

# Glochidiosis and behaviour

Sebastian L. Rock





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Faculty of Health, Science and Technology

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Biology

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Jocko Willink

## Abstract

Freshwater mussels in the order Unionida are a highly endangered and globally distributed taxon of parasitic bivalves. Consequently, many conservation and reintroduction projects have emerged to protect this valuable order. Adult mussels release parasitic larvae (glochidia) that affix themselves to their hosts, typically the gills of fish, where they become encysted in the tissue and metamorphose into juveniles; later, excysting to develop into free-living adults in the sediment, completing the lifecycle. As Unionids are well-known ecosystem engineers, reintroduction efforts are generally met with support. However, members of the public unfamiliar with the scientific literature often have reservations when learning that the restoration project aims to introduce parasites to their local waterways. Little is known about the impacts of glochidiosis on host fishes; however, most effects are negative. With the growth of mussel conservation projects, more fish will be exposed to these negative impacts.

In this dissertation, I explore the parasitic interactions of two of Europe's most endangered mussels with some of their respective host fishes. I initially produced a general literature review to summarize all previous work on the topic and better understand which aspects needed the most attention (**Paper I**). From this, I surmised that the behavioural and molecular impacts of glochidiosis were the least studied and that there was a general over-representation of the interaction between the freshwater pearl mussel (*Margaritifera margaritifera*) and its salmonid hosts, a highly specialized interaction not well-suited for cross-species generalizations. I followed **Paper I** with an investigation into the impacts of infestation by the thick-shelled river mussel (*Unio crassus*) on the schooling behaviour of its host minnow (*Phoxinus phoxinus*; **Paper II**), and the impacts of both adult and larval life stages of *U. crassus* on the predator-prey

interactions of its host bullhead (*Cottus gobio*) with a prey gammarid (**Paper III**). The results of **Papers I, II and III** suggested that unionid mussels may express an extended phenotype and manipulate host behaviour; to test this hypothesis, I conducted a year-long field study was conducted on the movement patterns and habitat use of brown trout (*Salmo trutta*) when infested with glochidia from *M. margaritifera* (**Paper IV**), the species most likely to express an extended phenotype, as speculated in **Paper I**. This investigation provided evidence in support of an expressed extended phenotype by a unionid mussel on its host fish.

## Populärvetenskaplig sammanfattning

Sötvattensmusslor inom ordningen Unionida är en starkt hotad och globalt förekommande grupp av parasitiska bivalver. Unionider är viktiga ekosystemingenjörer eftersom de bidrar med ett brett spektrum av ekosystemtjänster i sina livsmiljöer. Som ett resultat av musslornas betydelse och för att skydda dem har flera bevarande- och återintroduktionsprojekt initierats. De vuxna musslorna släpper ut parasitiska larver (glochidier) vilka fäster på en eller flera värdfiskarter och utvecklas till juvenila musslor. När musslorna är färdigutvecklade släpper de från sin värdfisk och utvecklas till vuxna musslor, vilket fullbordar livscykeln. Eftersom musslorna har visat sig tillhandahålla ett stort antal ekosystemtjänster, stöds återintroduktionsinsatser vanligtvis av allmänheten, även om somliga kan ha reservationer mot restaureringsprojekt som syftar till att återinföra parasiter i lokala vattendrag. Glochidiernas effekter på värdfiskar är inte fullt kända, även om de flesta verkar vara negativa för fisken. Med det ökande antalet återintroduktionsprojekt kommer fler fiskar sannolikt att utsättas för denna negativa påverkan.

I denna avhandling utforskar jag de parasitiska interaktionerna mellan två av Europas mest hotade musslor och deras respektive värdfiskar. Jag inledde med att genomföra en litteraturöversikt för att sammanfatta tidigare forskning om ämnet samt för att bättre förstå vilka aspekter som behövde mest uppmärksamhet i framtida studier (**Paper I**). Utifrån resultaten drog jag slutsatsen att de beteendemässiga och biokemiska effekterna av glochidier var de minst studerade, och att det fanns en allmän överrepresentation av interaktionen mellan flodpärlmussla (*Margaritifera margaritifera*) och dess salmonidvärdar, en mycket specialiserad interaktion som inte är väl lämpad för generaliseringar för unionider som grupp. Jag följde upp **Paper I** med en undersökning



av effekterna av glochidier av tjockskalig målarmussla (*Unio crassus*) på simbeteendet hos dess värdfisk, elritsa (*Phoxinus phoxinus*; **Paper II**), samt effekterna av både vuxna och glochidier av *U. crassus* på predator-bytesdjursinteraktionerna mellan dess värdfisk, stensimpa (*Cottus gobio*), och ett vanligt byte, en gammarid märkräffa (**Paper III**). Resultaten från **Paper II** och **III** antydde att unionida musslor kan manipulera värdfiskens beteende. För att testa denna hypotes genomfördes en ettårig fältstudie av rörelsemönster och habitatval hos öring (*Salmo trutta*) när den var infekterad med glochidier från *M. margaritifera*, den art som är mest benägen att manipulera sin värdfisk (**Paper IV**). Resultatet av denna undersökning gav stöd för att en unionid mussla kan manipulera sin värdfisk.

