationsrisiko des Wirts beeinflussen, sondern auch die Interaktion des Wirts mit niedrigeren trophischen Ebenen durch Veränderung der Beutepräferenz.

Die Ergebnisse dieser Studie bestätigen, dass Trematoden eine wichtige Rolle in Nahrungsnetzen spielen können, indem sie das Fraßverhalten ihres Wirtes verändern. Darüber hinaus können Trematoden so die Stärke der Interaktion ihrer Wirte mit anderen Arten auf verschiedenen trophischen Ebenen beeinflussen. Der Schlüssel zum Verständnis, wie Populationen und die Dynamik von Lebensgemeinschaften durch die Interaktion einzelner Arten beeinflusst werden, ist ein solides Verständnis der Vielfalt der Wechselwirkungen zwischen allen beteiligten Arten. Die gründliche Untersuchung der Interaktionen in einzelnen Wirt-Parasit-Systemen und deren weiterreichende Auswirkungen auf andere Mitglieder im Nahrungsnetz ist eine Voraussetzung für die Erstellung realistischer Nahrungsnetz-Modellen, in denen Parasiten adäquat berücksichtigt sind.

Schlagwörter: Trematoden, Wirt-Parasit-Interaktionen, Fraßverhalten, Süßwasserschnecken, *Tylodelphys clavata*, Infektion der Augen mit Metazerkarien, *Perca fluviatilis*, Intraspezifische Konkurrenz, Intraspezifische Spezialisierung.

1. Introduction

1.1 Parasitism and trematodes: a big picture

The parasitic way of life is probably one of the most common life forms on earth. It has been estimated that approximately half of the species known to science are parasitic, being either obligatory parasites or having a parasitic stage in their life cycle (Windsor 1998; Dobson et al. 2008). The origins of parasitism go back several million years, as indicated by fossil evidence (Conway Morris 1981; Upeniece 2001). From these early records, parasites have greatly diversified and nowadays a wide variety of life cycles and adaptations to their parasitic existence can been seen in several taxa (Poulin and Morand 2000, 2004).

Parasites evolved from free-living ancestors. A permanent interspecific association required pre-adaptations for survival, feeding and reproduction on the host plus the reproductive success as a parasite must be greater than the success as a free-living animal (Poulin 2007, 2011). Phylogenetic evidence reveals that parasitism arose independently in several taxa (Poulin 2011; Weinstein and Kuris 2016). In the same way, evolutionary transitions from simple to complex life cycles have independently appeared in multiple groups (Blaxter et al. 1998, Herlyn et al. 2003; Cribb et al. 2003; Poulin 2011). For instance, an ancestral one-host life cycle in which the host became part of a new food chain because a new predator arrived on the scene. If the host was routinely eaten by the new predator, selection would have favoured any parasite capable of surviving inside the predator and subsequently made adjustment to their developmental schedule so that adulthood became linked with the ingestion by the predator. In this scenario a new definitive host would be added to the cycle (upward incorporation). Contrarily, the inclusion of an intermediate host (downward incorporation) occurred, for instance, when the parasite evolved to infect a second species that routinely consumed the parasite's transmission stages (e.g. eggs) (Parker et al. 2003; Poulin 2011; Auld and Tinsley 2015). After such historical events that affected the transmission of the parasite or the survival of its host, selection favoured those parasites capable to adjust to the new conditions (Poulin 2007, 2011).

Trematoda is a widespread and large class of parasites with one of the most complex life cycles involving many morphologically distinct forms, distinctive generations and various different ways to infect their hosts (Cribb et al. 2003; Poulin 2007). The class is divided into two subclasses, the Aspidogastrea and the Digenea. The former is a small group present only in aquatic ecosystems infecting molluscs, fish and chelonians (Gibson et al. 2002). On the other hand, the Digenea is a large and diverse group distributed worldwide that normally uses molluscs as intermediate hosts and vertebrates as final hosts. Digeneans are found in all classes of vertebrates but are less diverse in agnathans and chondrichthyans (Gibson et al. 2002; Kostadinova and Pérez del Olmo 2014).

The vast majority of digenean life cycles involve three hosts and transmission challenges. Firstly, eggs are released from adult worms in the definitive host and hatch into miracidia (ciliated and often free-swimming larva), which must find a suitable mollusc (the first intermediate host), where the trematode larvae reproduce asexually to produce cercariae. Then cercariae emerge from the first intermediate host and must locate a suitable second intermediate host, in which the metacercariae develop. Finally, metacercariae and second intermediate host must be ingested by an appropriate definitive host to complete the life cycle (Poulin and Cribb 2002; Cribb et al. 2003) (Figure 1). To face these transmission challenges several adaptations have been favoured by natural selection, such as efficient host-finding mechanisms in miracidia and cercariae, as well as parasite-mediated mechanisms to increase the susceptibility of the second intermediate host to predation (Haas 1992, 2003; Combes et al. 1994; Moore 2002; Sukhdeo and Sukhdeo 2004; Hughes *et* al. 2012). However, in particular digenean families, the life cycle has been reduced to two hosts (e.g. Schistosomatidae) or in some cases just one (e.g. Cyathocotylidae: *Mesostephanus haliasturis*) (Barker and Cribb 1993; Combes et al. 2002; Poulin and Cribb 2002).

Parasites with multiple-host life cycles, necessarily link them to several different taxa of surrounding animal populations. There is mounting evidence that parasites influence the interaction strength between the host and other species, having important effects on the functional role of hosts in the ecosystem and the structure of animal communities and food webs (Minchella and Scott 1991; Marcogliese and

Cone 1997; Thompson et al. 2005; Hernandez and Sukhdeo 2008; Dick et al. 2010; Hatcher and Dunn 2011). Recent food webs studies have shown that the inclusion of parasites alters network structure and affects species richness, connectance, and linkage density, among other food web statistics (Lafferty et al. 2006; Lafferty et al. 2008; Dunne et al. 2013). Additionally, parasites can account for a substantial proportion of both biomass and productivity, contributing directly to the energy flow in the system (Thieltges et al. 2008; Soldánová et al. 2016). Although there is no longer the need to argue that parasites must be included in ecological models, there is still no satisfactory way to insert parasites into food webs (Sukhdeo 2010, 2012). For example, from case studies few generalizations have emerged among different host-parasite systems and some key assumptions, such as size-based trophic cascades disallow parasites in food web models because parasites are smaller than their food (hosts) (Marcogliese and Cone 1997; Thompson et al. 2005; Lafferty et al. 2008; Warren et al 2010). It has been suggested that a correct incorporation of parasites into food webs requires data on the effects of parasites in energy or biomass flows (Sukhdeo 2010), and there is still a big gap in knowledge.

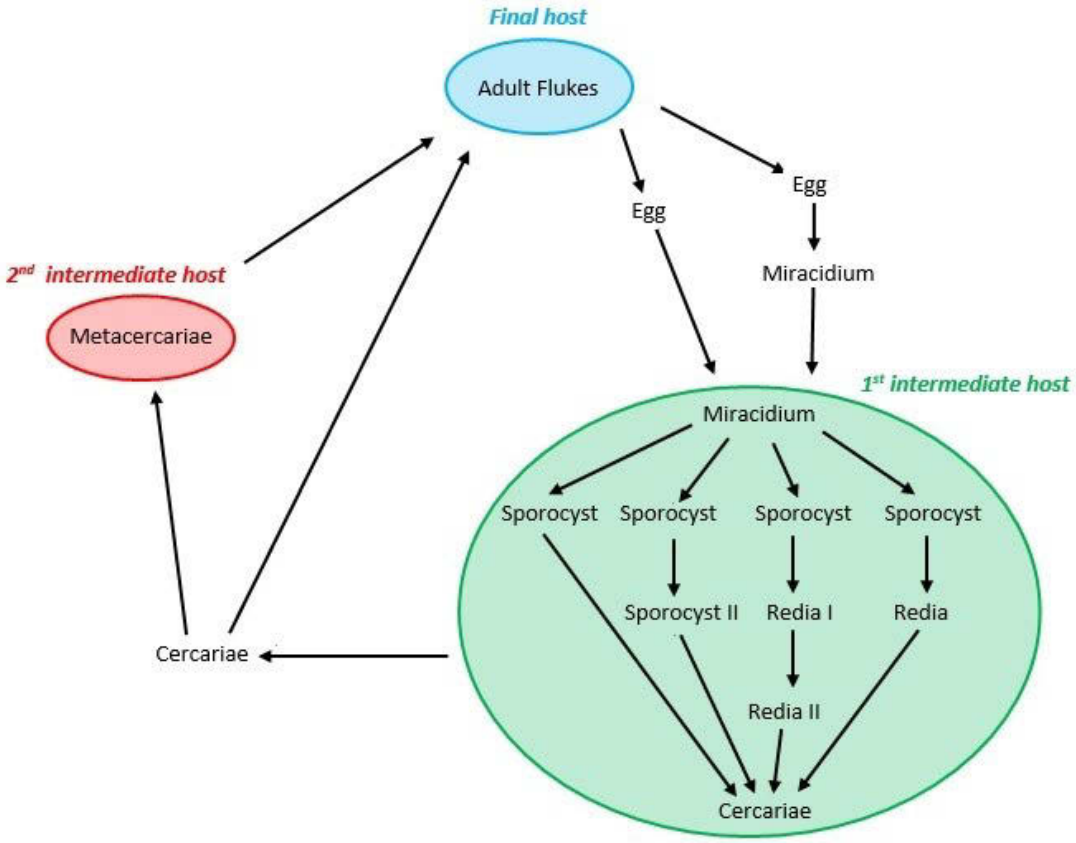

Figure 1. Diagram of common pathways of digenean life cycles.

1.2 Digenean trematodes and their molluscan host

Due to the almost exclusive use of molluscs as first intermediate host, with the exception of a few marine sanguinicolid trematodes that use annelids, they can be considered as keystone species for digeneans (Dillon 2000; Esch et al. 2001). The first larval stage of digeneans, the miracidium, seeks for and actively penetrates an appropriate mollusc host or, in some species, the eggs are directly consumed by a suitable mollusc and the miracidium hatches in the gut of its host. The final infection sites of the parasite are hepatopancreas, gonads or mantle, where the larva transforms into a sporocyst which acts as a germinal sac and produces either daughter sporocysts or rediae (Malek 1980; Esch et al. 2001). The uptake of nutrients by the sporocyst takes place through the tegument. However, in the redia apart from the uptake through the tegument, there is also a direct consumption of host tissue since it possesses a mouth and a primitive gut (Figure 2) (Malek 1980; Mehlhorn 2008; Skála et al. 2014). All intramolluscan embryogenesis is asexual and leads finally to the production of numerous cercariae, depending on the species, within the sporocyst or the redia (Esch et al. 2001) (Figure 2). Cercarial production varies greatly between digenean species, with some species releasing less than 500 cercariae snail^{-1} day^{-1} (e.g. *Cryptocotyle concavum*) and others producing a much larger number of cercariae, up to 30000 or 60000 cercariae snail^{-1} day^{-1} (e.g. *Trichobilharzia szidati* and *Diplostomum spathaceum*, respectively) and well beyond have also been reported, up to 250000 or 500000 cercariae snail^{-1} day^{-1} (e.g. opecoelid cercariae) (Lyholt and Buchmann 1996; Haas 2003; Karvonen et al. 2004a; Cribb 2005; Thieltges et al. 2008; Soldánová et al. 2016).

Asexual intramolluscan reproduction is an impressive evolutionary adaptation of the digeneans. It probably explains the difference in the success (species richness) between the two trematode subclasses. The aspidogastreans have no asexual reproduction in the mollusc host and from the more than 15000 trematode species less than 100 species belong to this subclass (Cribb 2005; Kostadinova and Pérez del Olmo 2014). However, with this remarkable asexual reproduction, digeneans need to acquire space to accommodate the increasing number of developing parasites leading to a parasitic invasion on average of 20 – 30 % and up to 50 % of the biomass within

a snail's shell (Figure 3) (Bernot and Lamberti 2008; Hechinger et al. 2009). Additionally, they also need to obtain enough energy for their own maintenance, growth and multiplication, which imposes energetic constraints modifying their hosts' energetic budget and energy allocation patterns (Theron and Gerard 1994; de Jong-Brink et al. 2001; Hechinger et al. 2009).

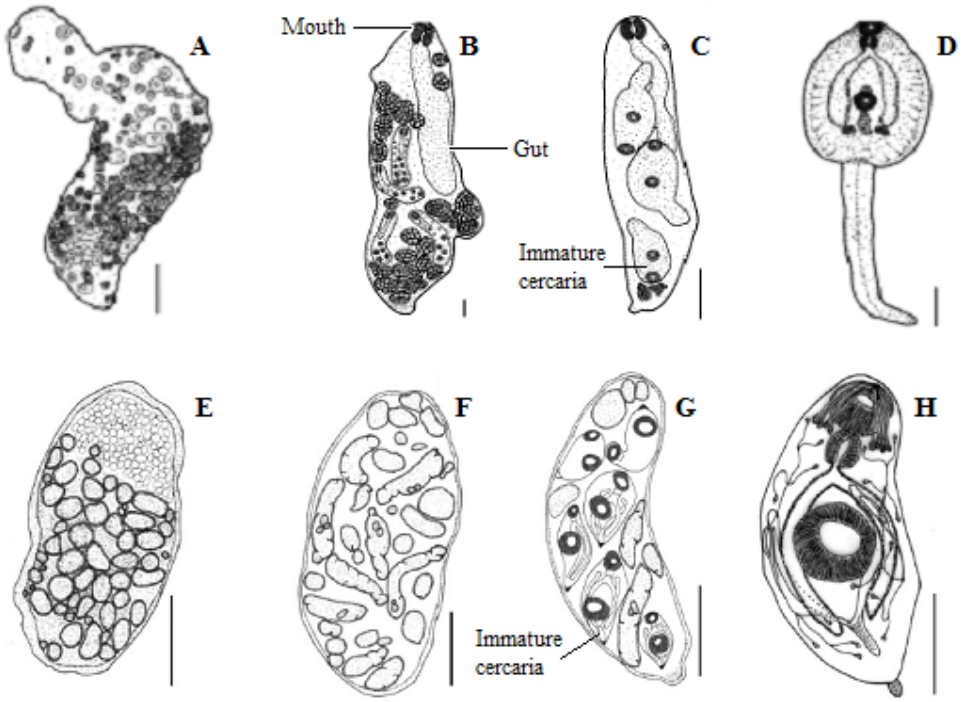

Figure 2. Illustration of the intramolluscan development of two digenean species, *Fasiola gigantica* (A-D) and *Proctoeces maculatus* (E-H). **(A)** and **(E)** Sporocyst containing germinal balls; **(B)** mother redia; **(C)** daughter redia; **(D)** cercaria of *F. gigantica*; **(F)** mother sporocyst containing daughter sporocysts; **(G)** daughter sporocyst; **(H)** cercaria of *P. maculatus*. Scale bars: (A) = 30 µm; (B-D) = 100 µm; (E-G) = 200µm; (H) = 50 µm (modified from Phalee et al. 2015 and Antar and Gargouri 2015).

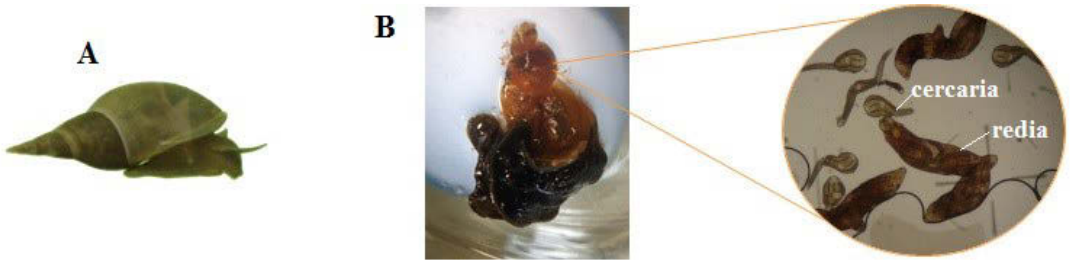

Figure 3. Intramolluscan invasion of *Echinoparyphium aconiatum* **(A)** *Lymnaea stagnalis,* **(B)** dissected snail infected with *E. aconiatum*, the posterior part of the snail's body (in orange) shows the extensive invasion of *E. aconiatum* and the magnified section displays both cercariae and rediae of *E. aconiatum*.

Within the molluscan host, digeneans typically occupy either the hepatopacreas or the gonadal space (or both) having important physiological effects, which vary

among parasite-host systems (Malek 1980; Pratt and Barton 1941; Cheng and Snyder 1962a; Probst and Kube 1999). One of the most distinctive impacts is the partial or completely castration of the host (Cheng and Snyder 1962a; Probst and Kube 1999; de Jong-Brink et al. 2001; Sorensen and Michella 2001; Faro et al. 2013). Parasitic castration implies that the animal is "evolutionarily dead". Indeed, it continues living and feeding but it will no longer produce descendants. Sometimes infection leads to parasitic gigantism where the infected host grows larger than non-infected conspecifics (Mouritsen and Jensen 1994; Sorensen and Michella 1998; Probst and Kube 1999). Both inhibition of reproductive activity and enhancement of abnormal growth of its host are advantageous strategies for obtaining the energy and space needed by the parasite. Additionally, several biochemical and histopathological alterations have been observed in infected snails (Pratt and Barton 1941; Cheng and Snyder 1962a, b; Malek 1980; Faro et al. 2013). For instance, reduction in the glycogen levels and total protein content, displacement of hepatopancreatic tubules and breakdown of cell membranes have commonly been reported in different host-parasite systems (Malek 1980; Joosse and Van Elk 1986; Pinheiro et al. 2009; Faro et al. 2013).

Apart from physiological alterations digeneans can also impact host survival (Jokela et al. 1999; Karvonen et al 2004a; Żbikowska 2011; Żbikowska and Cichy 2012) and even induce behavioral alteration in order to enhance transmission efficiency (Curtis 1990; Levri 1999; Levri et al. 2007; Voutilainen 2010). The shedding of *Gynaecotyla adunca* cercariae is restricted to night-time and infected snails (*Ilyanassa obsoleta*) showed a peculiar low tidal nocturnal migration pattern towards the beach, where the target intermediate host (crustaceans beach-hoppers, *Talorchestia longicornis*) is present. This migration enhances both spatial and temporal overlap between the cercariae and the next host in their life cycle, as *T. longiscornis* is mostly active at night (Curtis, 1990). Considering all mentioned effects, it is undoubtedly that digeneans influence host fitness and ultimately can impact host population dynamics. Moreover, they may indirectly affect host interactions with other species escalating their impact on community and ecosystem level (Thomas et al. 1998; Dunn et al. 2012; Sargent et al. 2014).