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## **Abbreviations**

<b>ANOVA</b>	Analysis of variance
<b>ANCOVA</b>	Analysis of co-variance
<b>DM</b>	Distance moved
<b>dpi</b>	Days post infestation
<b>GLMM</b>	Generalized linear mixed model
<b>K</b>	Fulton's condition factor
<b>LMM</b>	Linear mixed model
<b>NND</b>	Nearest neighbour distance
<b>PCA</b>	Principal component analysis
<b>PIT</b>	Passive integrated transponder
<b>RFS</b>	Regression factor score
<b>RPC</b>	Rotated principal component
<b>TKE</b>	Turbulent kinetic energy
<b>SGR</b>	Specific growth rate

## List of papers

This dissertation is based on the following papers, which will be referred to by their roman numerals from here on:

### Paper I

Rock, S. L., Watz, J., Nilsson, P. A., Österling, M. (2022). Effects of parasitic freshwater mussels on their host fishes: a review. *Parasitology*, 149, 1958–1975.  
<https://doi.org/10.1017/S0031182022001226>

### Paper II

Rock, S. L., Blomqvist, M., Watz, J., Nilsson, P. A., Calles, O., & Österling, M. (2025). Parasitic freshwater mussels impact the shoaling behaviour and habitat use of their host fish. *Manuscript*

### Paper III

Rock, S. L., Elmlund, A., Watz, J., Nilsson, P. A., Calles, O., & Österling, M. (2025). A habitat and a parasite: The impact of adult and larval parasitic freshwater mussels on habitat choice and predator-prey interactions between a host fish and its prey. *Submitted*

### Paper IV

Rock, S. L., Watz, J., Nilsson, P. A., Calles, O., & Österling, M. (2025). Parasitic mussels induce upstream movement in their fish hosts: early evidence of extended phenotype. *In Press*

## **Author contributions**

### **Paper I**

SLR and MÖ conceived the general idea behind the review. SLR carried out the majority of the work of screening and reviewing the body of literature on which this study is based, analysed and synthesized the studies and drafted the manuscript. JW, PAN and MÖ assisted SLR in the literature search, helped carrying out the analysis and synthesis and provided important comments on the draft.

### **Paper II**

SLR and MÖ conceptualized the study design and methodology. SLR and MB collected the data. FT ran the hydrological models. SLR led statistical analysis with support from JW and PAN. SLR led the writing of the manuscript supported by all other authors.

### **Paper III**

SLR, MÖ and PAN conceived the ideas and designed the methodology. SLR and AME collected the data. SLR lead statistical analysis with support from JW and PAN. SLR lead the writing of the manuscript supported by all other authors.

### **Paper IV**

SLR and MÖ conceived the initial study idea. SLR primarily collected data in the field, supported by MÖ and PAN. SLR led statistical analysis with support from JW and PAN. SLR led the writing of the manuscript supported by all other authors.

## Associated publications

The following papers were produced over the duration of the doctoral period but are not included in the dissertation. Not all publications in this list pertain to the subject matter of the dissertation, relevant papers are cited as standard.

1. Rock, S. L., Rodenburg, F., Schaaf, M. J., & Tudorache, C. (2022). Detailed analysis of zebrafish larval behaviour in the light dark challenge assay shows that diel hatching time determines individual variation. *Frontiers in Physiology*, 13, Article 827282. <https://doi.org/10.3389/fphys.2022.827282>
2. Rock, S. L., Oudendijk, Z., Kürten, F. T., Veglia, L., Tyukosova, V., Bourtzi, I., Verzé, N., & Sloggett, J. J. (2023). The effect of stress on rates of asexual reproduction in an invasive planarian. *Ecotoxicology*, 32(10), 1201-1208. <https://doi.org/10.1007/s10646-023-02713-z>
3. Rock, S. L. (2024a). Aquarium setup for the long-term housing of *Pseudanodonta complanata* (Bivalvia: Unionidae) towards captive breeding success. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 34(7), Article e4218. <http://dx.doi.org/10.1002/aqc.4218>
4. Rock, S. L. (2024b). First observation of a spawning mantle display in a European unionid mussel. *Ecology and Evolution*, 14(7), Article e70016. <https://doi.org/10.1002/ece3.70016>
5. Rock, S. L., & Townsend Jr, V. R. A scanning electron microscopy based survey of the impact of infestation by parasitic freshwater mussel glochidia upon the gill morphology of two species of salmonid fish. *Parasitology International*, Article 103071. <https://doi.org/10.1016/j.parint.2025.103071>



## Introduction

### Host-parasite interactions

The relationships between parasites and their hosts are among the most complex and specialized forms of organism interactions on the planet. Interest in these interactions has grown rapidly since the inclusion of parasitology in evolutionary ecology as parasites have been shown to play a key role in regulating population size (Scott & Dobson, 1989; Tompkins *et al.*, 2002), host behaviour (Berdoy *et al.*, 2000; Wesołowska & Wesołowski, 2014), host ecology (Poulin & FitzGerald, 1989), the evolution of mutualistic relationships (Parratt & Laine, 2016; Rook, 2007), and have even been proposed as a driving factor behind the evolution of sexual reproduction (Hamilton *et al.*, 1990). While there are many interpretations of the term "parasite," the most widely accepted definition is "an organism that lives in or on another organism, the host, and causes it some harm by exploiting it through a structurally adapted way of life" (Poulin, 2007). This definition can be applied to plants, fungi, animals, viruses, bacteria, and, some argue, even to specific DNA strands (Combes, 2001; Poulin, 2007).

Studies on parasitism have recently been incorporated into evolutionary ecology, as parasite presence is ubiquitous in every ecosystem, with almost every species having at least one parasite. Parasites are highly coevolved with their hosts, as there is an underlying evolutionary race in which the parasite evolves to better exploit the host, while the host adapts with better defences for avoidance and self-preservation (Poulin, 2007). The study of parasitic interactions can provide insights into the evolution of host biology, behaviour, and habitat use (Marcogliese, 2004). Parasites are involved in up to 75% of the links in any given food web, and up to 40% of all described species are parasitic; some even suggest that parasitic



species outnumber free-living organisms (Dobson *et al.*, 2008; Price, 1980; Sukhdeo, 2012).

Organisms may have adopted parasitic life-history strategies for a variety of reasons; however, all parasites must have had some previously adapted traits that allowed them to become parasitic, utilizing these traits to reap a fitness advantage from another organism (Poulin, 2007). This increase in fitness may be the result of higher nutrient intake by feeding from the host (Bouchet & Perrine, 1996; Williams & Bunkley-Williams, 1994), higher dispersal rates by using the host as a means of transportation (Anderson, 1984; Athias-Binche, 1993), or others, and often in combination (Poulin, 2007). Given the vast diversity of parasitic organisms, the literature often categorizes them according to the strategies they have evolved. Among the factors taken into account when describing a parasite are the location on the host where the parasite infests, the number of hosts the parasite requires to complete its life cycle, and the proportion of its lifetime spent as a parasite (see Box 1).

**Box 1:** Collection of terms with which to describe parasites [from appended **Paper I**]

Endoparasite: Lives internally in the host, in contact with host homeostasis.

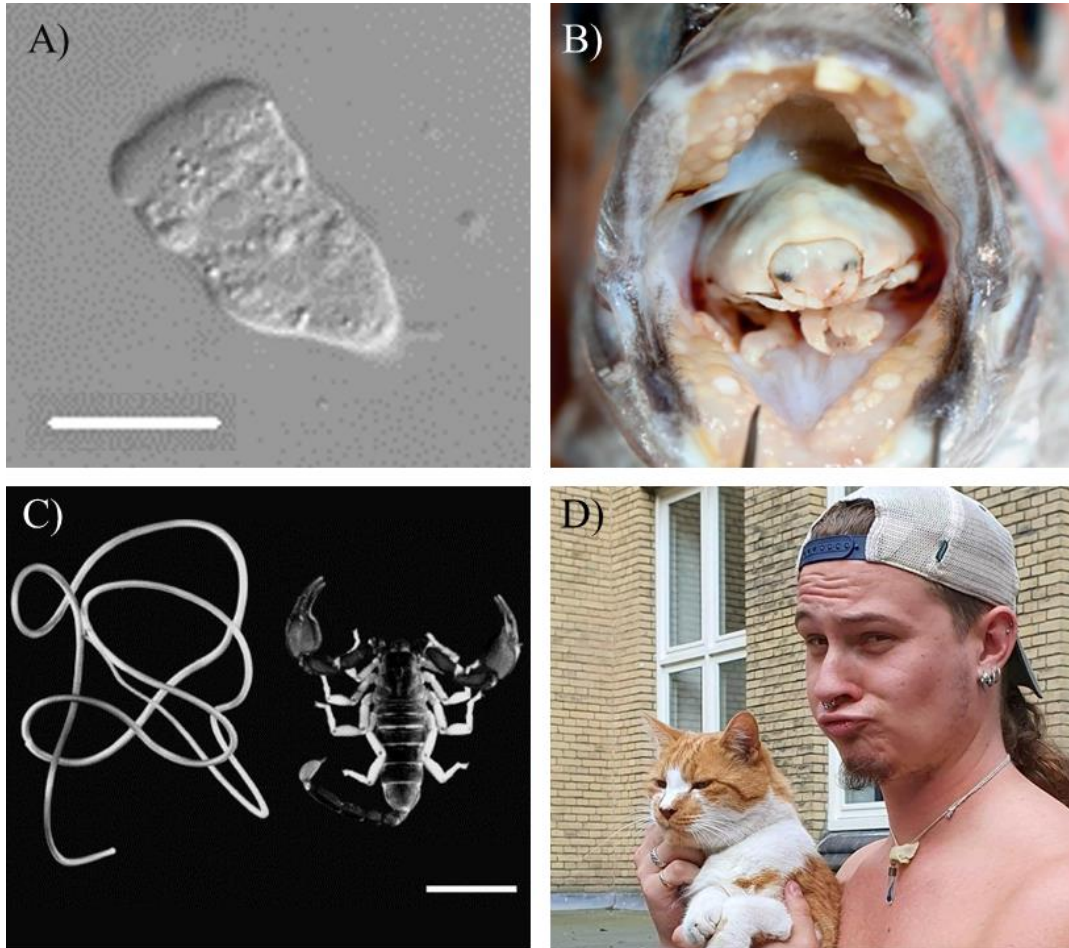
Ectoparasite: Lives externally on the host, in contact with the outside environment.

Monoxenous (direct) parasite: One host species required for full development.

Heteroxenous (indirect) parasite: Multiple host species required for full development.

Facultative parasite: Does not require a host to complete the life cycle, but can be parasitic.

Given the complexity of host-parasite interactions, the traits outlined in Box 1 can be combined in a variety of ways. For example, the brain-eating amoeba (*Naegleria fowleri*; Fig. 1A) is a free-living protozoan commonly found in warm, still waters. Occasionally, the protozoan infects humans, consuming the brain after entering the body through the nose, causing primary amoebic meningoencephalitis (Siddiqui *et al.*, 2016). As such, we may call it a facultative monoxenous endoparasite. The tongue-eating louse (*Ceratothoa famosa*; Fig. 1B) is an isopod that enters the mouth of a fish through the gills, severs the tongue and replaces it, later feeding on host tissue as it releases juveniles into the water column to infest a new host (Hadfield *et al.*, 2025). As such, we may call it a total monoxenous ectoparasite. Certain horsehair worms (Fig. 1C) will lay their eggs on the edge of water bodies to be accidentally ingested by terrestrial arthropods. Following ingestion, the nematode will develop into an adult and induce suicidal drowning in the host, allowing the nematode to reach an aquatic habitat where it can complete its life cycle (Schmidt-Rhaesa *et al.*, 2005). As such, we may call it a partial monoxenous endoparasite. The common housecat (*Felis catus*; Fig. 1D) is a highly invasive, free-living mammal responsible for tens of billions of wildlife kills annually in the United States alone, causing significant harm to overall biodiversity (Loss *et al.*, 2013; Trouwborst *et al.*, 2020; Nilsen *et al.*, 2023). The feline also possesses soft fur and large eyes, which it uses to gain favour with one or multiple *Homo sapiens* individuals or social groups, to then extract nutrients, shelter, and a dispersal vector to novel habitats (Medina *et al.*, 2011). Although the degree to which *F. catus* is parasitic can be debated, we may call them a facultative heteroxenous ectoparasite.