When removing the parasites from the picture, molluscs are by themselves an important component of benthic communities in aquatic ecosystems. In many streams and lakes, snails are dominant grazers feeding commonly on periphytic algae/bacteria/detritus complexes and on decaying macrophyte tissues (Brönmark 1990). Additionally there is evidence that they can have a strong impact on periphyton community structure by affecting biomass, productivity and species composition (Lowe and Hunter 1988; Brönmark 1989; Vermaat 1994; Krist and Charles 2012). As a result of their high grazing rate, snails reduce the shading effect of periphyton on macrophytes and thus play a major role in top-down control of this key structural element (Brönmark 1985; Brönmark and Weisner 1992; Jones et al. 2002; Jones and Sayer 2003; Li et al. 2009), contributing to the maintenance of high water clarity in lakes and rivers (Scheffer et al. 1993, Hilt et al. 2011). A decrease in snail abundance, for example by predation, can cause a cascading effect increasing periphyton biomass and consequently, through shading and competition for nutrients, leading to a decrease in macrophyte biomass (Brönmark et al. 1992; Brönmark 1994; Jones and Sayer 2003).

In the same way as predation, digeneans that compromise snail reproduction may modulate top-down periphyton control in benthic communities. Furthermore, taking into account the pathological alterations and the energetic demand of both parasite and host, it is quite likely that digeneans can indirectly affect periphyton community structure by changing the grazing activity of their snail hosts. Two studies have shown that infection of snails with digeneans can result in either decreased or increased feeding rate of the hosts. For the marine snail *Littorina littorea* the feeding rate is reduced by 40 % in individuals infected with *Cryptocotyle lingua* (Wood et al. 2007). On the other hand, infection with *Posthodiplostomum minimum* increased the periphyton grazing rate of the freshwater snail *Physa acuta* (Bernot and Lamberti 2008). Considering that aquatic benthic communities are in fact complex trematode assemblages within various mollusc species, the indirect effects of digeneans on periphyton community structure, as mediated by snails, remains unclear. Further research with various snail-trematode systems is required to unravel the role of parasitism in the snail-periphyton interaction.

1.3 The eye fluke *Tylodelphys clavata*

Tylodelphys clavata (Diplostomidae) has a typical trematode life cycle involving three host species. Sexual maturity is reached in the gastrointestinal tract of grebes (*Podiceps* spp.), the final bird hosts. The aquatic snails *Lymnaea stagnalis* and *Radix* spp. serve as first intermediate hosts and *T. clavata* cercariae can infect a wide range of fish species, which act as second intermediate hosts (Kozicka and Niewiadomska 1960; Faltýnková and Haas 2006; Faltýnková et al. 2007). However, high prevalence and intensity levels in European perch (*Perca fluviatilis*) populations are common (Vivas Muñoz 2014). For instance, mean intensities of 425 and 308 metacercariae per fish were reported in perch populations from Slapton Ley (England) and Lake Sığırcı (Turkey), respectively (Kennedy 1981; Soylu 2013). For this reason, perch is considered to be the primary host of *T. clavata* and other fish species that are usually less severely infected are secondary hosts of this species (Kozicka and Niewiadomska 1960). Once the cercariae penetrate the skin or gill filaments of the fish, they shed their tail and migrate through the host tissues settling in the eye. Here they transform into metacercariae. In the earliest stage the larva is relatively small (body length: 0.21 mm) and retains morphological features of the cercaria. Progressively, the larva grows and doubles its size by the time full development is completed (Kozicka and Niewiadomska 1960). Within the eye *T. clavata* infect the vitreous humour. Metacercariae are mobile and active between the fish's lens and retina (Stumbo and Poulin 2016). The life cycle is completed when an infested fish is eaten by the final avian host (Figure 4).

Trophically transmitted parasites, such as *T. clavata*, can alter the intermediate hosts' behaviour or other phenotypic traits to increase susceptibility to predation by the target host. This strategy to increase transmission success would not only be favoured by natural selection, but can also severely influence host ecology (Moore 2002; Lafferty and Kuris 2012). In general, phenotypic and behavioural alterations observed in infected hosts that appear to increase parasite fitness have been called "host manipulation" and described in several aquatic and terrestrial parasite-host systems (Moore 2002; Hughes et al. 2012).

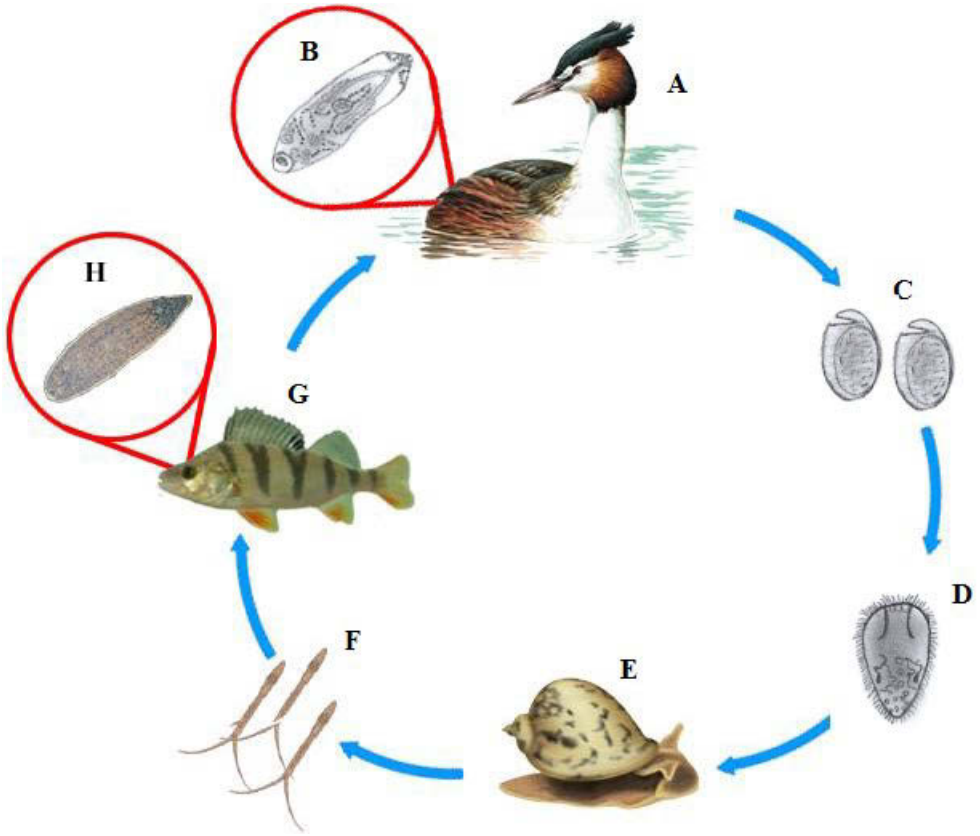

Figure 4. Life cycle of *Tylodelphys clavata*. **(A)** Final host (*Podiceps* spp.); **(B)** adult, which infects the gastrointestinal tract of the bird host; **(C)** eggs; **(D)** free-swimming miracidium; **(E)** snail first intermediate host (*Radix* spp.); **(F)** free-swimming cercariae; **(G)** fish second intermediate host; **(H)** metacercaria, which develops in the fish eyes (modified from Vivas Muñoz 2014).

Numerous studies have associated parasitic infection with changes in a wide range of fish behaviour, for example habitat selection, competitive ability, foraging efficiency and swimming performance (Barber et al. 2000; Barber and Wright 2005). However, there are only a limited number of experimental studies that can prove the causal relationship between parasite infection and behavioural changes (Barber 2007). Various diplostomatid trematodes infect the eyes of their fish host and can potentially impair their visual performance (Shariff et al. 1980; Stumbo and Poulin 2016). Consequently, eye flukes provide a suitable model to study host manipulation and behavioural changes.

The internal structure of the eye represents an immune privileged structure (Caspi 2013) and thereby eye fluke can escape the host immune defence. Different parts of the fish eye, such as the lens, vitreous humour and retina are a target of *Diplostomum* spp. and *Tylodelphys* spp. Histological damages to the choroid layer, pigment

epithelium and photoreceptors have been recently documented in fish infected with *Diplostomum* spp., targeting the retina (Padros et al. 2018; Ubels et al. 2018). However, the most notorious pathological effect from eye fluke infection is lens opacity (cataracts), caused by metabolic excretions of lens infecting fluke species (Figure 5a, Shariff et al. 1980; Karvonen et al. 2004b). In both cases, these parasite-induced alterations on the optical tissues have been associated with impaired visual function (Shariff et al. 1980; Karvonen et al. 2004b; Padros et al. 2018; Ubels et al. 2018).

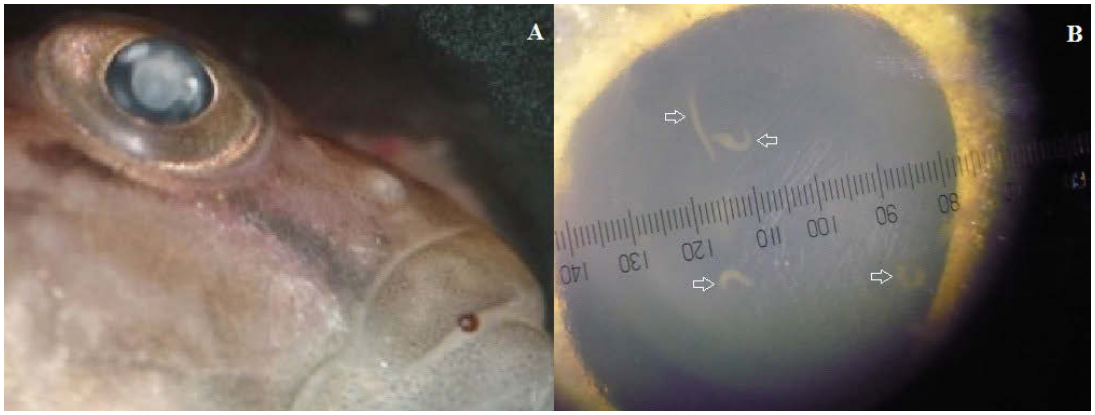

Figure 5. Eyes of fish infected with two different types of eye flukes. **(A)** Round goby (*Neogobius melanostomus*) infected with *Diplostomum* sp. (lens infecting fluke) caused in this individual a cataract, **(B)** Eye of European perch infected with *Tylodelphys clavata* (vitreous humour dwelling fluke), metacercariae (white arrows) are in the anterior chamber of the eye, in front of the visual field (modified from Flink et al. 2017 and Vivas Muñoz 2014).

Behavioural studies have shown that the lens infecting *Diplostomum* spp. have important consequences on, among others, foraging efficiency, habitat selection, shoaling and antipredator behaviour (Table 1) (Crowden and Broom 1980; Owen et al. 1993; Seppälä et al. 2004, 2005a, 2005b, 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 humour 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*) showed that the presence of *Tylodelphys* sp. metacercariae in front of the visual field causes retinal obstruction. Additionally, considering the semi-transparent body of the metacercariae, the active movement of

multiple flukes may lead to a shifting of light intensity over the retina (Figure 5b, Stumbo and Poulin 2016). Retinal 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).

Only one study described behavioural changes associated to the non-lens infecting fluke *T. clavata*. Vivas Muñoz et al. (2017) using naturally infected European perch (*P. fluviatilis*) showed that foraging efficiency declined with increasing infection intensity of *T. clavata*. 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).

It is conceivable, that 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*) infected with plerocercoids of the cestode *Schistocephalus solidus* which also decrease the foraging competitive ability of the host (Milinski 1984; Barber and Huntingford 1995). When competing with non-infected conspecifics for differently-sized *Daphnia magna*, infected sticklebacks mostly fed on the smaller sized prey for which the non-infected fish had no preference (Milinski 1984). Additionally, 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).

Table 1. Summary of fish behavioural changes associated with eye fluke infections.

Behaviour category	Host	Parasite	Behavioral change observed	Experimental or natural infection	Reference
Aggression	Rainbow trout *Oncorhychus mykiss*	*Diplostomum spathaceum*	Reduced aggression when parasite pre-infective, increased aggression when parasites became infective for final host	Experimental	Mikheev et al. (2010)
Competition	Rainbow trout *O. mykiss*	*D. spathaceum*	Infected fish lost contests for a territory against the control fish	Experimental	Mikheev et al. (2010)
Antipredator behaviour	Rainbow trout *O. mykiss*	*Diplostomum pseudospathaceum*	Reduced escape response, impaired crypsis, decreased shoaling behaviour and cohesiveness of the shoals after a simulated avian attack	Experimental	Seppälä et al. (2004, 2005a, 2008)
Antipredator behaviour	Rainbow trout *O. mykiss*	*D. pseudospathaceum*	Fish harboring pre-infective parasites less vulnerable to simulated predation and less active	Experimental	Gopko et al. (2015)
Antipredator behaviour	Rainbow trout *O. mykiss*	*D. pseudospathaceum*	Fish harboring infective parasites increased activity and reduced activity latency after a simulated avian attack.	Experimental	Gopko et al. (2017)
Antipredator behaviour	Round goby *Neogobius melanostomus*	*Diplostomum* spp.	Reduced escape response to simulated aerial attack	Natural	Flink et al. (2017)
Habitat selection	Rainbow trout *O. mykiss*	*D. pseudospathaceum*	Fish harboring infective parasites preferred to stay close to the water surface	Experimental	Gopko et al. (2017)
Habitat selection	Dace *Leuciscus leuciscus*	*D. spathaceum*	Spent more time at the water surface. Infection intensity correlated positively with the time-at-surface	Natural	Crowden and Broom (1980)
Foraging	Three-spined stickleback *Gasterosteus aculeatus*	*D. pseudospathaceum*	Infected fish experience reduce visual acuity, shorter reactive distance to prey	Natural	Owen et al. (1993)
Foraging	Dace *L. leuciscus*	*D. spathaceum*	Infection intensity correlated negatively with the reactive distance to prey and positively with the amount of time spent feeding	Natural	Crowden and Broom (1980)
Foraging	Artic charr *Salvelinus alpinus*	*D. spathaceum*	Decreased success rate with increasing cataract coverage	Experimental	Voutilainen et al. (2008)
Foraging	European perch *Perca fluviatilis*	*Tylodelphys clavata*	Infection intensity correlated negatively with the reactive distance to prey and decreased foraging success under competition	Natural	Vivas Muñoz et al. (2017)

European perch is widely distributed in the Palearctic region and one of the most common fish species in northern-temperate lakes (Craig 2000). 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. During ontogenetic development, perch undergo habitat and dietary shifts. After hatching, larvae move out to the pelagic zone (offshore) where they feed on zooplankton. After at least one month inshore migration starts; when juvenile perch return to the littoral zone they form shoals and gradually change to a diet of different macroinvertebrates. Afterwards, when large enough, they shift again to a diet mainly consisting of fish (Craig 1978; Guma'a 1978; Persson 1986; Wang and Eckmman 1994; Imbrock et al. 1996; Hejlm et al 2000). Intraspecific diet specialization in perch has been associated with habitat and resources use. In general, it has been described that individuals specialize in feeding on either littoral or pelagic prey types. This specialization has been related to morphological intraspecific variation in favour of better utilization of different habitats and/or diets (resource polymorphism). In lakes, the littoral juvenile perch that feed mainly on macroinvertebrates have deeper bodies than the pelagic ones that feed on zooplankton (Hjelm et al. 2001; Svanbäck and Eklöv 2002, 2003, 2004). However, within-habitat individual diet specialization has also been observed among juvenile perch, especially in the littoral zone, which is assumed to reduce intraspecific competition (Quevedo and Olsson 2006; Quevedo et al. 2009; Frankiewicz and Wojtal-Frankiewicz 2012). There is evidence that prey selection and the degree of individual diet specialization of juvenile perch is influenced by resource availability, interspecific competition and predation pressure (Persson 1986; Persson and Greeneberg 1990; Dielh 1993; Svanbäck and Persson 2004; Eklöv and Svanbäck 2006; Svanbäck and Bolnick 2007; Sharma and Borgstrøm 2008; Svanbäck et al. 2008). Yet, the effect of eye fluke infection on prey preference has never been evaluated.

1.4 Study aims

By altering diet preference or feeding behaviour, parasites can influence the interaction strength between the host and other species and consequently may affect

energy transfer through communities via trophic cascades (Hatcher and Dunn 2011). In this study, the role of digeneans on their host's feeding behaviour is evaluated at two trophic levels: First the impact of trematode infection on grazing activity of freshwater snails (primary consumers) and second the impact of eye fluke infection on feeding behaviour and food preferences of European perch (secondary consumer).

Freshwater snails are important drivers of benthic communities as their grazing activity can influence the competition between primary producers (Brönmark 1985; Brönmark and Weisner 1992). Effects of parasitism on host grazing activity can potentially have a cascading effect throughout the food web (Minchella and Scott 1991). In this study, the impact of trematode infection on periphyton grazing activity was examined in different freshwater snail-trematode systems. This approach allows testing whether a general pattern can be detected for the impact of trematode infections or whether the impact is snail-trematode species-specific.

Having as baseline the negative impact of *T. clavata* infection on perch foraging ability in naturally infected fish (Vivas Muñoz et al. 2017), in this study experimentally infected perch were used to prove the causal relationship between infection and foraging behaviour. To test whether perch's prey preference might be influenced by infection status under intraspecific competition, feeding behaviour and competitive ability of perch were evaluated in small groups of four individuals under competition for two different prey species (*Asellus aquaticus* and *D. magna*). Additionally, since light intensity can also affect visual performance of fish and influence predator-prey interactions (Sandström 1999); feeding behaviour was recorded at two light intensities (600 and 6 lx). It was hypothesized that decreasing light intensity should intensify the impact of *T. clavata* on perch's visual performance 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.

Lastly, considering the evidence of individual diet specialization among juvenile perch (Quevedo and Olsson 2006; Quevedo et al. 2009; Frankiewicz and Wojtal-Frankiewicz 2012), to evaluate whether perch alter their prey preferences as a compensatory mechanism for reduced foraging efficiency and competitive ability

caused by *T. clavata* infection, young of the year (YOY) perch from Lake Müggelsee (Berlin, Germany) were sampled and their diet was evaluated using stomach content analysis (SCA) and stable isotope analysis (SIA) of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). In this lake, there is a high variability in infection intensity of *T. clavata* among juvenile perch (Vivas Muñoz 2014). Additionally, in habitats containing high abundance of reeds, it has been observed that some individuals forage exclusively on zooplankton while others have mixed diets with zoobenthos and zooplankton (Okun and Mehner 2005). Therefore, it was predicted that individual diet preferences may be influenced, to some extent, by eye fluke infection intensity.

Using two distinct techniques, SCA and SIA, enables to study the trophic ecology of perch over different timescales. SCA gives a short-term dietary "snapshot" of recently ingested items (Hyslop 1980). On the other hand, SIA provides temporally integrated information on dietary habits, reflecting what was actually assimilated by the consumer (Peterson and Fry 1987). The heavy isotopes of nitrogen and carbon, ^{15}N and ^{13}C, enrich in the food chains in relation to the lighter isotopes, ^{14}N and ^{12}C, respectively. $\delta^{15}N$ increases by 3 – 5 ‰ per trophic level (trophic enrichment factor), and is often used to estimate the trophic position of a consumer. On the other hand, $\delta^{13}C$ increases by 0 – 1 ‰ per trophic level and allows the identification of food sources (Minagawa and Wada 1984; Peterson and Fry 1987; Post 2002, 2003). Differences in nitrogen and carbon isotope ratios reflect variance in diet and can reveal intra-population differences in diet preferences and give an indication whether an omnivorous population actually consists of generalist feeders or specialists with different preferences (Beaudoin et al. 1999; Bolnick et al. 2003; Bearhop et al. 2006). To estimate the contribution of specific prey items to fish diets, isotope data can be used in mixing models (Phillips and Gregg 2003; Parnell et al. 2010, 2013). However, for these models, prior knowledge of the potential prey is necessary; therefore, the combined use of SCA and SIA provide a robust analysis in the evaluation of intra-population differences in diet preferences.