**Figure 1:** Tiled image of several parasites. A) Trophozoite form of *Naegleria fowleri*, bar measures  $10\ \mu\text{m}$  [modified from Siddiqui et al., 2016; used with permission]. B) Preserved *Ceratothoa famosa* in the mouth of a host fish [modified from Hadfield et al., 2025; used with permission]. C) Horsehair worm (*Spinochordodes tellinii*) next to host scorpion (*Euscorpium flavicaudis*), bar measures 1 cm [modified from Schmidt-Rhaesa et al., 2005; used with permission] D) *Felix catus* seeking shelter with a host *Homo sapiens*.

## Parasite ecology

Parasitic organisms, by definition, negatively affect the fitness of their hosts. Consequently, they have generally been regarded as negative factors in healthy ecosystems and are regularly the target of eradication efforts. However, arguments against the widespread eradication of parasites have begun to emerge (Marcogliese, 2005). First, parasites may play a central role in the normal functioning of the host immune system, particularly in cases where parasitic infestation is common throughout the population (Flohr *et al.*, 2009; Pizzi, 2009). Given that hosts have evolved to tolerate the parasitic infestation, a lack of the effects caused by or induced from infestation may lead to secondary deleterious effects in the host (Flohr *et al.*, 2009; Pizzi, 2009; Rook, 2007). Additionally, the survival of a parasite may be dependent on the (temporary) survival of the host; it is thus not always advantageous for the parasite to exhibit an overly exaggerated effect on host fitness such that it affects survival (Poulin, 2007).

Second, as parasites can have significant effects on host tissue, behaviour, or both, parasite presence - or lack thereof - can alter the community structure in which the hosts exist (Mouritsen & Poulin, 2003, 2005). Such effects are typically referred to as extended phenotypes. This concept proposes that phenotypes are more than simply physical characteristics or protein synthesis, and can be extended to all effects a genotype might have beyond the body of the organism (Dawkins, 1982). Dawkins (1982) cites two principal categories of examples for this claim. The first is the capacity of animals to manipulate their environment, such as in the case of termite mounds or beaver dams (Gurnell, 1998; Butler & Malanson, 2005; Korb, 2010; Bonachela *et al.*, 2015). The second, of particular interest here, is the manipulation of other organisms: referring to the capacity of a parasite to induce changes in the host (often behavioural) that increase parasite

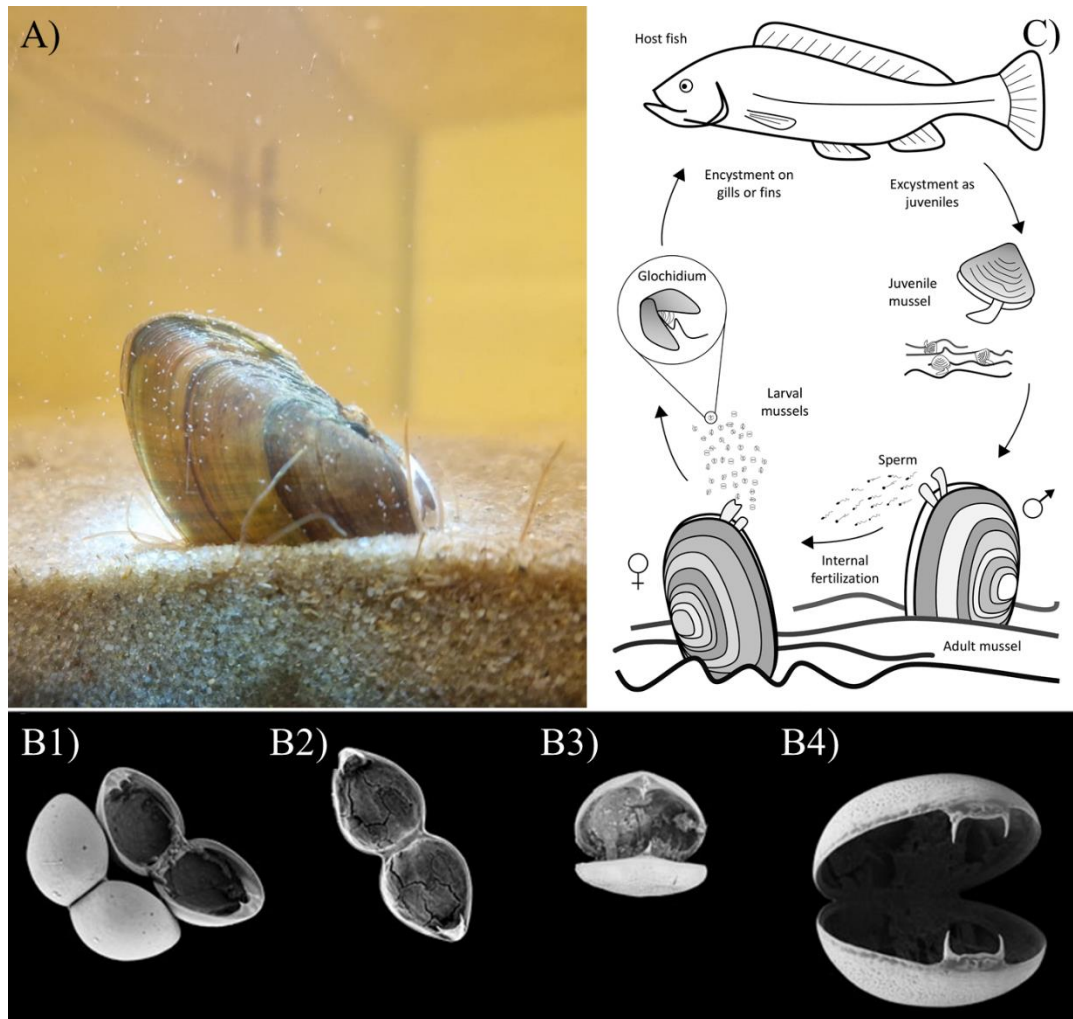
fitness and can be of direct detriment to the host. In certain heteroxenous parasites, this process is referred to as parasite-induced trophic transmission, wherein the parasite enacts a behavioural change to the first host, directly or indirectly, which increases the likelihood of its transmission to the next (Webster, 2007; Luong *et al.*, 2014; Wesołowska & Wesołowski, 2014).