2. Materials and methods

2.1 Periphyton grazing rates of freshwater snails

A total of four snail-trematode systems were used for feeding experiments: *Planorbarius corneus* (Planorbidae) - *Cotylurus* sp. (Strigeidae), *L. stagnalis* (Lymnaeidae) - *Diplostomum pseudospathaceum* (Diplostomatidae), *L. stagnalis – T. szidati* (Schistosomatidae) and *Radix lagotis* (Lymnaeidae) - *Trichobilharzia regenti* (Table 2, Figure 6).

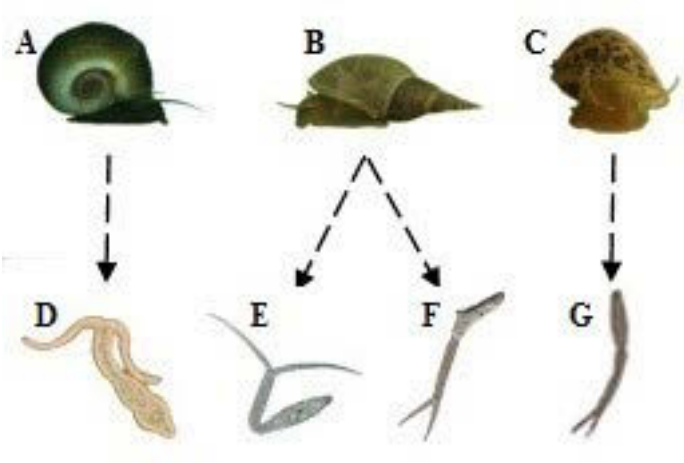

Figure 6. Snail and trematode species used to examine the impact of parasitism on periphyton grazing activity. **(A)** *Planorbarius corneus*; **(B)** *Lymnaea stagnalis*; **(C)** *Radix lagotis*; **(D)** *Cotylurus* sp.; **(E)** *Diplostomum pseudospathaceum*; **(F)** *Trichobilharzia szidati*; **(G)** *T. regenti*.

2.1.1 Naturally infected snails

P. corneus and *L. stagnalis* snails were collected along the shoreline of Lake Grimnitzsee (Brandenburg, Germany) in July and August 2015, respectively. In order to detect trematode infection in the laboratory, snails were placed individually into plastic test tubes with copper-free tap water and exposed to light for 24 hours to stimulate shedding of cercariae. Live, freshly emerged cercariae were observed under a light microscope (100x – 1000x magnification). Morphological identification of cercariae was based on the keys by Niewiadomska and Kieseliene (1994), Faltýnková et al. (2007, 2008a) and Mikeš (2001). Individuals that did not shed cercariae within 24 hours under light exposure were classified as non-infected.

After inspection, snails with the most prevalent trematode species were chosen for the feeding experiment. In July, these were *Cotylurus* sp. with a prevalence of 28 % in 73 examined *P. corneus* and in August *D. pseudospathaceum* with a prevalence of 20 % in 325 examined *L. stagnalis*. Infected snails and non-infected snails were kept separately as groups in 15 L glass aquaria with aerated copper-free tap water at a water temperature of 21 ± 1 °C until the experiment started. Snails were fed ad libitum with fresh lettuce and periphyton that was incubated as described below. Considering that the collected snails' age was unknown, the individuals for the experiments were chosen depending on their wet weight attempting to have similar size in both infected and non-infected groups (Table 2). After the feeding experiment, the snails assigned to be non-infected were dissected to confirm the absence of a trematode infection.

Table 2. Four snail-trematode systems used for feeding experiments with their respective origin. Mean wet weight (WW) ± S.D. of infected and non-infected snails. Significant differences are indicated by an asterisk ($P < 0.05$, Mann-Whitney U-test). GS, Lake Grimnitzsee; Lab, laboratory-reared and experimentally infected; n = number of individuals.

Snail	**Trematode**	**Origin**	**Snails WW (g)**	
			Infected	**Non-infected**
Lymnaea stagnalis	*Diplostomum pseudospathaceum*	GS	2.6 ± 0.5 n = 10	2.5 ± 0.5 n = 10
Planorbarius corneus	*Cotylurus* sp.	GS	4.6 ± 1.1 n = 8	4.5 ± 0.9 n = 10
L. stagnalis	*Trichobilharzia szidati*	Lab	4.5 ± 0.9 n = 9	2.9 ± 0.5* n = 9
Radix lagotis	*Trichobilharzia regent*	Lab	0.26 ± 0.1 n = 7	0.17 ± 0.05 n = 6

2.1.2 Experimentally infected snails

For the experiments with *Trichobilharzia* spp. laboratory reared snails from the Charles University (Prague, Czech Republic) were used. Juvenile snails of *L. stagnalis* (6 - 10 mm) and *R. lagotis* (5 - 8 mm) were infected with miracidia of *T.*

szidati and *T. regenti*, respectively. Snails were placed individually into wells of a 24-well culture plate (Thermo Fischer Scientific, Waltham, USA) containing tap water and exposed to 3 – 8 miracidia for 5 hours. After the pre-patent period (eight weeks), infection success was assessed by stimulating shedding of the cercariae with a light source. Ten infected and ten non-infected snails of the same age per species were transported to Germany, where they were maintained in the same conditions as described above for the wild collected snails.

After arrival, snails were maintained for at least one and a half weeks in the German laboratory before the experiment. Feeding experiments were carried out 13 weeks post-infection (w.p.i.) and 11 w.p.i. for *L. stagnalis* and *R. lagotis*, respectively. Until snails were used for the experiments infected *L. stagnalis* and *R. lagotis* achieved a larger size than their similar aged non-infected conspecifics (Table 2) and did not lay egg batches. Cercariae shedding during the experiment confirmed the persistent infection of experimentally infected snails.

2.1.3 Feeding experiment

To measure grazing rates on periphyton, snails were offered naturally developed periphyton on transparent polypropylene strips (10 x 5 cm), (General Binding Corporation, Chicago, Illinois). One centimetre on both sides of each strip was covered with a water proof sticky tape (Tesa, Norderstedt, Germany) which was removed after harvest for better handling. Strips were exposed for two weeks at a water depth of 0.5 m in the littoral of eutrophic Lake Müggelsee. Periphyton of this lake is dominated by diatoms (Roberts et al. 2003; unpublished data). On the experiment day, periphyton strips were collected and taken to the laboratory in a humid chamber avoiding desiccation and damage. Subsequently, periphyton strips were placed vertically into 1 L glass beakers filled with carbonated water for 3 minutes to remove all grazers.

The experimental table (180 x 75 cm) was illuminated with four fluorescent daylight tubes (Osram Biolux 36 W/965; Munich, Germany) on a 12 h dark-light cycle and covered by a dark curtain. A total of 30 spots were marked on the table for

positioning the 1 L experimental glass beakers, in which light intensity ranged from 64 to 66.5 μE m^{-2} s^{-1} (measured using a spherical sensor, Biospherical Instruments, QSPL210),which is sufficient to saturate periphyton photosynthesis (Hill 1996).

The snails were starved for 12 h before the experiment started. Ten infected and ten non-infected snails were selected from the holding tanks, weighed and randomly distributed one by one to the experimental beakers filled with 0.5 L of copper-free tap water. One periphyton strip was vertically introduced to each of the 30 experimental beakers. From this moment, snails were allowed to feed for 24 h at a water temperature of 22 °C. Five beakers were left free of snails to calculate periphyton growth in the absence of grazing (controls) and compared to periphyton biomass of five fresh strips that served as a baseline.

Initial (5 strips) and final periphyton biomass were determined by removing all periphyton from the strips with a toothbrush and suspending it in a defined volume of tap water. After homogenization, subsamples were filtrated onto pre-dried (105 °C, 12 h), pre-weighted GF/F glass fibre filters (Whatman, Maidstone, UK). Periphyton dry weight (DW) was determined after drying the samples for 12 h at 105 °C to constant weight.

2.1.4 Data analysis

Since periphyton DW of control samples from before and after the grazing experiment did not differ significantly in any case, the mean DW of all controls within an experiment was considered as the initial periphyton biomass which ranged from 5-25 g DW m^{-2} (Table 3). The individual-specific grazing rate of each snail was determined from the difference between initial and final periphyton DW. The mass-specific grazing rate was calculated dividing the grazing rate by the snail's wet weight, which includes biomass of the parasites.

Pairwise comparisons between treatments with and without trematodes were performed with the Mann-Whitney U- test. Differences were considered statistically

significant when $P \leq 0.05$ (two-tailed). Statistical analyses were performed using R version 3.5.1 program (R Core Team 2018).

Table 3. Mean dry weight (DW) ± S.D. of initial periphyton biomass prior to the four grazing experiments and month in which periphyton was incubated in Lake Müggelsee.

Snail	Trematode	Initial periphyton biomass (g DW m^{-2})	Periphyton incubation (month)
Lymnaea stagnalis	*Diplostomum pseudospathaceum*	12.2 ± 2.1	Aug.
Planorbarius corneus	*Cotylurus* sp.	12.8 ± 1.3	Jul.
L. stagnalis	*Trichobilharzia szidati*	25.9 ± 4.4	Apr.
Radix lagotis	*Trichobilharzia regenti*	5.0 ± 1.6	Oct.

2.2 Feeding behaviour of experimentally infected European perch

2.2.1 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. Egg ribbons were hung in two 45 L glass aquaria (50 x 30 x 30 cm), water was supplied by a drip system to the surface in a flow-through system at 15± 1°C. Perch fry hatched within five days and were fed ad libitum with live *Artemia salina* nauplii (Micro Artemia Cysts, Ocean Nutrition, Essen, Belgium) once their yolk sack reserve was exhausted.

Approximately one month post-hatching fish were transferred into a recirculating system with nine 200 L aquaria (100 x 40 x 50 cm). Each of the holding tanks was aerated and illuminated with a 1 m LED strip (eco + LED-strip DAY 5500K, 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 two weeks. Food size was then progressively increased up to 3 mm (Aller silver 3mm, Aller aqua, Christiansfeld, Denmark). Additionally, one

month before the behavioural 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.

2.2.2 Experimental infection and tagging

Snails of the genus *Radix*, which are potential hosts for *T. clavata* were collected from Lake Grimnitzsee. In the laboratory, snails were inspected for trematode infections by stimulating shedding of the cercariae with a light source. Live, freshly emerged cercariae were observed under a light microscope (100x – 1000x magnification) and morphological identification of *T. clavata* cercariae was based on the description of 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 ± 1 °C with a natural photoperiod. Snails were fed ad libitum with fresh lettuce.

Experimental infection was carried out eight months post-hatching. 12 hours before the procedure, a snail was removed from the holding tank, placed into a 0.5 L beaker and cercariae shedding was again 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 hours. 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 (8x – 20x 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 ± SD: 167 ± 41), which was within the range of previous records in naturally infected juvenile perch (Kennedy 2001; Vivas Muñoz et al. 2014).

Nine months post-infection, infected and non-infected fish were tagged for identification. Fish were anaesthetized 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.

2.2.3 Behavioural experiment

The experiments were carried out in a glass aquarium (100 × 40 × 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 5500K, 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 programed using an automatic light control system (SIMU-LUX, LEDaquaristik). 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 the small prey (*D. magna*) and the colored tags of the fish could be clearly identified on the video recordings. Additionally, a green background containing 1 x 1 cm grid was placed behind the back and under the base of the aquarium.

Ten months post-infection the experiment started. Fish were tested in ten groups of four, size-matched individuals (2 infected and 2 non-infected) with well distinguishable VIE tags. Although individuals within groups were size-matched (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 one week and were fed once a day with dry food, live *A. aquaticus* and *D. magna* until 24 h before the experiment began.

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 behaviour of the fish was recorded simultaneously using two cameras (Sony α 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 five minutes 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.

2.2.4 Video and data analysis

2.2.4.1 Feeding behaviour of perch

Reaction distance 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 to calculate the reaction distance, corrected for perspective distortion, using Pythagoras' theorem.

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, light intensity (high vs. low) and infection status (infected vs. non-infected) were included, 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 a 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 LMM (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, the influence of infection status (infected vs non-infected) on the tendency to feed was evaluated by categorizing the fish that fed and the ones that didn't (yes vs. no) and compared using Pearson's Chi-square test per each light intensity.

2.2.4.2 Activity level of prey organisms

To observe if the light intensity had an influence on the activity level of *A. aquaticus*, the top view video was used 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. A comparable method to determine the activity level of *D. magna* was not successfully achieved

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

2.3 Dietary habits of naturally infected European perch

2.3.1 Study area

Lake Müggelsee is a shallow, eutrophic and polymictic lake, located at the eastern border of Berlin, Germany (52°26' N, 13°39' E). It is the largest lake in the city with a surface area of 7.4 km^2 and a mean water depth of 4.9 m (maximum depth: 8 m). The lake is categorized as a flow-through lake. Consequently, the quantity and quality of water is mainly controlled by the inflowing lowland river Spree (catchment area: 7000 km^2, water retention time of the lake: about 40 days) (Driescher 1993).

The lake has a disc-like shape with a relatively regular shoreline, which is characterized by the presence of dense belts of common reed (*Phragmites australis*) (Driescher 1993). The fish community of Lake Müggelsee mainly consists of perch,

roach (*Rutilus rutilus*), bream (*Abramis brama*), ruffe (*Gymnocephalus cernuus*), bleak (*Alburnus alburnus*) and pikeperch (*Sander lucioperca*) (Okun and Mehner 2005).

2.3.2 Fish sampling

YOY perch were sampled in 2014 and 2016 in the littoral area in two reed zones, one located at the southern shoreline ("South") and the other at the northern shoreline ("North") (Figure 7). Fish were caught by electrofishing at the "South" on the 19th of August 2014 and at the "North" on the 28th of August and 9th of September 2014. In 2016 fish were caught only at the "North" on the 8th of August.

Figure 7. Map of Lake Müggelsee, Berlin, Germany. Displayed are the two sampling sites "North" and "South" (red starts) (modified from google maps).

Immediately after capture, YOY perch were killed and placed on ice. In the laboratory, all fish were measured to the nearest 1 mm (total length, TL) and weighted to the nearest 0.01 g (wet weight, WW). The eyes were removed, dissected, and entirely examined for the presence of parasites using a stereo microscope (8x – 20x magnification). All parasites were counted and identified to the lowest taxonomic level possible based on morphological characteristics according to the

descriptions of Kozicka and Niewiadomska (1960), Dönges (1969), Kennedy (1987) and Höglund and Thulin (1992). Only trematode species were found and the data from both eyes was combined for each fish as metacercariae do not exhibit a preference for either left or right eye (Kennedy 2001; Soylu 2013). Prevalence and mean intensity of the parasites were calculated according to Bush et al. (1997).

Considering that fish caught at the northern shore in the two sampling dates of 2014 had similar size range and parasite loads, these two samples were combined. Morphological parameters of the sampled fish are summarized in Table 4.

Table 4. Number of YOY-perch (*Perca fluviatilis*) sampled from lake Müggelsee with their respective sampling year and site. Total length (TL) and wet weight (WW) are given as means ± SD.

Sampling Year	Sampling site	*n*	TL (cm) Mean ± SD	WW (g) Mean ± SD
2014	"South"	90	6.0 ± 0.53	2.05 ± 0.62
2014	"North"	259	6.2 ± 0.8	2.17 ± 1.04
2016	"North"	119	5.1 ± 0.5	1.35 ± 0.42

The stomachs were removed and preserved in 70 % ethanol. Stomach contents of each fish were identified to order, family, or species and counted under a stereo microscope (8x – 20x magnification). Most of the prey items were intact and easy to determine and count. However, if some preys were broken down into parts, for instance in the case of chironomid larvae, only the heads were counted to quantify the prey number, as this body part is easily detectable.

In 2016 a sample of muscle tissue was taken from under the dorsal fin of each fish and frozen at –20 °C for stable isotope analyses.

2.3.3 Stable isotope analysis

A total of 22 fish were selected to evaluate their isotopic signatures. Individuals were chosen according to the infection intensity of *T. clavata* and divided into two groups: low infected (average intensity ± SD: 5 ± 3 metacercariae per fish) and high infected

(average intensity ± SD: 39 ± 13 metacercariae per fish). Total length was also considered for the selection as stable isotope ratios increase with body length in perch (Mustamäki et al. 2014; Linzmaier et al. 2018). TL of the selected fish ranged from 4.0 to 4.9 cm and there was not size difference between the two groups (Mann-Whitney U-test: W = 45.5, $n_1 = n_2 = 11$, $P = 0.33$).

Additionally, zooplankton and benthic invertebrates were collected from the sampling site "North" to estimate prey isotopic signatures. Zooplankton was caught using a conical plankton net (100 µm mesh) and the benthic invertebrates, *Dikerogammarus villosus*, *Chelicorophium curvispinum* and Chironomidae larvae, were hand-collected from aquatic vegetation and stones. After collection prey samples were frozen at –20 °C. Both perch muscle samples and prey samples were transported to the University of Duisburg-Essen where the stable isotope analyses were carried out.

Prior to the analysis, all samples were freeze-dried and grounded to a fine powder. Then, per sample triplicates of 400–700 µg were weighed into 4 × 6 mm tin foil capsules for solids (IVA Analysentechnik e.K., Meerbusch, Germany). The samples were analyzed using an elemental analyser (PYRO Cube EA; Elementar Analysensysteme, Langenselbold, Germany) coupled with an isotope ratio mass spectrometer (IsoPrime 100 IRMS; Elementar Analysensysteme Langenselbold, Germany). The experimental procedure was carried out as described by Nachev et al. (2017) and the results were obtained following the principle of identical treatment and normalization according to Werner and Brand (2001).

Isotope ratios are expressed in the δ-notation, in per mil units (‰), which describes the isotope ratio in the sample in relation to an international reference substance, according to the following equation:

$$\delta^{h}E_{s,ref} = \left[\frac{R(^{h}E/^{l}E)_{s}}{R(^{h}E/^{l}E)_{ref}} - 1 \right] \text{x } 10^{3}$$

where, $R(^{h}E/^{l}E)_{s}$ is the ratio of the heavy and light isotope (here $^{13}C/^{12}C$ as well as $^{15}N/^{14}N$) in the sample, and $R(^{h}E/^{l}E)_{ref}$ is the ratio in the reference material. The

normalization of the laboratory internal standard (acetanilide) was performed using international standards USGS40 and USGS41 (both International Atomic Energy Agency, Vienna). The instrument drift was controlled and corrected with the internal standard, whereas after every three replicates an acetanilide standard was measured.

2.3.4 Data analysis

2.3.4.1 Stomach content analysis

For the analysis the prey items were separated into six categories: (1) zoopankton (cladocerans and copepods), (2) *Dikerogammarus villosus*, (3) *Chelicorophium curvispinum*, (4) pelagic macroinvertebrates (pupae of Chiromonidae and Culicidae) and benthic insect larvae were separated into two groups: (5) Predator-sensitive (PS) insect larvae, which consisted of organisms living on macrophytes, branches or on other substrates and included Ephemeroptera and Plecoptera. These taxa are relatively large, conspicuously visible and thus sensitive to fish predation (Persson et al. 1996). The other group was (6) Chironomid larvae, which are often cryptically coloured, tube-builders living on or within the substrate (Pinder 1986), making them less sensitive to visual fish predation (Persson et al. 1996).

A linear regression was used to investigate the relationship between infection intensity of *T. clavata* and perch size (TL) per sampling date. Since significant relationships were found, the residuals from the regressions were used, to correct for fish size, in the evaluation of perch's prey preferences. The relationships between infection intensity and the number of consumed items for each prey category (log + 1 transformed) were analyzed using Spearman rank correlation.

2.3.4.2 Condition factor and body surface area

Fulton's condition factor (K) for each fish was calculated according to the following equation:

$$K = 100 \times (W / TL^3)$$

where W = wet weight (g) and TL = total length (cm). Spearman rank correlation was used to evaluate the relationship of *K* with infection intensity of *T. clavata*.

Additionally, for each fish body surface area (BSA) was calculated according to Thompson (1942), using the equation:

$$BSA = K \times (W^{2/3})$$

where W = wet weight (g) and K = is a constant for the particular species, here it was used K = 7.52 value that has been determined for common carp (*Cyprinus carpio*) (Ling et al. 2008) as there is not available information for European perch.

2.3.4.3 Stable isotope analysis

For the analysis $\delta^{13}C$- and $\delta^{15}N$-values of perch were corrected for trophic fractionation by 1 ‰ for carbon and 3.4 ‰ for nitrogen (Vander Zanden and Rasmussen 2001; Vanderklift and Ponsard 2003; Fry 2006).

To compare the isotopic signatures among perch a linear model (LM) was used having as independent variable infection intensity (low infected vs. high infected). Differences in the isotopic signatures between the prey types were also evaluated with a LM; in this case the independent variable was the taxon (*D. villosus*, *C. curvispinum*, Chironomidae larvae, and zooplankton). Tukey's test was used, as post-hoc test, to determine pairwise differences in the $\delta^{13}C$-values between the prey items.

To quantify the proportion of the different prey items in diets of low and high infected perch, stable isotope mixing model was run using the package SIAR (Parnell and Jackson 2013) for R. Within a Bayesian framework, SIAR calculates the most likely set of dietary proportional contributions given the isotopic ratios in a set of potential food sources and consumers (Parnell et al. 2010).

Considering the diversity of feeding modes that exist within subfamilies of chironomid larvae (e.g. detritivores, filter feeders, periphyton grazers and predators) (Berg 1995; Henriques-Oliveira 2003) and that the sampled chironomids used for

SIA were only identified to family, the results of SIAR Bayesian mixing models are given excluding this prey type.

For all analyses, significance was accepted when $P \leq 0.05$. All statistical analyses were performed using R version 3.5.1 program (R Core Team, 2018).

3. Results

3.1 Periphyton grazing rates of freshwater snails

Mass-specific periphyton grazing rates of *P. corneus* infected with *Cotylurus* sp. were significantly higher than those of non-infected conspecifics (Mann-Whitney U-test: W = 66, $n_1 = 8$, $n_2 = 10$, $P < 0.05$). Within 24 h, infected *P. corneus* consumed on average twice the amount of periphyton than their counterpart control snails (Figure 8A). In contrast, there were no significant differences between the mass-specific periphyton grazing rates of *L. stagnalis* infected with *D. pseudospathaceum*, and non-infected individuals (Mann-Whitney U-test: W = 53, $n_1 = n_2 = 10$, $P > 0.05$; Figure 8B).

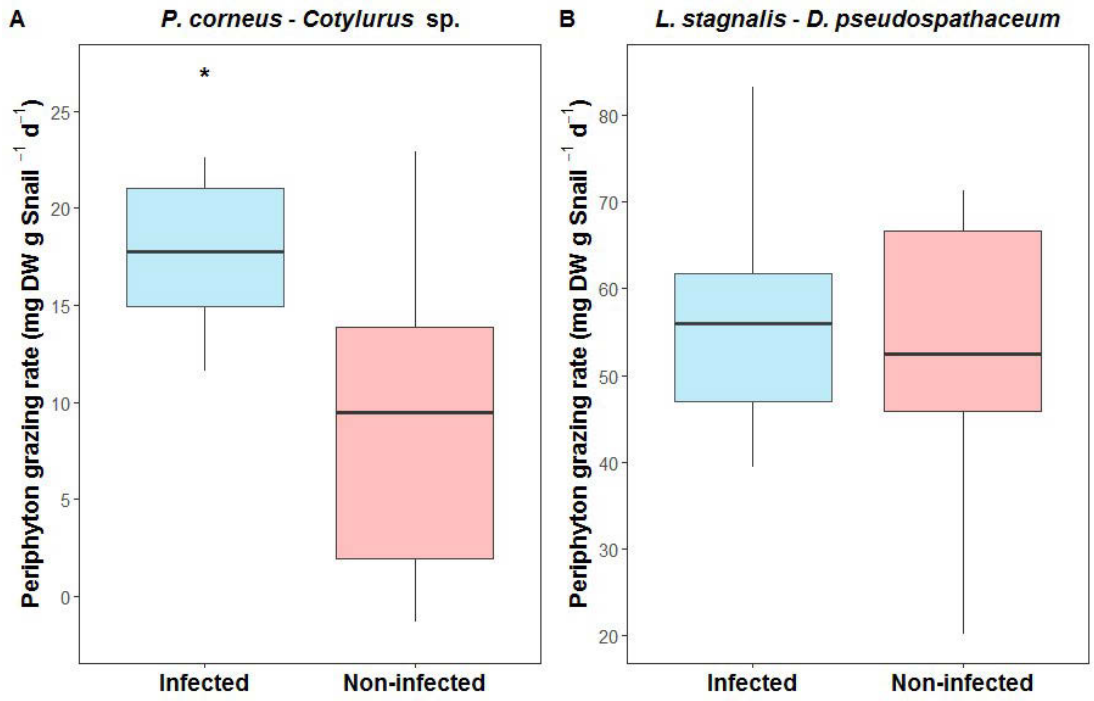

Figure 8. Mass-specific periphyton grazing rate of two naturally infected freshwater snail species. **(A)** *Planorbarius corneus* infected with *Cotylurus* sp. ($n = 8$) and non-infected ($n = 10$); **(B)** *Lymnaea stagnalis* infected with *Diplostomum pseudospathaceum* ($n = 10$) and non-infected ($n = 10$). Box plots show medians (horizontal thicker lines), first and third quartiles (box limits) and ranges (whiskers). Significant differences are indicated by an asterisk ($P < 0.05$, Mann-Whitney U-test).

The mean mass-specific periphyton grazing rate of *L. stagnalis* with a patent infection of *T. szidati* was approximately half that of the non-infected conspecifics, exhibiting a significant difference between the two groups (Figure 9A; Mann-

Whitney U-test: W = 0, $n_1 = n_2 = 9$, $P < 0.0001$). Even if the pronounced gigantism in infected *L. stagnalis* is not considered when calculating individual-specific grazing rates, infected and non-infected *L. stagnalis* still differ significantly by factor 1.4 (Figure 10A; Mann-Whitney U-test: W = 14, $N_1 = N_2 = 9$, $P < 0.05$). On the other hand, the mass-specific grazing rate of *R. lagotis* infected with *T. regenti* did not significantly differ from that of non-infected individuals (Mann-Whitney U-test: W = 22, $n_1 = 7$, $n_2 = 6$, $P > 0.05$; Figure 9B). However, due to parasite-induced gigantism, individual-specific grazing rates differed by factor 0.7, with the infected snails showing the higher periphyton consumption (Figure 10B, Mann-Whitney U-test: W = 33, $n_1 = 7$, $n_2 = 6$, $P > 0.05$).

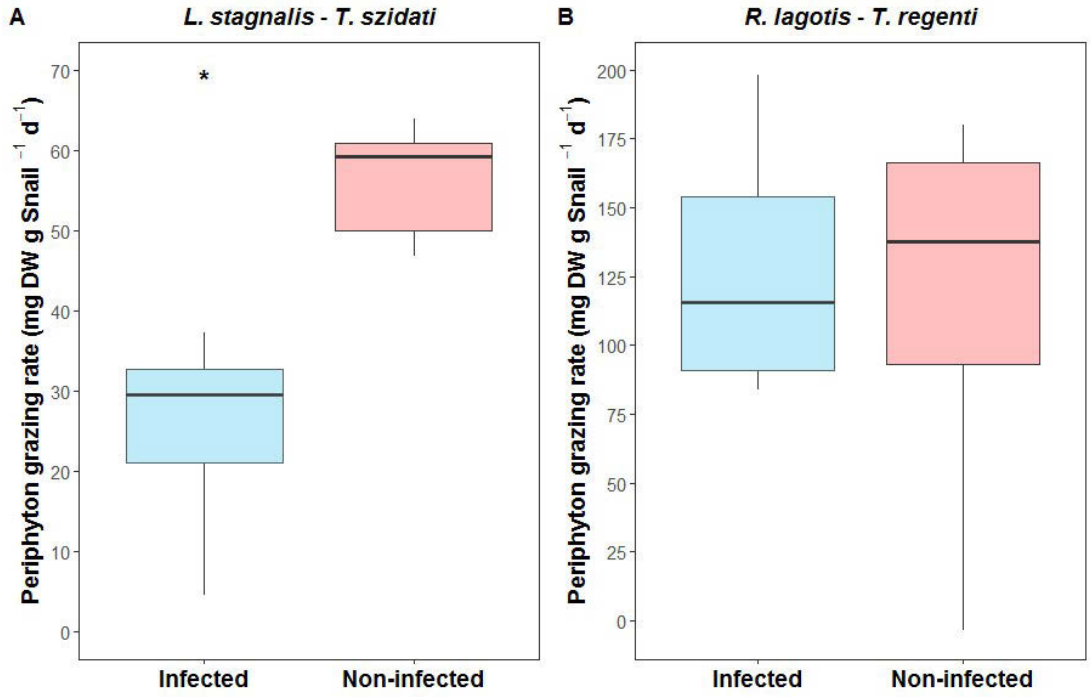

Figure 9. Mass-specific periphyton grazing rate of two laboratory-reared freshwater snail species. **(A)** *Lymnaea stagnalis* infected with *Trichobilharzia szidati* (n =9) and non-infected (n = 9); **(B)** *Radix lagotis* infected with *T. regenti* (n =7) and non-infected (n = 6). Box plots show medians (horizontal thicker lines), first and third quartiles (box limits) and ranges (whiskers). Significant differences are indicated by an asterisk ($P < 0.05$, Mann-Whitney U-test).

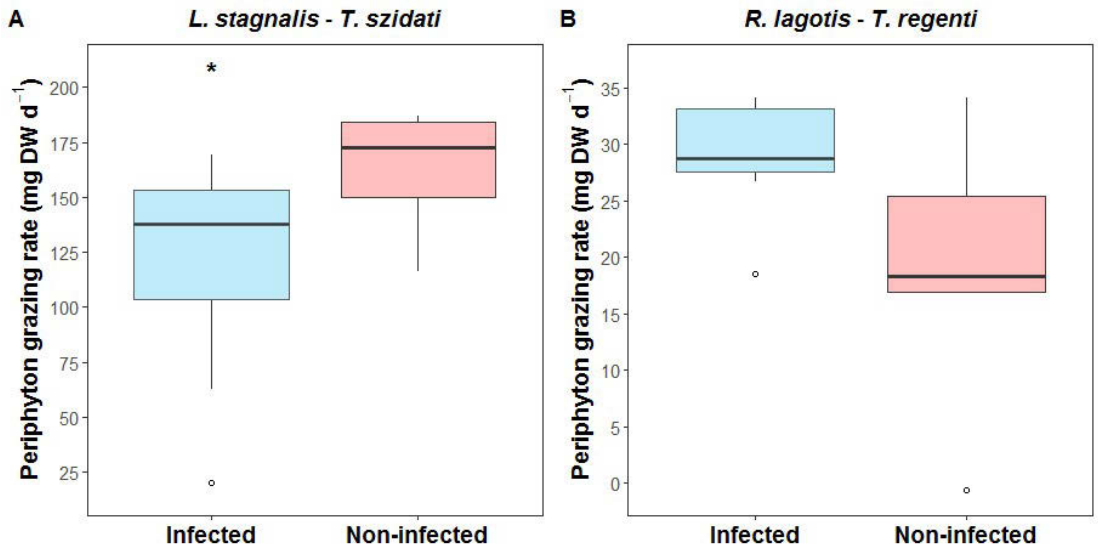

Figure 10. Individual-specific periphyton grazing rate of two laboratory-reared freshwater snail species. **(A)** *Lymnaea stagnalis* infected with *Trichobilharzia szidati* (n =9) and non-infected (n = 9); **(B)** *Radix lagotis* infected with *T. regenti* (n =7) and non-infected (n = 6). Box plots show medians (horizontal thicker lines), first and third quartiles (box limits), ranges (whiskers) and open circles (extreme values). Significant difference is indicated by an asterisk ($P < 0.05$, Mann-Whitney U-test).

3.2 Feeding behaviour of experimentally infected European perch

The infection intensity of experimentally infected fish ranged from 114 to 236 metacercariae per fish (mean ± SD: 168 ± 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. 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 where infected, infection status did not significantly affect the tendency to feed at both light intensities (Pearson's Chi-square test: high light intensity: χ^2_1 = 1.41; P = 0.235; low light intensity: χ^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; $P < 0.001$; Figure 11). 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).

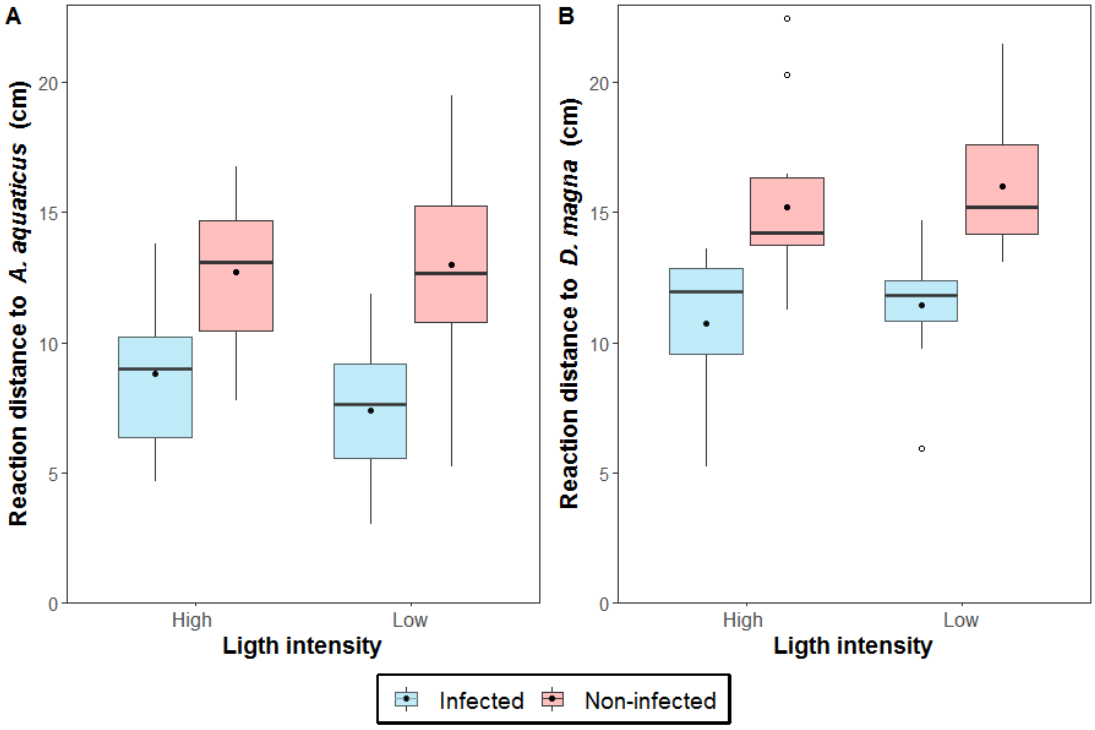

Figure 11. Reaction distance of non-infected and *Tylodelphys clavata*-infected juvenile European perch (*Perca fluviatilis*) under competition attacking **(A)** *Asellus aquaticus* and **(B)** *Daphnia magna* at two light treatments: high light intensity (600 lx) and low light intensity (6 lx). Box plots show medians (horizontal thicker lines), means (black circles), first and third quartiles (box limits), ranges (whiskers) and extreme values (open circles).

Attacks towards *D. magna* were almost always successful, regardless whether the fish were infected or not (99 % ± 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: $F_{1,30.3} = 1.68$; $P = 0.21$; Figure 12). Infected fish failed more frequently to make contact with the prey by snapping at it before the prey was within range or getting a stone of gravel instead of an *A. aquaticus* which was next to it.

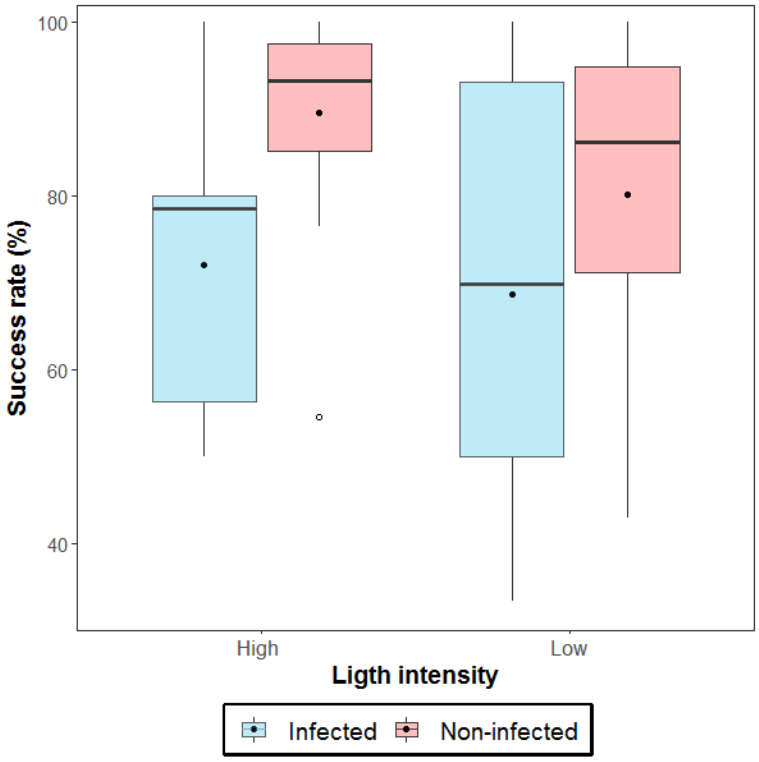

Figure 12. Percentage of successful attacks by non-infected and *Tylodelphys clavata*-infected juvenile European perch (*Perca fluviatilis*) under competition when attacking *Asellus aquaticus* under two light treatments: high light intensity (600 lx) and low light intensity (6 lx). Box plots show medians (horizontal thicker lines), means (black circles), first and third quartiles (box limits), ranges (whiskers) and extreme values (open circles).