Direct effects on behaviour can be exemplified by the parasitic flatworms in the genus *Leucochloridium*, whose brood sacs infest the eyes of snails. This infestation changes both the appearance and behaviour of the snail, making it more visible to avian predators, the definitive host, and thereby facilitates transmission (Wesołowska & Wesołowski, 2014). Extended phenotypes can be applied to non-trophically transmitted parasites as well, such as in the case of the previously described horsehair worms.

Indirect effects on the ecosystem and community structure induced by parasitic infestation may be demonstrated through a case study of the parasitic flatworm *Curtuteria australis* that infests the foot of the marine bivalve *Austrovenus stutchburyi*. These flatworms have been shown to significantly reduce the ability of the host bivalve to burrow and move across the substrate, thereby resulting in relatively low bioturbation of the upper sediment (Mouritsen & Poulin, 2003, 2005). In a field study where the population of the parasite was artificially lowered, bioturbation increased, ultimately leading to a reduction in species richness and density of benthic macroinvertebrates (Mouritsen & Poulin, 2005). Such secondary trait-mediated effects lead many to argue that stable ecosystems have a rich diversity of parasites (Dobson *et al.*, 2006; Hudson *et al.*, 2006; Marcogliese, 2004; Mouritsen & Poulin, 2005; Pizzi, 2009; Rózsa, 1992).

## **Mussels as parasites**

Freshwater mussels in the order Unionida (Fig. 2A) can be found on every continent with the exception of Antarctica and are characterized by the presence of a parasitic life stage (Fig. 2B). Unlike their marine relatives, unionid mussels do not synchronously release eggs and sperm into the water column for external fertilization. Rather, males release sperm, which is filtered from the water by females and used for internal fertilization. In most cases, fertilized eggs are brooded in modified gill pouches for later release as parasitic larvae, called glochidia. Glochidia affix themselves to the gills, fins, and/or skin of a host fish (occasionally amphibians) where they remain encysted for a metamorphosis period before excysting as juvenile mussels and falling to the substrate, where they bury themselves and, over time, develop into adults (Strayer, 2008; Fig. 2C).



**Figure 2:** A) *Unio tumidus* in an aquarium at Karlstad University surrounded by other benthic invertebrates. B) Scanning electron microscope images of 1) *Cucumerunio novaehollandiae*, 2) *Hyridella australis*, 3) *Echyridella aucklandica* and 4) *Hyridella glenelgensis*. (no scale provided; modified from Klunzinger et al., 2023; CC BY 4.0). C) Generalized unionid life cycle. Adult males release sperm in the water column for internal fertilization of the eggs within the female. Larvae are then released and affix themselves to the host, where they metamorphose into juveniles and detach from the host to develop into adults on the bottom substrate [from appended **Paper I**].

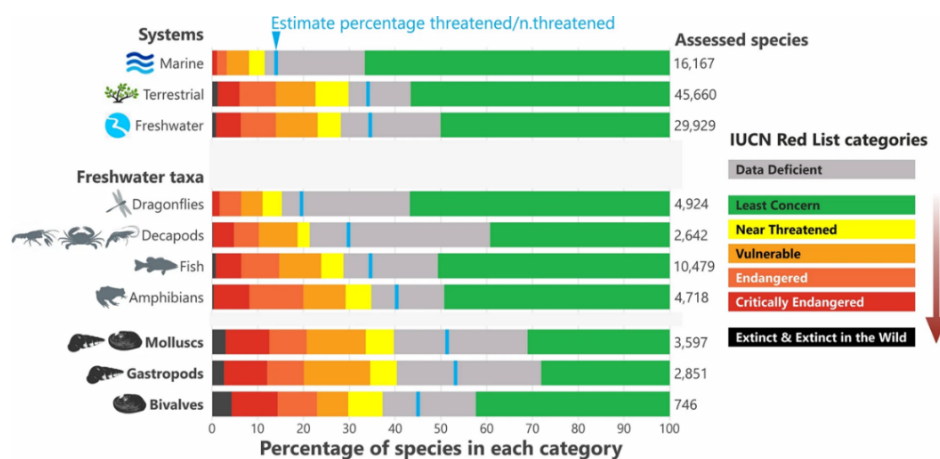
Many mussel species have developed highly specialized methods of infesting hosts, ranging from the release of glochidia coagulates in the shape of host prey items to the use of lures to attract host fish for a more direct infestation (Haag & Warren, 2003). While the majority of these lure-species live in North America, reports of specialized infestation strategies have been observed in both Europe and Asia (Klunzinger *et al.*, 2023; Rock, 2024). This parasitic larval life stage is typically regarded as a mechanism for up-river colonization by freshwater mussels, as adults have limited mobility, and the release of gametes and larvae into the water column of a flowing river inherently disperses the species directionally downriver (Schwalb *et al.*, 2010, 2012). Given the specific fitness advantage of this life-history adaptation and the cost associated with high larval mortality, unionids are almost exclusive to freshwater habitats, with few species known to tolerate brackish water (Wächtler *et al.*, 2001; Korniuschin & Glaubrecht, 2003; Haag, 2012; Graf, 2013). Female mussels can have very high fecundity, with some species releasing millions of glochidia at a time. While larval mortality is exceptionally high, so too are the rates of infestation prevalence and intensity (Wächtler *et al.*, 2001).

Unlike other parasites which can grow significantly while on their host, glochidia are very small in relation to their hosts, as the primary purpose of infestation appears to be dispersal, typically not growth (Graf, 2013; Jansen *et al.*, 2001; Taeubert *et al.*, 2012). Studies on the effects of glochidiosis on host fish have only recently become of interest (**Paper I**). In short, encysted glochidia extract some nutrients from their hosts (e.g., Denic *et al.*, 2015) but glochidiosis causes little to no effects on overall host growth (e.g., Marwaha *et al.*, 2019) despite typically increasing metabolic rate (e.g., Filipsson *et al.*, 2017). Very little is known on the behavioural or molecular effects of glochidiosis (see **Paper I**). Glochidia do not gain a fitness advantage by inducing



an overly dramatic effect on host fitness, as death of an infested host equates to the death of all the affixed glochidia, which can potentially number in the thousands.