In general, infected fish consumed less of the available prey than the non-infected fish (Figure 13). Regarding the consumption of *A. aquaticus,* non-infected fish clearly outcompeted their infected conspecifics during the trial with high light intensity. The number of *A. aquaticus* consumed by non-infected fish was independent of the light intensity while infected fish increased the consumption of *A. aquaticus* at low light intensity (LMM: significant interaction between light intensity and infection status: $F_{1,75} = 9.99$; $P = 0.002$; Figure 13A). 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 (LMM: $F_{1,76} = 0.90$; $P = 0.35$) (Figure 13B). In all analyses, body size of the experimental fish had no significant influence on the results.

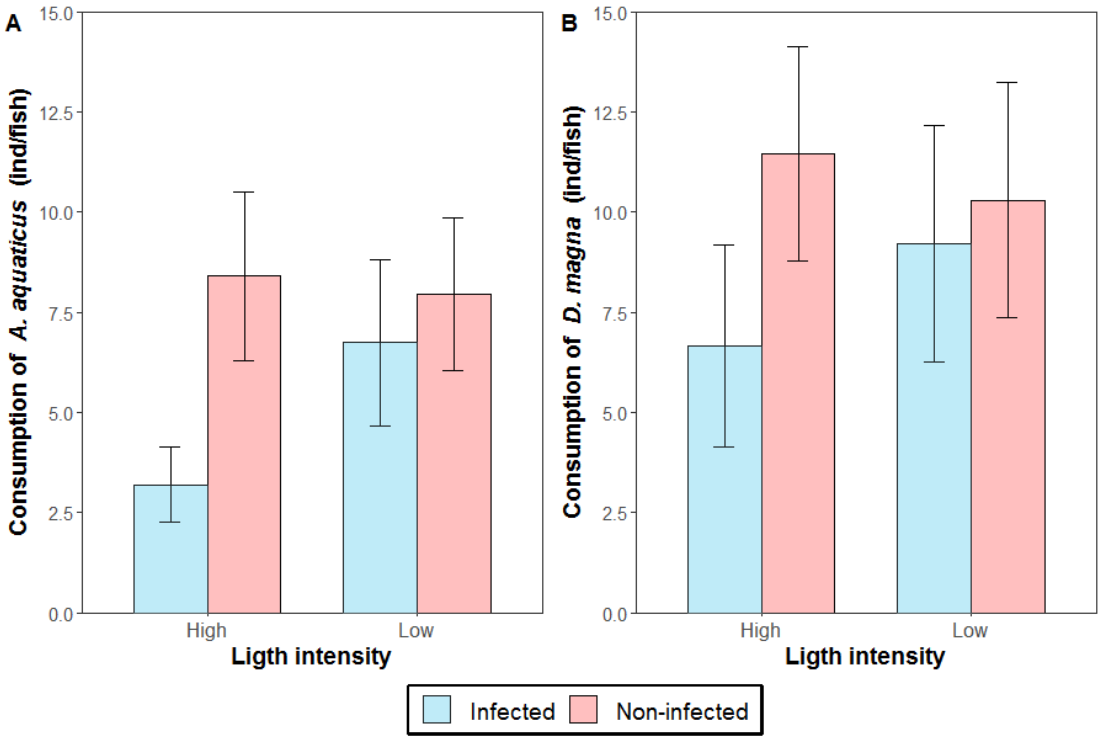

Figure 13. Consumption of **(A)** *Asellus aquaticus* and **(B)** *Daphnia magna* by non-infected and *Tylodelphys clavata*-infected juvenile European perch (*Perca fluviatilis*) under competition at two light treatments: high light intensity (600 lx) and low light intensity (6 lx). Bars indicate mean value ± standard error.

No influence of infection status on prey preference of the perch was detected. 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, $P = 0.97$; Figure 14).

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; $n_1 = n_2 = 10$; $P < 0.001$; Figure 15).

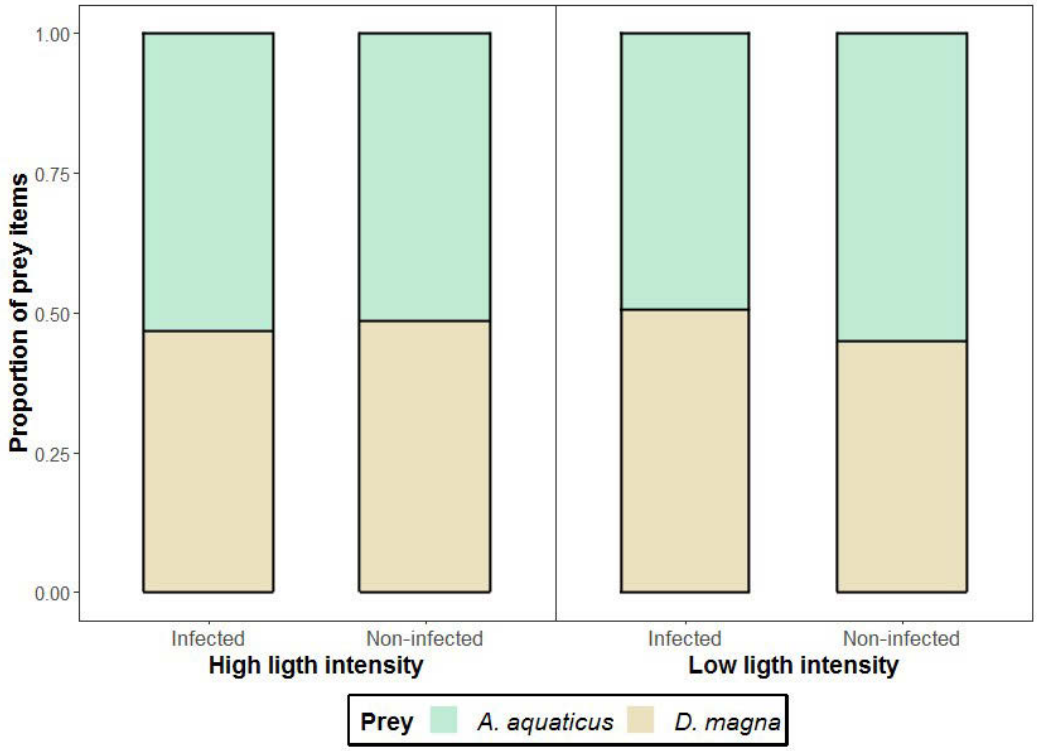

Figure 14. Proportion of *Asellus aquaticus* and *Daphnia magna* ingested by non-infected and *Tylodelphys clavata*-infected juvenile European perch (*Perca fluviatilis*) under competition at two light treatments: high light intensity (600 lx) and low light intensity (6 lx).

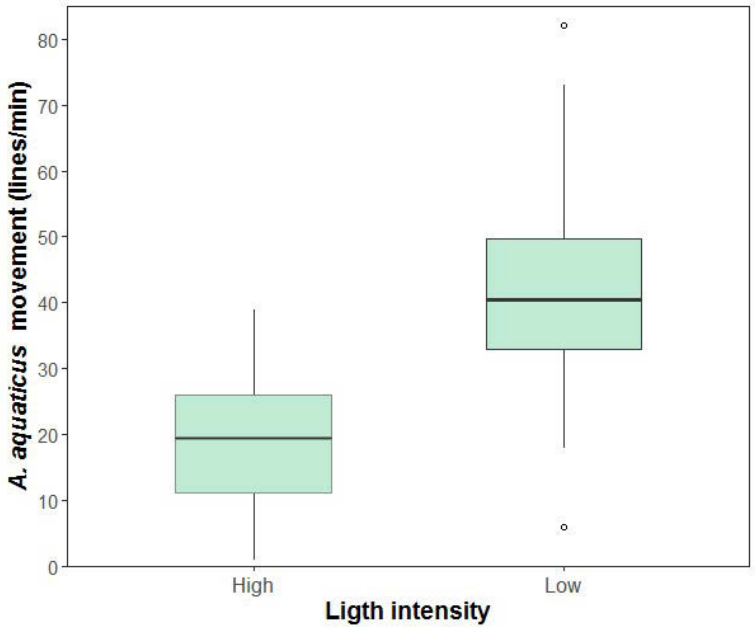

Figure 15. Activity level of *Asellus aquaticus*, measured as lines crossed per minute, at high light intensity (600 lx; $n = 50$) and low light intensity (6 lx; $n = 50$). Box plots show medians (horizontal thicker lines), first and third quartiles (box limits), ranges (whiskers) and extreme values (open circles).

3.3 Dietary habits of naturally infected European perch

YOY-perch from Lake Müggelsee were infected with six species of eye flukes: *T. clavata*, *Tylodelphys podicipina, D. baeri, D. spathaceum*, an unidentified *Diplostomum* sp. and *Posthodiplostomum brevicaudatum*. All sampled fish were infected with *T. clavata*, with the exception of one fish in 2016. Infection intensity of *T. clavata* varied greatly between the three sampling dates. In 2014, a location-dependent difference in the infection of *T. clavata* was found; infection intensity in the fish caught at the northern shore was seven times higher than in the fish caught at the southern shore. The highest number of metacercariae recorded in a single fish from the northern shore was 296, while fish from the southern shore harboured less than 50 metacercariae. Moreover, in 2016 the mean infection intensity of *T. clavata* at the northern shore was half of that recorded in 2014 at the same location (Table 5). In general, the occurrence of the other eye fluke species was considerably low. The second most common eye fluke species was the vitreous humour dwelling fluke *D. baeri* with a prevalence of 41 % in 2014. However, the infection intensity of this parasite was comparatively low (mean intensity ± SD: 1.6 ± 1.1 metacercariae per fish). The less frequent metacercariae species were the vitreous humour dwelling fluke *T. podicipina* and the lens infecting fluke *D. spathaceum* (Table 5).

Table 5. Prevalence and mean intensity ± S.D. of trematodes infecting the eyes of YOY-perch (*Perca fluviatilis*) from two locations ("South" and "North") of Lake Müggelsee in 2014 and 2016.

Species	Prevalence (%)			Intensity (metacercariae per fish)		
	South 2014	North 2014	North 2016	South 2014	North 2014	North 2016
Tylodelphys clavata	100	100	99.2	12.8 ± 9.5	92.1 ± 55.5	41.2 ± 19.0
T. podicipina			0.8			1.0 ± 0.0
D. baeri	17.8	41.3	4.2	1.3 ± 0.6	1.6 ± 1.1	2.0 ± 1.7
D. spathaceum	1.1		0.8	1.0 ± 0		1.0 ± 0.0
Diplostomum sp	2.2	0.4	4.2	1.0 ± 0.0	1.0 ± 0.0	1.4 ± 0.5
Postodiplostomum brevicaudatum	13.3	2.7	3.4	1.7 ± 1.2	1.1 ± 0.4	1.5 ± 0.6

A positive relationship was found between the infection intensity of *T. clavata* and the body size of YOY-perch in all sampling dates (South 2014: R^2= 0.12, $F_{1,88}$ = 12.59, $P < 0.001$; North 2014: R^2= 0.06, $F_{1,257}$ = 15.90, $P < 0.0001$; North 2016: R^2= 0.33, $F_{1,117}$ = 56.75, $P < 0.0001$; Figure 16). The size-dependent infection intensity of *T. clavata* among the two sampled years in the northern shore differed in magnitude but maintained relatively similar slope (Figure 16).

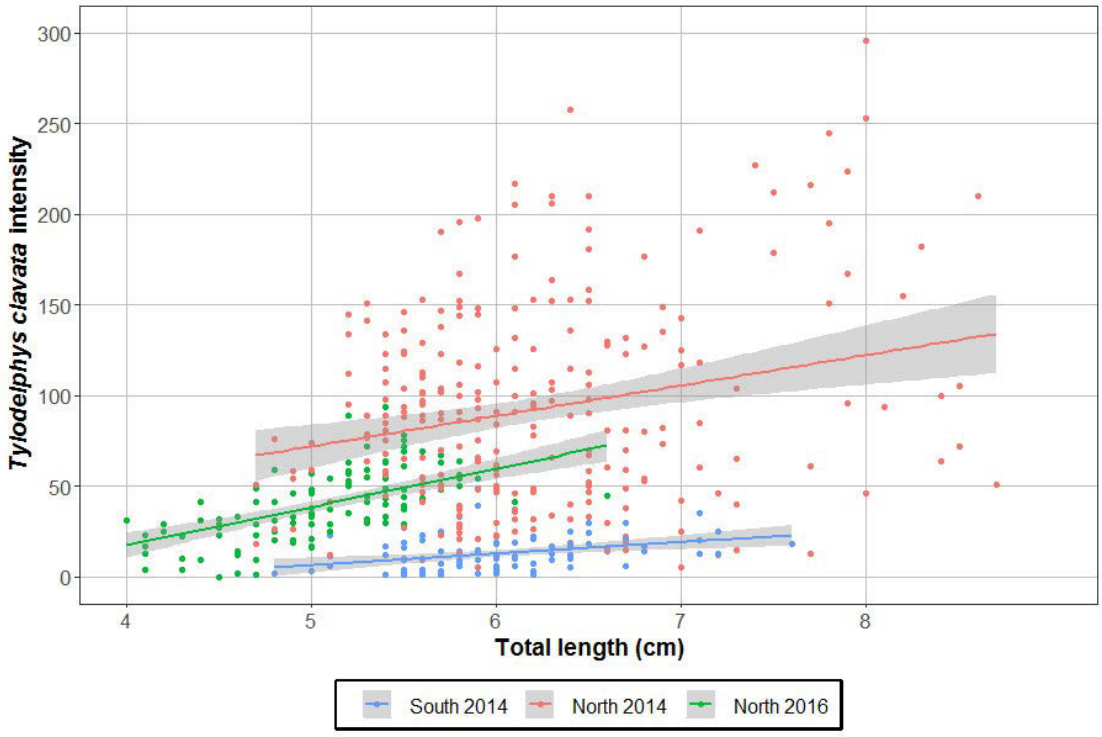

Figure 16. Relationship between infection intensity of *Tylodelphys clavata* and the total length of YOY-perch (*Perca fluviatilis*) from two locations of Lake Müggelsee ("South" and "North") in 2014 and 2016. The lines represent the best linear fit (South 2014: $y = 6.30x - 25.16$; North 2014: $y = 16.80x - 12.03$; North 2016: $y = 21.20x - 67.57$). The grey shading represents 95 % confidence intervals.

Body surface area (BSA) of YOY-perch increased exponentially with total length ($y = 1.67e^{0.32x}$, R^2= 0.93; Figure 17). When comparing all sampled fish together, the positive increments of both *T. clavata* infection intensity and BSA with fish size exhibited rather similar slopes (Figure 17).

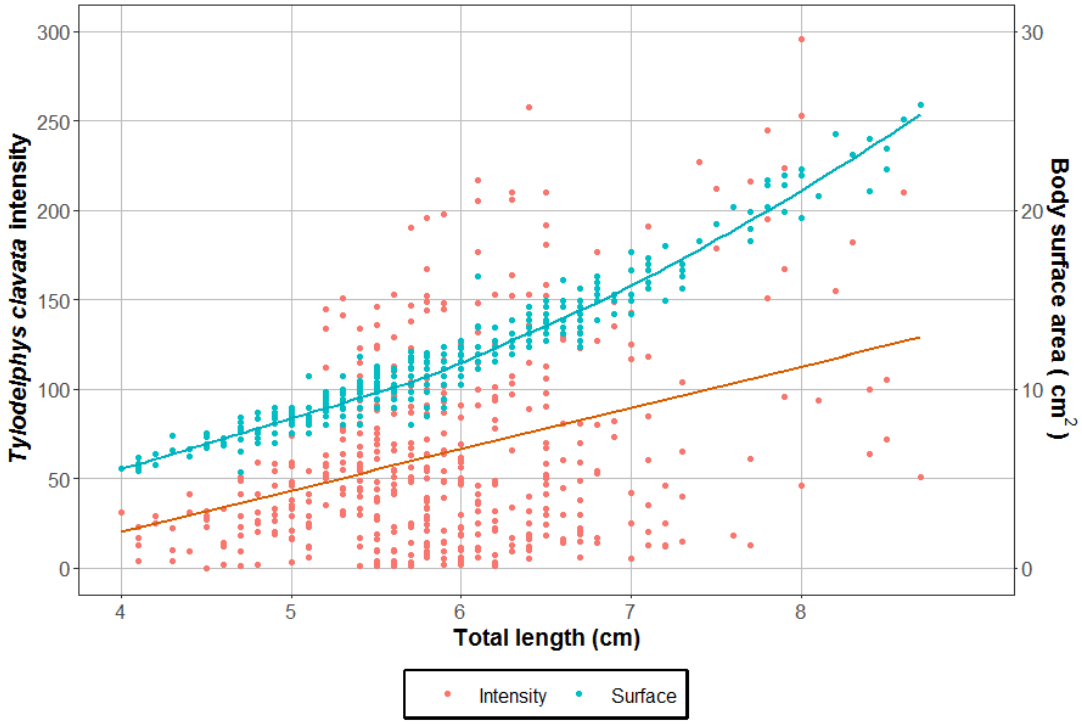

Figure 17. Relationship between infection intensity of *Tylodelphys clavata* and body surface area (cm^2) with total length of YOY-perch (*Perca fluviatilis*) from Lake Müggelsee. The lines represent the best model fit (Infection intensity: $y = 23.12x - 71.31$; Body surface area: $y = 1.67e^{0.32x}$)

The results did not reveal a negative impact of *T clavata* on the condition factor (*K*) of YOY-perch, instead a positive relationship between infection intensity (corrected for fish size) and *K* was detected for the two sampling locations in 2014 (Spearman's rank correlation, South: $r_s = -0.419$, $n = 90$, $P < 0.0001$; North: $r_s = 0.398$, $n = 259$, $P < 0.0001$; Figure 18A and B). In 2016, there was no significant correlation between parasite load (corrected for fish size) and *K* ($P > 0.05$; Figure 18C).

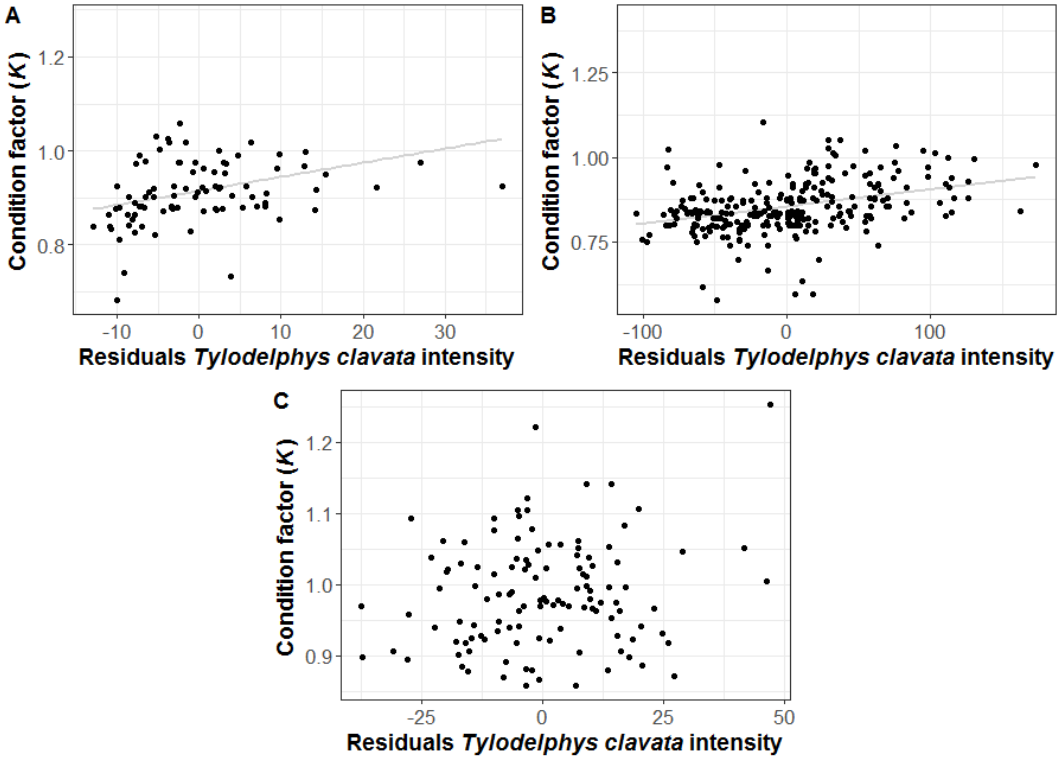

Figure 18. Relationship between *Tylodelphys clavata* intensity corrected for fish size (residuals from the regression in Figure 16) and condition factor (*K*) of YOY-perch (*Perca fluviatilis*) from two locations of Lake Müggelsee ("South" and "North") in 2014 and 2016. **(A)** "South" in 2014, **(B)** "North" in 2014 and **(C)** "North" in 2016. The lines represents the best linear fit (South 2014: $y = 0.0029x + 0.914$; North 2014: $y = -0.00050x + 0.854$).

The diet of YOY-perch was dominated by zooplankton and benthic macroinvertebrates for all sampling dates. In 2014, the most common prey item in fish caught at the southern shore were chironomid larvae, which occurred in 85.6 % of the stomachs, followed by *D. villosus* and predator-sensitive (PS) insect larvae (Ephemeroptera and Plecoptera) with an occurrence of 56.7 % and 52.2 %, respectively. In the same year, more than 70 % of the fish from thee sampling site "North" contained zooplankton and chironomid larvae in their stomachs. Additionally, the two amphipod species, *D. villosus* and *C. curvispinum* were also important prey items (occurrence > 40 %). In 2016, both zooplankton and chironomid larvae occurred in more than 95 % of perch stomachs. Also frequently present were the amphipod *D. villosus* and diverse meiobenthos organisms (ostracods and harpacticoid copepods) with an occurrence of 84.9 % and 78.2 %, respectively. For all sampling dates, chironomid and culicid pupae were present in less than 50 % of the fish. Adult stages of Ephemeroptera, Odonata and Trichoptera (terrestrial prey types) were rarely consumed and found in less than 5 % of the stomachs. Other

invertebrates such as snails and leeches were only present in the diet of YOY-perch from the northern sampling site (Figure 19).

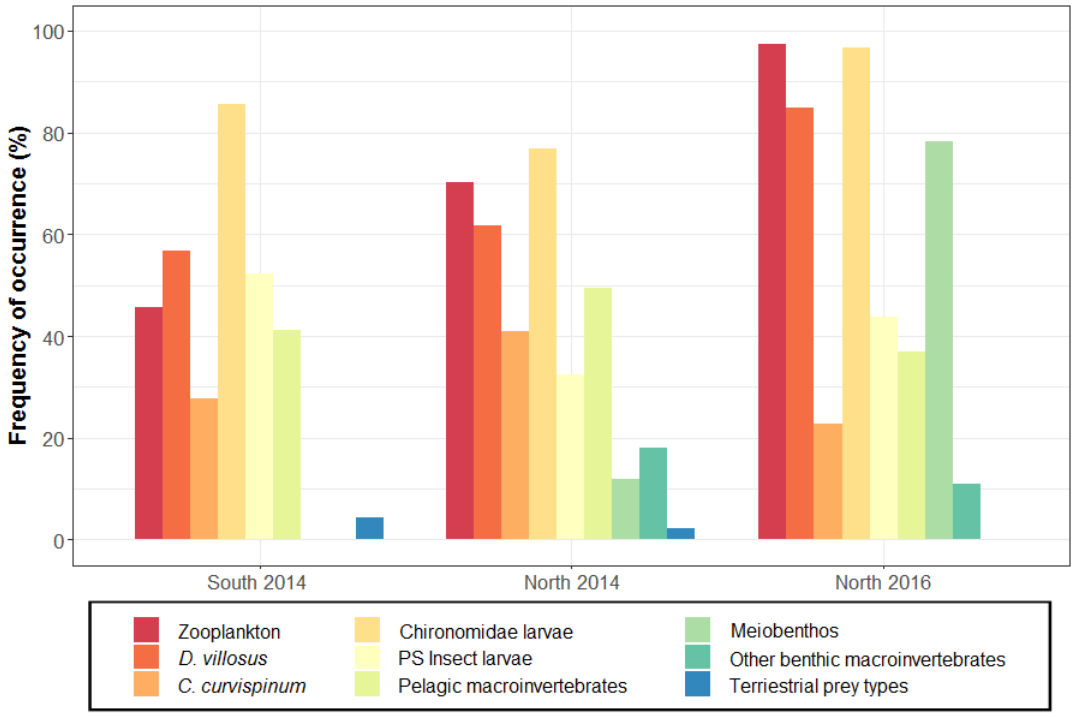

Figure 19. Frequency of occurrence (%) of preys in the diet of YOY-perch (*Perca fluviatilis*) from two locations of Lake Müggelsee ("South" and "North") in 2014 and 2016. Zoopankton: cladocerans and copepods; pelagic macroinvertebrates: Chiromonidae and Culicidae pupae; predator-sensitive (PS) insect larvae: Ephemeroptera and Plecoptera; meiobenthos: Ostracoda and Harpacticoids; other benthic macroinvertebrates: snails and leeches; terrestrial prey types: adult stages of Ephemeroptera, Odonata and Trichoptera.

In 2014, infection intensity of *T clavata* (corrected for fish size) was negatively correlated with the amount of zooplankton consumed by YOY-perch from the southern shore (Spearman's rank correlation: $r_s = -0.208$, $n = 90$, $P = 0.048$; Figure 20C), while no significant relationship was detected with neither the two amphipod species nor the different categories of insect larvae ($P > 0.05$; Figure 20). On the other hand, more relationships were found between the consumption of the prey animals from different prey categories and infection intensity (corrected for fish size) of perch from the northern shore. In the case of amphipods, as infection intensity of *T. clavata* increased fish consumed more *D. villosus* (Spearman's rank correlation: $r_s = 0.309$, $n = 259$, $P < 0.0001$; Figure 21A) and less *C. curvispinum* (Spearman's rank correlation: $r_s = -0.215$, $n = 259$, $P < 0.001$; Figure 21B). Additionally, infection intensity was negatively correlated with the amount of consumed zooplankton (Spearman's rank correlation: $r_s = -0.179$, $n = 259$, $P < 0.01$; Figure

21C), chironomid larvae (Spearman's rank correlation: $r_s = -0.188$, $n = 259$, $P < 0.01$; Figure 21D) and pelagic macroinvertebrates (Spearman's rank correlation: $r_s = -0.19$, $n = 259$, $P < 0.01$; Figure 21F). In 2016, no significant correlation was found between infection intensity (corrected for fish size) and the different prey categories ($P > 0.05$; Figure 22).

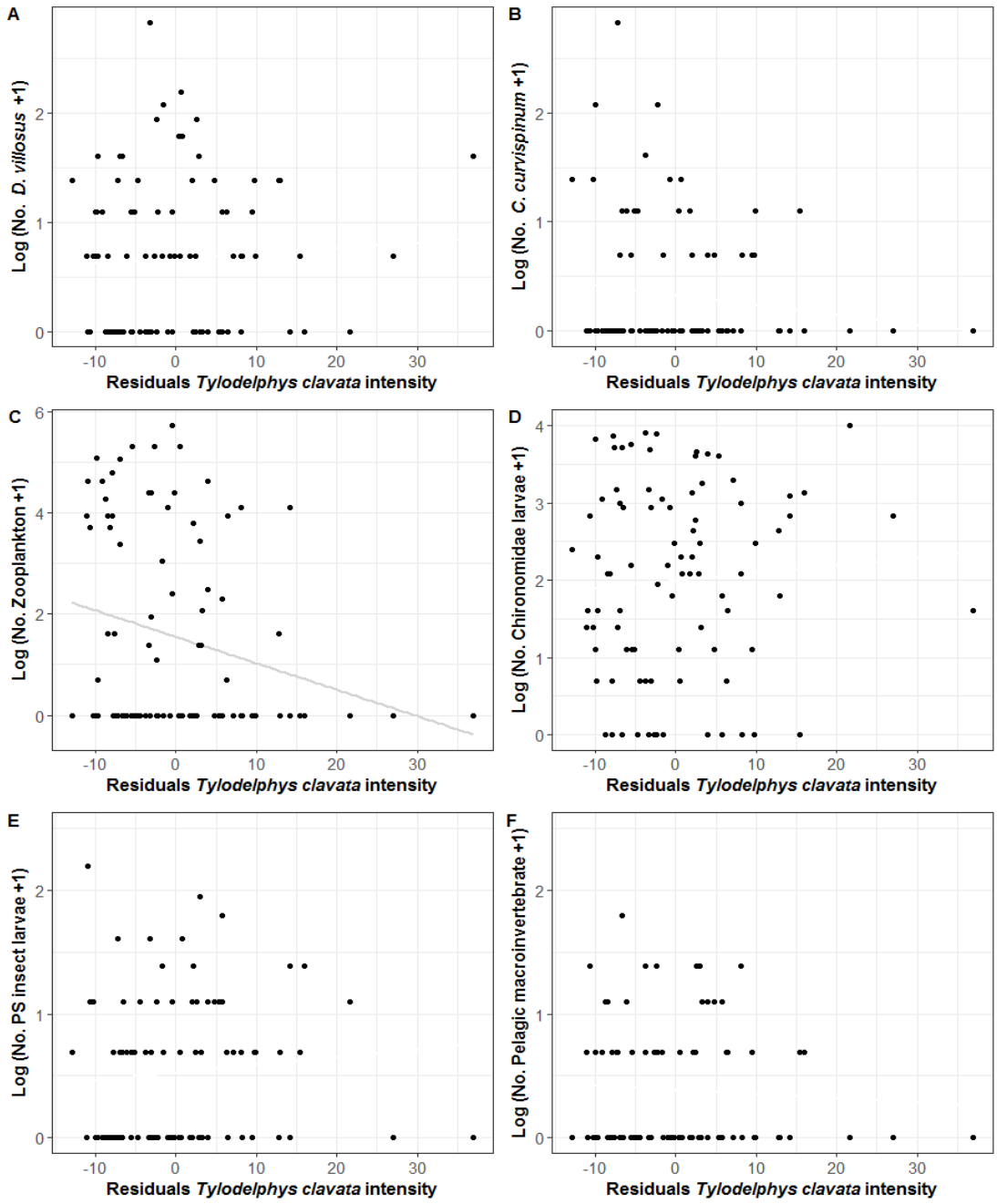

Figure 20. *Tylodelphys clavata* intensity corrected for fish size (residuals from the regression in Figure 16) from perch (*Perca fluviatilis*) caught at the southern shore of Lake Müggelsee in 2014 as a function of number of consumed **(A)** *Dikerogammarus villosus*, **(B)** *Chelicorophium curvispinum*, **(C)** zooplankton, **(D)** Chironomidae larvae, **(E)** Predator-sensitive (PS) insect larvae and **(F)** pelagic macroinvertebrates. All prey categories are log + 1 transformed. Line represents the best linear fit (Zooplankton: $y = -0.052x + 1.551$).

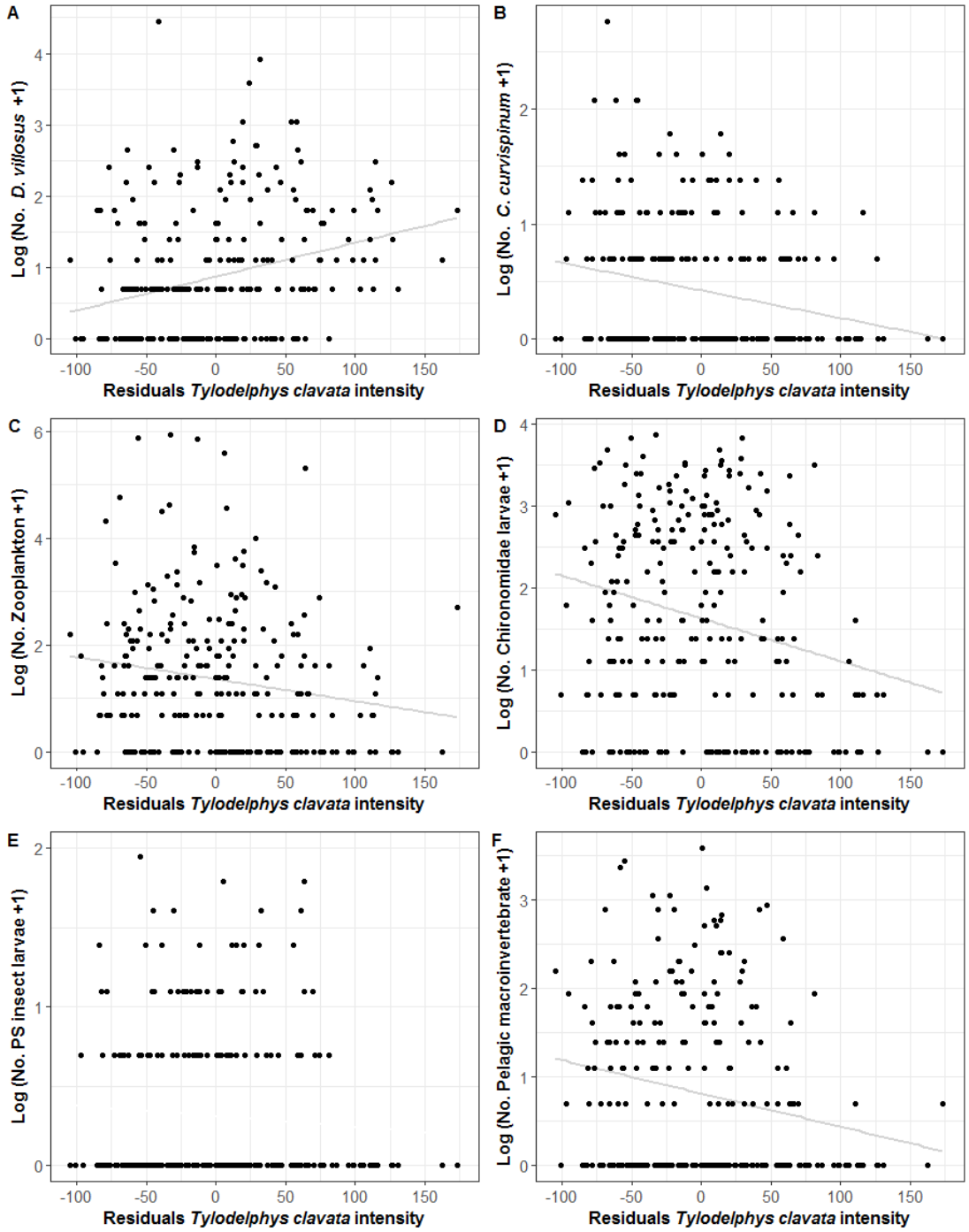

Figure 21. *Tylodelphys clavata* intensity corrected for fish size (residuals from the regression in Figure 16) from perch (*Perca fluviatilis*) caught at the northern shore of Lake Müggelsee in 2014 as a function of number of consumed **(A)** *Dikerogammarus villosus*, **(B)** *Chelicorophium curvispinum*, **(C)** zooplankton, **(D)** Chironomidae larvae, **(E)** Predator-sensitive (PS) insect larvae and **(F)** pelagic macroinvertebrates. All prey categories are log + 1 transformed. Lines represents the best linear fit (*D. villosus*: $y = 0.0047x + 0.864$; *C. curvispinum*: $y = -0.0024x + 0.418$; Zooplankton: $y = -0.0041x + 1.363$; Chironomidae larvae: $y = -0.0052x + 1.628$; Pelagic macroinvertebrates: $y = -0.0037x + 0.813$).