Freshwater mussels have seen drastic population declines in recent years and are among the most endangered taxa, globally and within Europe (Lopes-Lima *et al.*, 2018; Haag, 2019; Lopes-Lima *et al.*, 2021; Fig. 3). The dramatic decrease in mussel populations has been attributed to a myriad of factors, among the most commonly cited being general environmental degradation and overall habitat loss, which in combination threaten 25% of all freshwater taxa with extinction (Lopes-Lima *et al.*, 2018; Haag, 2019; Sayer *et al.*, 2025). As populations of freshwater fish have also decreased dramatically, so too has unionid recruitment, further threatening population numbers (Dudgeon *et al.*, 2006; Arthington *et al.*, 2016; Modesto *et al.*, 2018). Moreover, cases of mussel mass mortality events are increasingly commonly reported (McDowell & Sousa, 2019; Wengström *et al.*, 2019; Richard *et al.*, 2021; Cossey *et al.*, 2025).



**Figure 3:** Current extinction risk in different species groups. Data was extracted from the IUCN Red List (IUCN 2021). The graphic appearance was adapted from IPBES (2019) [caption and figure from Lopes-Lima *et al.*, 2021; used with permission].

## **Unionids in the ecosystem**

Like most bivalves, freshwater mussels are filter feeders and are regarded as important ecosystem engineers for the habitats they inhabit, as they can significantly alter both the nutrient dynamics and physical structure of their ecosystems (van der Schatte Olivier *et al.*, 2020; Zieritz *et al.*, 2022). As mussels filter particulates from the water column and excrete material into the sediment, water clarity and sediment nutrient concentrations can become significantly higher, increasing both micro- and macrophyte production and boosting benthic and riparian biodiversity (Aldridge *et al.*, 2007; Carroll *et al.*, 2008; Allen *et al.*, 2012; Atkinson *et al.*, 2013; Chowdhury *et al.*, 2016; DuBose *et al.*, 2020; Benjamin *et al.*, 2022).

Mussels can also significantly affect the physical structure of their surrounding environment, both while alive and dead, increasing surface area and roughness, effectively acting as a freshwater reef (Fig. 4). The aggregation of mussel shells increases substrate structural complexity, which provides refuge opportunities from high water flows and predation for benthic fauna (Ziuganov *et al.*, 1994; Stewart *et al.*, 1998; Gutiérrez *et al.*, 2003; Strayer, 2008; Spooner *et al.*, 2013). Lower substrate water velocities around mussel beds can increase sedimentation, thereby decreasing erosion and increasing nutrient availability for benthic fauna. Moreover, mussels often reposition and burrow in new locations within the substrate; this activity bioturbates the surrounding benthic environment, increasing oxygen penetration in the sediment and further supporting benthic biota (Quijón & Pino, 1996; Sephton *et al.*, 1980; Vaughn & Hakenkamp, 2001; Gutiérrez *et al.*, 2003). Increases in benthic invertebrate densities associated with mussel beds are often correlated with increases in vertebrate communities as well. The increase in detritivores provides more food sources for the host fishes of mussels, which, combined with the

improved water conditions, leads to higher potential mussel recruitment as a function of host abundance (Ziuganov *et al.*, 1994; DuBose *et al.*, 2020). Moreover, many macroinvertebrates that benefit from freshwater mussel beds later metamorphose into terrestrial insects, moving nutrients from the aquatic to the terrestrial environment and increasing biodiversity in riparian habitats (Allen *et al.*, 2012; Novais *et al.*, 2015).



**Figure 4:** Aggregation of nine *Margaritifera margaritifera* in Vasslabäcken, a stream in Örebro County, Sweden.

## Objectives

This dissertation aims to investigate the effects of parasitism by glochidia (glochidiosis) on the ecology of host fish. I have addressed the aims of this dissertation with one published review paper (**Paper I**), two submitted manuscripts (**Papers III and IV**), and one manuscript in preparation (**Paper II**). **Paper I** is a general review of the impacts of glochidiosis on host fish to summarize the current global knowledge on glochidiosis. Following the review, I chose to focus on the behavioural effects of glochidiosis. **Paper II** is a laboratory study which investigated the impacts of the thick-shelled river mussel (*Unio crassus*) on the shoaling behaviour and habitat preference of Eurasian minnows (*Phoxinus phoxinus*). I predicted that infested minnows would shoal as-normal but prefer habitats with calmer water. **Paper III** is a second laboratory study that investigated impacts of *Unio crassus* on the habitat preference and predatory behaviour of the European bullhead (*Cottus gobio*). I predicted that infested bullhead preferred more heterogeneous mussel habitats and predate less. **Papers I, II and III** suggest that unionid mussels may express an extended phenotype on their host fish by altering host behaviour. To test this hypothesis, I conducted a year-long mark-recapture study (**Paper IV**) during a reintroduction effort for the freshwater pearl mussel (*Margaritifera margaritifera*) where brown trout (*Salmo trutta*) from a population naïve to *M. margaritifera* were allowed to freely distribute themselves and juvenile mussels within their native stream habitat. I predicted that infested trout would prefer slower flowing sections of the river and distribute themselves further upstream. The results from this dissertation improve the global understanding of the behavioural effects of glochidiosis, better informing conservationists on the downstream ecological consequences of unionid mussel reintroduction.

## **Methods**

### **Literature review**

Two literature searches were performed on September 20<sup>th</sup>, 2021 in both Web of Science (Karlstad University library subscription) and Google Scholar with the following search string: “ALL= ((glochid\* OR mussel larv\* OR parasitic mussel OR margaritifera OR unio) AND (effect OR causes OR impairs OR improves OR increases OR decreases) AND (host OR fish OR salmon OR trout OR bass OR salmonid OR minnow OR darter))”, which returned 786 and 72 hits, respectively. A third search on Google Scholar on the same date with the search string: “glochidia” “effect on host” returned 39 hits.

Of the 897 total hits recovered, an initial selection was made based on their title and abstract to exclude studies with no relevance to unionid mussels. Papers on the host preference of glochidia were excluded, because they did not specifically relate to the impacts of glochidia on their host. Reading of the remaining papers resulted in 35 studies being classified as relevant for the review as they investigated the direct impact of glochidiosis on host behaviour and/or physiology, including one publicly available Master’s thesis. Further, the reference list and cited-by list of all 35 papers were investigated for additional relevant studies not discovered by the previous search strings; this revealed 28 additional studies, including another publicly available Master thesis. Five public access Bachelor’s and Master’s thesis reports from within Karlstad University not revealed by the literature searches were also included as they investigated the impact of glochidia on host behaviour and/or physiology.

## **Animal studies**

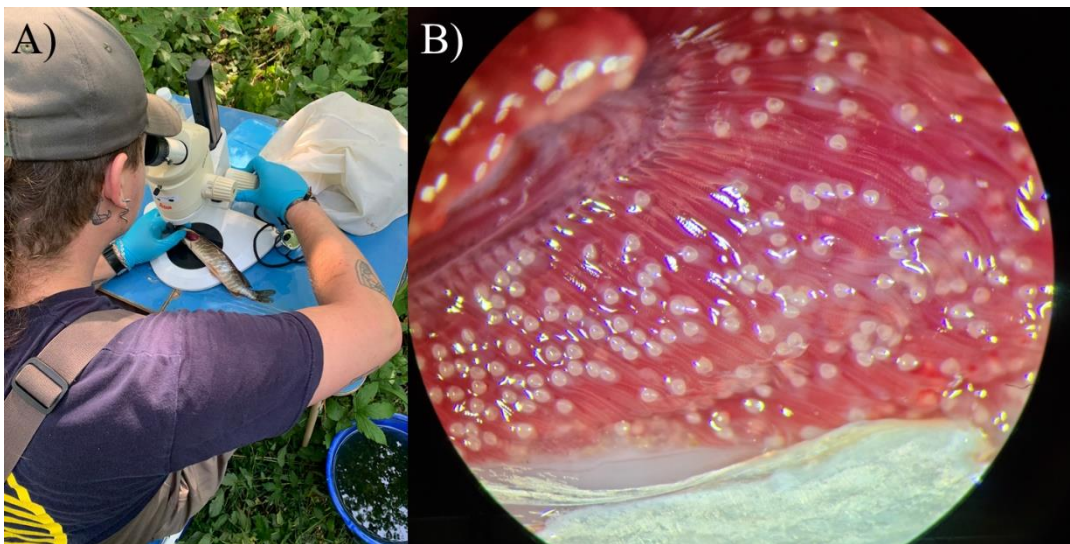
I carried out the three animal studies in both field and lab environments, between May 2021 and June 2023. **Paper II** was conducted in the aquarium laboratories of Karlstad University, Karlstad, Sweden. These facilities offer a wide range of aquaria and behavioural analysis equipment. In particular, I used the camera equipment (Canon video cameras), several large flume systems, holding tanks, and both plastic and glass aquaria. The study was additionally supported by hydrological models of water flow within the test arenas run at the Politecnico di Torino, Torino, Italy. **Paper III** was conducted at the 'MusselLAB' in Hemmestorpsmölla, Sjöbo, Sweden, a remote lab operated by Länsstyrelsen Skåne (county administrative board Skåne) in partnership with Skogsstyrelsen (Swedish Forestry Board). This facility is equipped with a variety of aquaria and a water treatment system to prepare river water for use in the lab. The study additionally used aquaria and substrate from Lund University. **Paper IV** was a field study conducted at the Söderåsens National Park in Skåne, Sweden, supported by the park rangers, with aquaria and PIT-tag equipment from both Karlstad and Lund universities.

The three animal studies were performed under the following ethical permits:

- **Paper II:** 001673 - Göteborgs djurförsöksetiska nämnd
- **Paper III:** 001673 - Göteborgs djurförsöksetiska nämnd
- **Paper IV:** 001530 - Göteborgs djurförsöksetiska nämnd

## Infestation methods and monitoring

Similar glochidia infestation strategies were used for all three animal studies. These involved allowing gravid mussels to naturally release glochidia while in captivity, then diluting the larvae to a known concentration (see methods of appended papers for specifics). Test fish were then placed into a glochidia bath for a time to ensure successful parasitism; control fish were subjected to sham treatments. Monitoring of infestation rates followed the same procedure across all studies: fish were heavily anaesthetized (euthanized when not needed for further trials) with benzocaine or MS-222, after which they were placed under a stereomicroscope (Fig. 5A). The operculum covering the gill was gently lifted for anesthetized fish or completely removed for euthanized fish, and the visible glochidia on one or both sets of gills were counted (Fig. 5B).



**Figure 5:** A) An anesthetized pike (*Esox Lucius*) being monitored for infestation from *U. crassus*. B) Glochidia from *M. margaritifera* encysted on the gills of an anesthetized *S. trutta*.