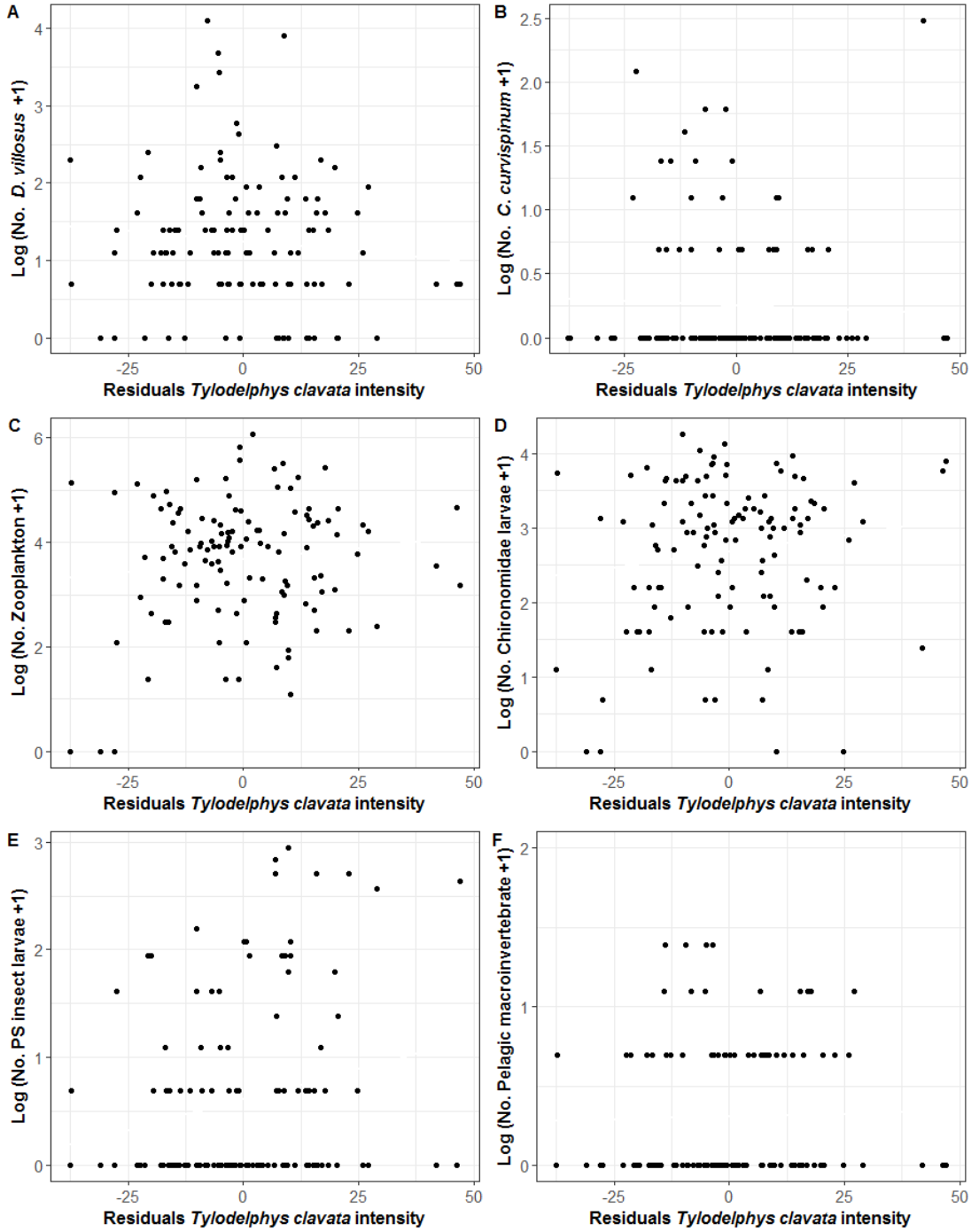

Figure 22. *Tylodelphys clavata* intensity corrected for fish size (residuals from the regression in Figure 16) from perch (*Perca fluviatilis*) caught at the northern shore of Lake Müggelsee in 2016 as a function of number of consumed **(A)** *Dikerogammarus villosus*, **(B)** *Chelicorophium curvispinum*, **(C)** zooplankton, **(D)** Chironomidae larvae, **(E)** Predator-sensitive (PS) insect larvae and **(F)** pelagic macroinvertebrates. All prey categories are log + 1 transformed.

The results from the stable isotope analysis revealed a significant difference in the $\delta^{13}C$ signature of individuals harbouring low and high numbers of *T. clavata* metacercariae ($F_{1,20} = 45.87$; $P < 0.001$; Figure 23). Less intensively infected perch

exhibited a lower $\delta^{13}C$ signature (average ± SD: -28.81 ± 0.74 ‰) in comparison with more intensively infected conspecifics (average ± SD: -26.33 ± 0.95 ‰). Regarding the $\delta^{15}N$ signature no significant difference was detected between fish with low (average ± SD: 12.11 ± 0.22 ‰) and high (average ± SD: 11.87 ± 0.37‰) infection intensity ($F_{3,8} = 3.24$; $P = 0.087$).

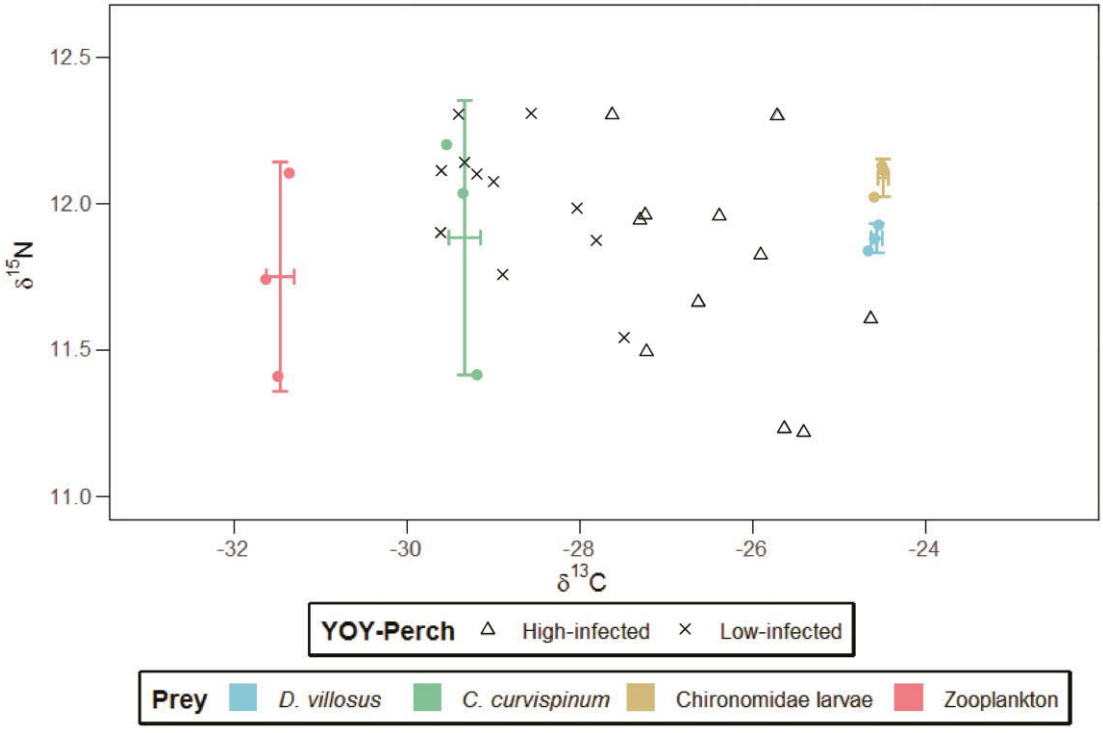

Figure 23. Stable isotope biplot of individual YOY-perch (*Perca fluviatilis*) and mean prey categories sampled at the northern shore of Lake Müggelsee in 2016. Fish are divided in two categories based on infection intensity of *Tylodelphys clavata*: low-infected fish (△) = 5 ± 3 metacercariae per fish (average ± SD) and high-infected fish (×) = 39 ± 13 metacercariae per fish (average ± SD). Perch $\delta^{13}C$ and $\delta^{15}N$ signatures were corrected for fractionation by 1 ‰ and 3.4 ‰, respectively. Prey stable isotope signatures are shown as mean ± SD.

Among the prey categories significant differences were found for $\delta^{13}C$ ($F_{3,8} = 2789$; $P < 0.001$) but not for $\delta^{15}N$ ($F_{3,8} = 0.78$; $P > 0.05$). Zooplankton had the lowest $\delta^{13}C$ signature of - 31.47 ± 0.14 ‰. At the opposite end of the spectrum, *D. villosus* and chironomid larvae both had the highest $\delta^{13}C$ signatures and were not significantly different from one another (Tukey's test: $P > 0.05$; Table 6).

Bayesian isotopic mixing model (SIAR) showed that the contribution of the prey groups to the diet of YOY-perch strongly varied between individuals with different *T. clavata* infection intensity. The amphipod *D. villosus* formed the bulk of highly

infected perch diet (average 70 %), while the dietary contributions of both C. *curvispinum* and zooplankton were considerably low (average < 20 %; Figure 24). On the other hand, less intensively infected perch were less selective and the three prey categories had similar importance. In average the contributions of *D. villosus*, Zooplankton and *C. curvispinum* were 26 %, 30 % and 42 %, respectively (Figure 24).

Table 6. Mean values (± SD) of $\delta^{13}C$ and $\delta^{15}N$ of the different prey categories collected from the northern shore of Lake Müggelsee

Prey	$\delta^{13}C$ (± SD)	$\delta^{15}N$ (± SD)
Zooplankton	- 31.47 ± 0.14	11.75 ± 0.35
Chelicorophium curvispinum	- 29.33 ± 0.16	12.12 ± 0.12
Dikerogammarus villosus	- 24.57 ± 0.06	11.88 ± 0.04
Chironomidae larvae	- 24.29 ± 0.05	12.09 ± 0.06

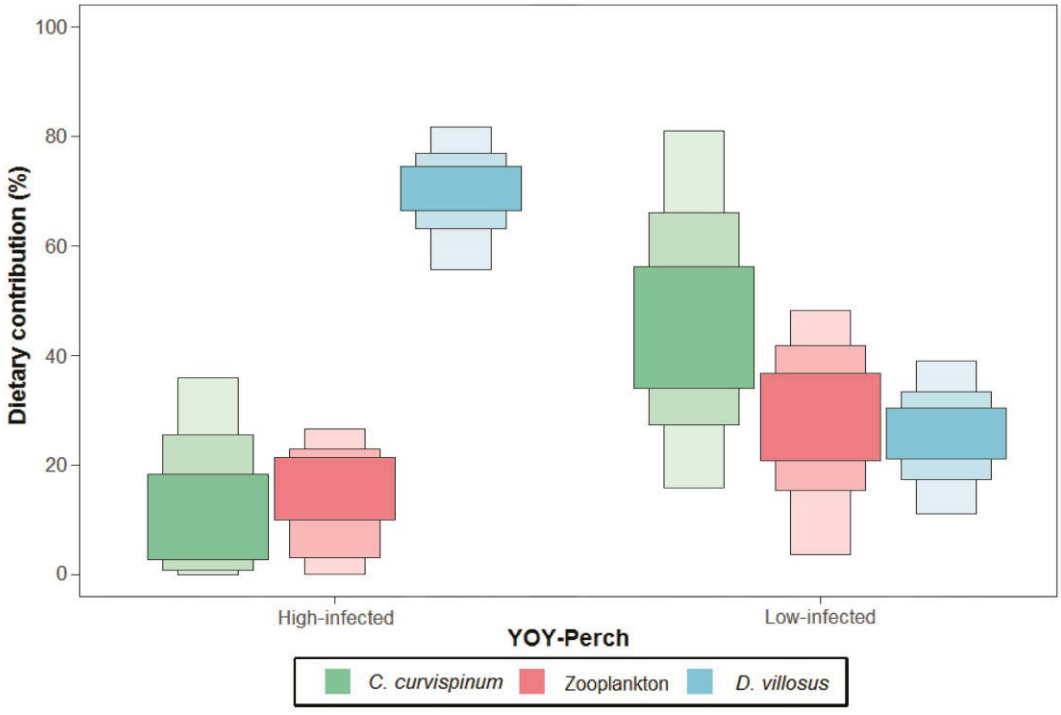

Figure 24. Result of SIAR Bayesian mixing model, based on $\delta^{13}C$ values, showing estimated contributions (%) of *Chelicorophium curvispinum*, zooplankton and *Dikerogammarus villosus* to the diet of YOY-perch (*Perca fluviatilis*) with different infection intensity of *Tylodelphys clavata* at the northern shore of Lake Müggelsee in 2016. *T. clavata* intensity: low-infected fish = 5 ± 3 metacercariae per fish (average ± SD) and high-infected fish = 39 ± 13 metacercariae per fish (average ± SD). The plot shows 25 % (inner box), 75 % and 95 % (outer boxes) credibility intervals.

4. Discussion

4.1 Role of trematodes on snail-periphyton interaction

The results from the experiments with the molluscan host show that trematode infections can significantly affect periphyton-grazing activity of freshwater snails. It thus adds to the existing studies showing that parasites can impact host ecology and play a major role in the structure of food webs (Minchella and Scott 1991; Lafferty et al. 2006; Hatcher and Dunn 2011). A general pattern however, could not be found among the four tested snail-trematode systems, since infected snails consumed more, less or equally as much periphyton compared to the non-infected snails. The variation across studied systems may result from differences on how the parasite utilizes the resources of the snail host.

The remarkable capacity of intramolluscan reproduction of digenean trematodes leads to an invasion on average of 20 – 30 % and up to 50 % of the biomass within the shell (Bernot and Lamberti 2008; Hechinger et al. 2009). This usually results in a partial or total destruction of the gonads and sometimes leads to partial replacement of the hepatopancreas (Probst and Kube 1999). Infection of the hepatopancreas leads to pathological alterations such as karyolysis, breakdown of cell membranes, sloughing of tissue, formation of fibromata and granulomata, alteration of cells from columnar to squamous type and displacement of hepatopancreatic tubules. In connection with these histological changes, decreased glycogen storage, secretion of histolytic excretory products by the larvae and direct ingestion of hepatopancreatic tissue by redia larvae have been observed (Pratt and Barton 1941; Cheng and Snyder 1962a, b; Faro et al. 2013; Skála et al. 2014). Trematodes can massively affect the function of the hepatopancreas, as shown impressively in *Lymnaea columella*, where infection with *Echinostoma paraensei* reduced carbohydrate and total protein content of this organ by 60 % and 76 %, respectively (Pinheiro et al. 2009). Accordingly, Arakelova et al. (2003) suggested that the reduction in metabolism intensity of infected *Littorina saxatilis* was connected with structural changes in the hepatopancreas caused by trematode sporocysts. It is conceivable that pathological alterations and partial replacement of the hepatopancreas by trematode larvae affect the pace at which food is processed. This in turn may alter the snail's grazing rate.

As the degree of the histopathological effects differs among snail-trematode systems (Pratt and Barton 1941; Cheng and Snyder 1962a; Probst and Kube 1999), the effect of a trematode infection on the snail's grazing rate may differ in the same way.

Infection of the gonad can lead to the destruction of the tissue and up to the complete replacement by daughter sporocysts or redia, resulting in partial or total castration of the host (Pratt and Barton 1941; Cheng and Snyder 1962a; Probst and Kube 1999; Faro et al. 2013). Additionally, there is evidence for trematode-induced hormonal castration of infected snails (Hordijk et al. 1991; de Jong-Brink et al. 1988). Any mechanism leading to parasitic castration, either mechanical or hormonal, leaves energy allocated for reproduction, available to be harnessed by the parasite in order to meet its own energetic requirements. There are two possible scenarios: 1) the released energy may be enough to support both parasite and host. This may easily apply to the snail-trematode system of this study since it has been shown that egg production of *L. stagnalis* is costly in terms of carbohydrates and proteins in contrast to the cercarial production of *Trichobilharzia ocellata* (Bourns 1974). There may even be excess energy which could be reallocated to somatic growth. This is assumed to explain the phenomenon of gigantism that occurs in many snail species following parasitic castration (Wilson and Denison 1980; Mouritsen and Jensen 1994). In this case, the snail grazing rate may either not be affected by a trematode infection or may even decrease due to reduced energetic demands of the host. 2) The resources available are not enough to fulfil the energy needs of parasite and host. In this case, the energy deficit may be compensated by an increased grazing rate or reduced activity (e.g. mobility) levels of the snail.

The two mechanisms do not act independently. Variation in the impact of trematodes on the snails' grazing rates observed across snail-trematode systems may at least partly be explained by different developmental strategies of the parasites. *D. pseudospathaceum* invades the gonad and hepatopancreas (Żbikowska 2011). Infection of *L. stagnalis* with *D. pseudospathaceum* results in castration and somatic gigantism of the snail host (Żbikowska 2011; Seppälä et al. 2013), indicating that in this particular host-parasite system the reallocation of reproductive energy seems to free enough resources to meet the requirements of parasite and host. As a result, it may produce similar mass-specific grazing rates of infected and non-infected snails

with similar size as observed in the experiment. Taking into account that *D. pseudospathaceum* induces gigantism in *L. stagnalis* (Żbikowska 2011; Seppälä et al. 2013), this also means that the individual-specific grazing rate of infected snails increases in this host-parasite system, even if that was not explicitly shown in this study.

Similarly, the effect of *T. regenti* on *R. lagotis* can be explained, where mass-specific grazing rates of non-infected and infected snails did not differ, whilst individual-specific grazing rates showed a trend to be higher in infected specimens. Accordingly, it was observed that *T. regenti* caused parasitic castration and gigantism in the experimentally infected *R. lagotis* individuals.

The increased mass-specific grazing rate of *P. corneus* infected with *Cotylurus* sp. may be a compensatory mechanism to provide the energy needed to sustain the parasite and to fulfil its own demands. The present study provides no information whether infection with *Cotylurus* sp. induces energy reallocation by parasitic castration in *P. corneus*. However, for the well-studied planorbid snail *Biomphalaria glabrata*, it has been shown that infection with *Schistosoma mansoni*, despite of partial castration, leads to a depletion of glycogen resources (Faro et al. 2013) and a condition comparable to starvation (Becker 1980) that is compensated by increased feeding activity (Williams and Gilbertson 1983). This could also apply for *P. corneus* infected with *Cotylurus* sp.

Contrasting results were obtained for *L. stagnalis* with *T. szidati*, although sporocysts of *T. szidati* are also found in the gonad and hepatopancreas of *L. stagnalis* and also cause parasitic castration and gigantism as *D. pseudospathaceum* (Horák et al. 2002; Hordijk et al. 1991; Żbikowska 2005). The latter effects were also clearly observed in the experimentally infected *L. stagnalis* individuals. Despite the similarity with a *D. pseudospathaceum* infection, *T. szidati*-infected *L. stagnalis* snails showed lower mass-specific and individual-specific periphyton grazing rates than non-infected conspecifics. Both parasite species show obvious differences in the number of produced cercariae; however, this cannot explain differences in the hosts' grazing rates. A rough estimation suggests that cercarial biomass production is similar for both trematode species: the average daily production of *D. spathaceum* in *L.*

stagnalis exceeds 10000 cercariae per snail (estimated from Karvonen et al. 2004a, figure 1). Due to the host specificity of *Diplostomum* species as described by Faltýnková et al. (2007), one should assume that this publication actually describes the cercarial production of *D. pseudospathaceum*. On the other hand, an average daily production of 2600 cercariae per snail has been reported for *T. szidati* (Soldánová et al. 2016). However, the mean individual cercaria biomass of *D. pseudospathaceum* is approximately a quarter the biomass of *T. szidati* cercaria (0.4 µg and 1.7 µg, respectively, calculated according to Soldánová et al. 2016 and the measurements from Niewiadomska 1986 and Neuhaus 1952), which compensates for the difference in the number of produced cercariae. Another factor that may be responsible for differences in the energy demand between infected and non-infected snails is the possible effect of trematode infection on the host's locomotory activity, which has been demonstrated to be positive or negative in different snail-trematode systems (Mouritsen and Jensen 1994; dos Santos et al. 2013; Alberto-Silva et al. 2015). Furthermore, a reduced digestive capacity of the progressively destroyed hepatopancreas might also interfere with the parasite's production and the snail's grazing rate.

The experiments in this study were performed to examine the impact of patent infections on the host grazing rate. Beyond that, it is still not known if patterns reported here could be likewise observed during the pre-patent period of a trematode infection. It may be that from infection establishment throughout pre-patent and cercarial shedding period, the energetic demand of the snail-trematode system may be modified. Therefore, to understand if the developmental stage of infection may also influence the feeding rate of snails, further research is required.

Parasitological surveys in freshwater systems show that trematode prevalences exhibit great variations. It is common to find low prevalences ranging from 1 to10 % for some species, while others fluctuate between 20 – 40 %. Occasionally some species achieve prevalences of 50 % and up to 80 % (Esch et al. 2001; Faltýnková et al. 2008b; Voutilainen et al. 2009; Born-Torrijos et al. 2014). Looking at the example of Lake Grimnitzsee, 28 % of *P. corneus* snails were infected with *Cotylurus* sp. The results suggest this trematode species alone could increase the overall grazing activity of the *P. corneus* population by at least one third. In this example, trematode

infections facilitated periphyton grazing similar to findings by Bernot and Lamberti (2008) with the freshwater snail *P. acuta* infected with *P. minimum*, while lower grazing rates found in *L. stagnalis* with a patent infection of *T. szidati* also support the findings by Wood et al. (2007) indicating that feeding rate of the marine snail *L. littorea* infected with *C. lingua* decreased by 40 %.

The effects of parasitism on resources utilization, documented in the present study, may indirectly affect other species with which the hosts interact (Thomas et al. 1998; Dunn et al. 2012; Sargent et al. 2014). For instance, periphyton grazing activity of freshwater snails is an important driver in the competition between primary producers by reducing the shading effect of periphyton on macrophytes, which in turn enhances macrophyte growth (Brönmark 1985; Brönmark and Weisner 1992; Li et al. 2009). Moreover, snails have a strong impact on the periphyton community structure by influencing biomass, productivity and species composition (Lowe and Hunter 1988; Brönmark 1989; Vermaat 1994; Krist and Charles 2012). Therefore, trematode-induced modulation on the grazing activity of aquatic snails may affect their functional role as periphyton processors and the energy transfer through the ecosystem.

4.2 Role of *T. clavata* infection on feeding behaviour of European perch

The parasitological survey showed that, even though six trematode species infect the eyes of perch in Lake Müggelsee, the occurrence of the majority of species was considerably low. *T. clavata* was the most abundant and prevalent species, infecting almost all the fish examined (> 99 %). Similar patterns of eye fluke infection have been previously recorded in the same lake (Vivas Munoz 2014), which suggests the presence of a stable eye fluke component community dominated by *T. clavata*. High prevalence and infection intensity levels of *T. clavata* in perch populations are quite common throughout Europe (Kennedy and Burrough 1978; Kennedy 1981, 2001; Rolbiecki et al. 1999; Behrmann-Godel 2013; Soylu 2013; Valtonen et al. 2003). For instance in Lake Constance, trematode infections appeared after juvenile fish returned to the littoral zone (approximately eight weeks post-hatching) and

afterwards infection levels of *T. clavata* increased rapidly reaching a prevalence of 100 % within one month (Behrmann-Godel 2013). Considering the impressive recruitment rate and abundance of *T. clavata* in perch compared to other eye fluke species (Kennedy 2001; Behrmann-Godel 2013), *T. clavata* is presumably the most relevant eye fluke to evaluate infection-associated behavioural alterations in perch.

Infection of sensory organs may impair their performance and consequently affect fish' perception of the environment, which in turn may result in a modified behaviour (Barber et al. 2000; Barber and Wright 2005). Previously, an experimental study showed that infection intensity of *T. clavata* alters the ability to locate food and impaired foraging competitive ability of naturally infected perch (Vivas Muñoz et al. 2017). However, with that approach it remained unclear whether the observed behavioural 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 experiment with parasite free laboratory-reared and experimentally infected perch now provides 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 humour 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 constrains 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 this study, it was found that the distances at which infected perch attack both *A. aquaticus* and *D. magna* were shorter in comparison to non-infected conspecifics. Comparing the reaction distances of the experimentally infected perch with those of naturally infected perch, which were determined by Vivas Muñoz et al. (2017), it turns out to be within a similar range.

Additionally, it was 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*), where the reaction distances decreased as the infection intensity of the eye fluke *D. spathaceum* 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 and causing cataracts such as *Diplostomum* spp. but also by vitreous humour 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 antipredator behaviour. This has been observed in three-spined sticklebacks (*G. aculeatus*) infected with the cestode *S. solidus*, which resumed feeding activity faster than non-infected conspecifics after a simulated predator attack (Giles 1983). Additionally, in the presence of a predator, infected sticklebacks did not show an obvious reaction towards the predator (e.g. raising the dorsal spines) and fed in a closer proximity to the predator than non-infected conspecifics, which fed very hesitatingly (Milinski 1985). Risk taking behaviour 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 of the parasite to the final host (Seppälä et al. 2005a; 2005b; Gopko et al. 2017; Flink et al. 2017). Despite the lack of information on the influence of vitreous humour dwelling eye flukes on their hosts' anti-predatory behaviour, 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). It was initially hypothesized that decreasing light intensity would intensify the impact of *T. clavata* on the visual ability. However, in the 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*) greatly decreases when light intensity falls below 2 lx (Richmond et al. 2004). Consequently, the low illumination level of 6 lx, used in the experiments, 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.

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. Therefore, the increase in consumption of *A. aquaticus* by infected fish under low light intensity may be the result of an increase in the prey encounter rate caused by a higher activity level of *A. aquaticus*.

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 the experiments 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 non-infected fish.

During the 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*) it has been shown that some individuals can directly suppress the foraging rate of others through aggressive behaviour (Metcalfe 1986; Brännäs et al. 2001). On the other hand, within groups of young perch, overt aggressive behaviour 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 behaviour was observed during feeding experiments by Staffan et al. (2002). Although aggressive interactions between the experimental fish were not observed, and there was not 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 behaviour 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 behaviour of rainbow trout showed that individuals infected with *D. spathaceum* formed smaller shoals, divided more often 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 *D. pseudospathaceum* 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 behaviour 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.

Among YOY-perch from Lake Müggelsee a striking positive relationship between infection intensity of *T. clavata* and fish size was observed. This may be attributed to the body surface area, which increased with fish size in a similar manner as infection intensity. Greater surface area in larger fish may facilitate the encounter of the infective free-swimming cercariae. Previously, size-dependent infestation of *T. clavata* among perch individuals has been detected when examining fish over a wider size range than in this study (Kennedy and Burrough 1977, 1978). Cercariae encounter rate may also be affected by other factors such as fish activity or habitat use. Individuals that are more active or remain for long periods of time in areas with high cercaria density have potentially higher encounter rates. This may to some extend explain the large variability in infection intensity between fish of the same size.

Parasites are often expected to reduce fish body condition due to pathological effects of infection (Lemly and Esch 1984; Santoro et al. 2013). The detrimental effect on the visual performance together with the reduction of feeding efficiency makes eye flukes candidates to affect fish body condition. In this study a positive relationship between condition factor and infection intensity was observed for fish sampled in 2014 but this relationship was not detected in 2016. Whether eye flukes may impact fish condition is uncertain as the available information is not consistent. A negative impact on the condition factor of three-spined sticklebacks has been associated with

the infection of *Diplostomum gasterostei* (Pennycuick 1971). Contrarily, infection intensity of *Diplostomum* spp. was positively correlated with the condition factor of the Mesopotamian bream (*Acanthobrama marmid*) (Dörücü et al. 2002) and no relationship was observed with the condition factor of walleye (*Stizostedion vitreum*) and white sucker (*Catostomus commersoni*) (Marcogliese et al. 2001). A positive correlation was also described between the abundance of *Diplostomum* (*Austrodiplostomum*) *compactum* and the condition factor of the South American wolf fish (*Hoplias* aff. *malabaricus*) and the Pantanal eartheater (*Satanoperca pappaterra*) but no effect was detected in any of the other four fish species that were examined in the same study (Machado et al. 2005). It has been shown that the condition factor of fish varies with factors such as sex, seasonal fluctuations, spawning cycles, fullness of the stomach and even total parasite biomass (Weatherly 1972; Lagrue and Poulin 2015). Therefore, future research evaluating the impact of eye flukes on the condition factor of fish requires a more detailed assessment, taking also into account the other variables mentioned above in order to avoid bias, masking of actual infection effects or spurious correlations.

Intraspecific diet specialization is common in natural populations and may have important ecological and evolutionary consequences (Bolnick et al. 2003, 2011). Individual diet specializations observed in perch have been associated with variation in morphology between individuals using different habitats (littoral/pelagic) (Hjelm et al. 2001; Svanbäck and Eklöv 2002, 2003, 2004). However, less is known about the factors that drives within-habitat differences. The results of the field study provide evidence that infection with the eye fluke *T. clavata* plays also a role in individual diet specialization among juvenile perch in the littoral.

Diet composition of juvenile perch varies between lakes depending on habitat, food availability and the degree of inter- and intraspecific competition (Persson 1986; Persson and Greeneberg 1990; Horppila et al. 1999; Hjelm et al 2001). For instance, in some locations perch in the littoral feed mainly on zooplankton up to the length of ca. 15 cm (e.g. Horppila et al. 1999) while in other locations fish completed the shift from zooplankton to benthic macroinvertebrates at smaller sizes (> 7cm) (e.g. Allen 1935; Mustamäki et al. 2004). In the present study, the stomach content analysis showed that the main benthic preys of YOY perch were amphipods and chironomids

and as planktonic prey fish consumed cladocerans and copepods, which is in line with a previous study from Lake Müggelsee (Okun and Mehner 2005).

Individual diet specialization among YOY-perch in the littoral has been previously detected through substantial differences in carbon isotope signals (Quevedo and Olsson 2006) and diet characterization based on stomach contents, where it was observed that some individuals feed primarily on benthic macroinvertebrates, whereas others feed mostly on zooplankton (Frankiewicz and Wojtal-Frankiewicz 2012). In general, these differences in the resources utilization have been considered to be a strategy to reduce intraspecific competition (Bolnick et al., 2003; Quevedo and Olsson 2006; Frankiewicz and Wojtal-Frankiewicz 2012). Considering the impact of *T. clavata* infection on visual ability, it was initially hypothesized that infected fish may change their food preferences as a compensatory mechanism for reduced foraging competitive ability. The results revealed that as infection intensity of *T. clavata* increased the consumption of *D. villosus* increased while the consumption of *C. curvispinum*, zooplankton and chironomids decreased. Even though these relationships were not always detectable and correlations were quite weak, the broad range in the δ^{13}C-signals among individuals indicates the use of different food resources. Individuals from the same study site with the same main food source and similar body size have generally similar isotopic signature due to it reflects the diet over a long period of time (Peterson and Fry 1987; Post 2002). Therefore, the variability in the δ^{13}C-signals of juvenile perch indicates the presence of individual diet preferences (Bootsma et al. 1996; Beaudoin et al. 1999; Bolnick et al. 2003), which were related to infection intensity of *T. clavata*. On the other hand, stomach content analysis provides a short-term dietary "snapshot" (Hyslop 1980). The isotopic mixing model results further support the observations from the stomach content analysis showing that more intensively infected fish had a more selective diet, feeding mainly in *D. villosus*, in comparison to less intensively infected conspecifics.

Taking into account that individual diet specializations of YOY perch have been related to planktivorous vs. benthivorous habits, it is conceivable that by occluding the visual field *T. clavata* could affect prey detection, especially of small size items favoring the consumption of larger invertebrates. Additionally, this effect should be

intensified with infection intensity as the impact of *T. clavata* in perch's visual ability is intensity-dependent (Vivas Muñoz et al. 2017). Similar influence in the prey preferences of fish have been observed in another parasite-host system. Three-spined stickleback females infected with the *S. solidus* fed mostly on benthic invertebrates while non-infected females of the same population fed on planktonic cladocerans (Jakobsen et al 1988). *Schistocephalus solidus* does not infect a sensory organ but it decreases the foraging competitive ability by impairing swimming performance (Milinski 1984; Barber and Huntingford 1995). It was suggested that catching pelagic prey would energetically be more demanding for infected fish as high swimming activity is required (Jakobsen et al. 1988). Thus, parasites that impair foraging competitive ability can indirectly influence diet preferences of the host, which in turn may alter not only predator-prey interactions but also the host's functional role in energy transfer through the ecosystem.

The results did not reveal the typical diet specialization (planktivorous vs. benthivorous). Instead less heavily infected fish seem to be "generalists", as the different prey categories similarly contributed to their diet (Bolnick et al. 2003), while individuals with a higher infection intensity specialized on the consumption of *D. villosus*. Presumably, this preference may not only be driven by prey size but also by prey behaviour. The amphipod *C. curvispinum* has a similar size as *D. villosus*; however, its importance on the diet of more intensively infected fish was low (average diet contribution 17 %). This amphipod is a filter-feeder, which builds mud tubes on hard substrates, such as stones, wood structures and aquatic vegetation that can provide shelter against predators (Van den Brink et al. 1991; den Hartog et al. 1992). On the other hand, *D. villosus* is an opportunistic species, well known for its predatory behaviour on a wide range of other invertebrate species (Dick and Platvoet 2000; Platvoet et al. 2009). Both laboratory and field studies have described a practically continuous feeding activity of *D. villosus* without any distinctive diurnal rhythm or extended feeding interruptions (Platvoet et al 2009; Richter et al. 2018; Worischka et al 2018). Accordingly, given the difference on behaviour, *D. villosus* individuals may be more conspicuous than *C. curvispinum* and presumably easier to detect for heavily infected fish.

Among Chironomidae subfamilies there are different feeding guilds for the larvae, such as filter-feeders, grazers, detritivores and predators (Berg 1995; Henriques-Oliveira 2003). A high variability in the isotope signatures should reflect the use of different resources by chironomids (Peterson and Fry 1987; Post 2002). However, the results in the present study showed a low variance. Moreover, δ^{13}C-signals of chironomids greatly differed from the δ^{13}C-signals of the filter-feeder *C. curvispinum* but it did not differ from the δ^{13}C-signals of *D. villosus*. Probably, the sampling method may have led to an underrepresentation of the different feeding guilds as they were hand-picked from aquatic vegetation and stones. It is possible that the sample consisted of individuals belonging to the subfamily Tanypodinae, which have a predatory feeding behaviour and move freely on aquatic vegetation or substratum surface (Berg 1995; Syrovátka 2018). Because the uncertain composition of the chironomid sample, chironomids were excluded from the mixing model analysis and the estimation of its contribution to the diet of YOY-perch was only possible on the basis of the stomach contents. The results from stomach contents analysis showed a negative relationship between infection intensity of *T. clavata* and consumption of chironomids. However, further research taking into consideration the different feeding guilds of chironomid larvae and having a more differentiated collection for stable isotopes analysis is required to unveil the role of *T. clavata* infection on the consumption of chironomid larvae, which are an important prey for YOY-perch.

Although the field data showed that *T. clavata* infection has an influence on perch diet preferences, in the feeding experiments it was not observed that infection status affected prey preference of perch when having two prey types with a clear size difference (*D. magna* and *A. aquaticus*). This may be a consequence of the experimental conditions. For instance, before the experiment fish did not experience limited food availability; thus, fish may have encountered low intraspecific competition. Presumably, if the experimental conditions were maintained for an extended period of time, different prey preference patterns would have been detected considering the evidence that individual diet preferences intensify when resources are limited (Svanbäck and Persson 2004; Araujo et al. 2008; Svanbäck et al. 2011). Furthermore, some studies have pointed out the importance of leaning for diet specialization (Bence 1986; Bolnick et al. 2003). Both *A. aquaticus* and *D. magna* were offered to perch previous to the experiment. However, a large proportion of the

weekly feed consisted of dry food, which may have also influenced the lack of prey preferences during the experiment.

In summary, the present study provides first evidence that infection intensity of *T. clavata* indirectly influences diet preferences of perch, resulting in dietary clusters among individuals of the same population. European perch is widely distributed and one of the most common species in northern-temperate lakes (Craig 2000). Thus, parasite-induced dietary clusters may have important ecological implications and modulate food web dynamics. Revealing this kind of indirect effects significantly contributes to the comprehensive understanding of the role of parasites in aquatic communities.

5. Conclusions and perspectives

There is meanwhile broad consensus that food web concepts without parasites are incomplete and their inclusion increases richness, connectance and alters network structure (Lafferty et al. 2006; Lafferty et al. 2008; Dunne et al. 2013). The results presented here confirm that trematodes can play a relevant role within food webs by altering their host's feeding behaviour. The observed changes in host resources utilization can induce indirect effects on other species at the same or different trophic level in the community (Hatcher and Dunn 2011; Dunn et al. 2012). To disclose the extent to which these effects ramify throughout communities and influence the ecosystem is a challenge as the multiple-host life cycles link trematodes to several different taxa, influencing consumer-resource interactions at various trophic levels.

In general, host interactions with other species can be altered through density-mediated effects (resulting from parasite-induced reduction in host reproduction and survival) as well as trait-mediated effects (resulting from parasite-induced changes in host behaviour or physiology). The latter were the focus of this study. However, these effects are not mutually exclusive but often interact (Hatcher and Dunn 2011; Dunn et al. 2012; Sargent et al. 2014). Trematode infection in snails is a good example of this interaction by causing parasitic castration and behavioural alterations. The effect on grazing rate of freshwater snails described in this study can have a knock-on effect for the basal resource species, which can potentially influence benthic community structure (Wood et al. 2007; Bernot and Lamberti 2008). Directions and intensities of parasite-induced effects, however, are species-specific and cannot be generalized. Thus, incorporation only of this individual stage of trematode life cycle into aquatic food webs remains a complex task that requires more comprehensive studies at the species level including the fact that complex trematode assemblages occur within various mollusc species (Esch et al. 2001, 2002; Sorensen and Michella 2001).

By using experimentally infected perch, this study demonstrated the causal relationship between infection of *T. clavata* and the impact on foraging competitive ability and feeding efficiency of the host. These effects can be associated with

important consequences on other aspects of fish behaviour, such as shoaling and antipredator behaviour. Frequently, trophically transmitted parasites, such as *T. clavata*, alter host behaviour increasing vulnerability to predation by the next host in the parasite's life cycle (Moore 2002; Hughes et al. 2012). In this way, parasites influence energy flow from lower to upper trophic levels (Hadeler and Freedman 1989; Kuris et al. 2008). 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. However, an interesting question for further studies is whether infected fish may modify their risk taking behaviour as a compensatory mechanism for reduced foraging and 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 behaviour during foraging may increase predation risk and potentially enhance transmission success of *T. clavata* to the final bird host.

This study provides for the first time evidence that infection intensity of *T. clavata* has an extra indirect effect, influencing diet preferences of perch. Such hidden effects of parasites, leading to diet specialization among individuals within a population (dietary clusters) are underappreciated components of food webs (Bernot and Lamberti 2008). Nonetheless, they may modulate a substantial amount of energy flow through the system especially in populations with high infection intensity variability. Therefore, in aquatic ecosystems eye fluke infection may play an important role not only in the energy transfer to upper trophic levels, but also in the interaction of the host with lower trophic levels. Given the cosmopolitan distribution of eye flukes and the various roles fish play in freshwater ecosystems, the ecological implications of this parasite-host system are far-reaching.

Aquatic systems are intricate structures with numerous players and complex dynamics. As observed in the present study, trematodes are involved in indirect interactions at several trophic levels. To incorporate parasites within a broad ecological context, it is essential to thoroughly study host-parasite interactions on species level, and how both direct and indirect effects influence populations and community structure. Only by understanding patterns of biomass, species

abundances and interaction strength of all members of the food web, we will be able to create realistic models incorporating parasite into the overall web dynamics.

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Jenny Carolina Vivas Muñoz