## Experimental methodology

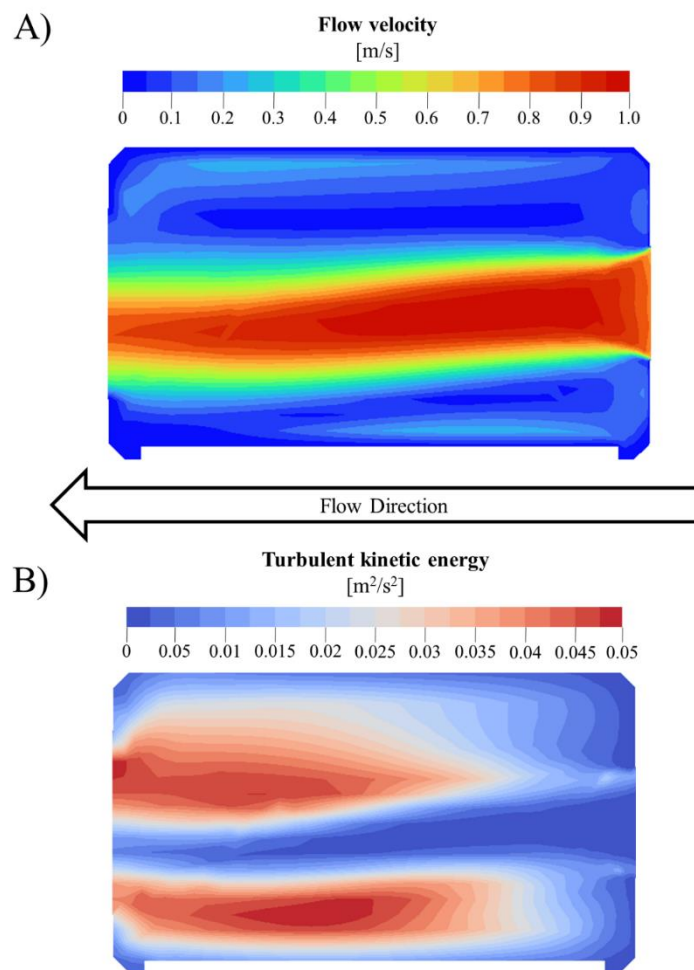
### *Paper II*

This study investigated the impact of glochidiosis on the shoaling behaviour of *P. phoxinus* when infested with *U. crassus*, and commenced in April 2021. Minnows were electrofished from the river Vramsån in the vicinity of the town Tollarp (Skåne, Sweden), brought into the Karlstad University aquarium facility and stored in large holding tanks. *U. crassus* were collected from the vicinity of the town Gärds Köpinge (Skåne, Sweden) on the same day and also brought to Karlstad University, and housed in several small plastic aquaria. All minnows were held in a holding tank until the mussels released viable glochidia, after which half were infested and placed in an adjacent, identical holding tank. At two points in time (14- and 28 days post infestation; dpi), the minnows were placed in large shallow flow-through arenas to observe their shoaling behaviour, filmed from above with video cameras. From these videos, screenshots were taken to measure the Nearest Neighbour Distance (NND) and shoal size (measured as the area of the 2D convex polygon delineated by the peripheral members, as per Barber & Huntingford, 1996). Distances were measured with ImageJ (version: v1.53e) calibrated with the internal dimensions of the experimental arena. Additionally, flow velocity and turbulence (turbulent kinetic energy; TKE) within the arenas were modelled. These models were used to assess the habitat preference of minnow shoals by averaging flow velocity and TKE within a 100-cell grid of the experimental arena and visually inspecting which cell each minnow was in (Fig. 6).

A group of minnows was determined to be forming a shoal (Yes/No) if four or more individuals were within four average body lengths of their nearest neighbour (188 mm). The number of isolated minnows, 'loners', defined as an individual beyond 188 mm from its



nearest neighbour, was also counted. From here, the NND of shoaling individuals (individuals within 188mm of their nearest neighbour) and shoal area were calculated, additionally, the area of all minnows (minnow area) was calculated. Average minnow flow velocity and TKE were calculated by averaging the values of all minnows, shoal flow velocity and TKE were calculated by averaging the flow velocity and TKE values of the shoaling individuals.

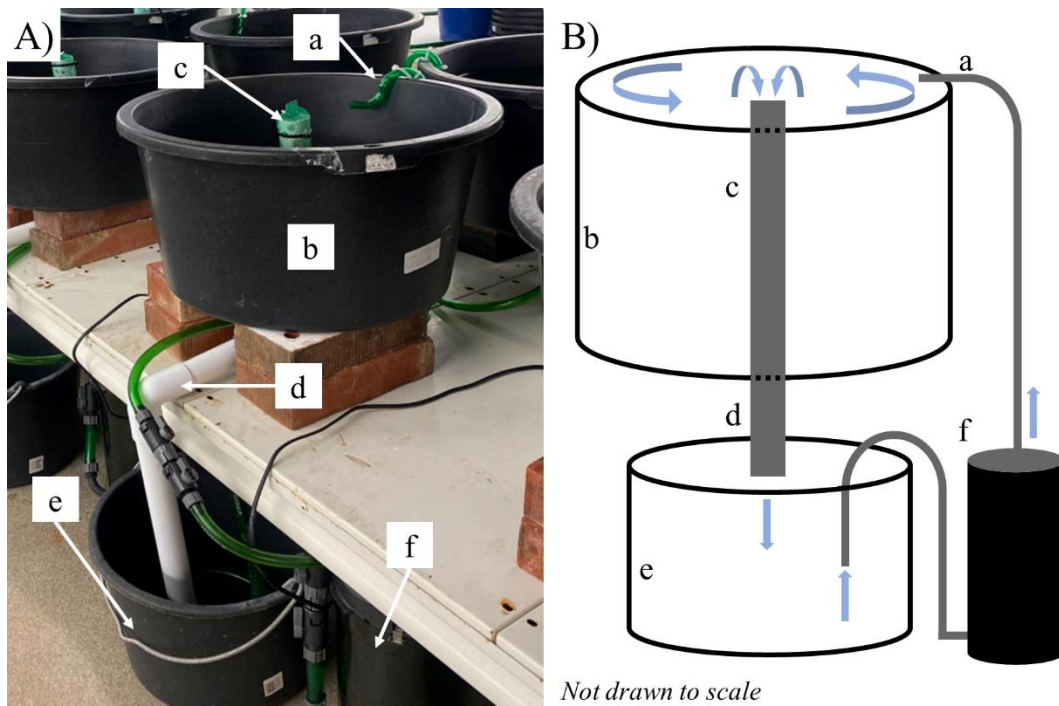


**Figure 6:** Heat map indicating the 2-dimensional variation of flow velocity (A) and turbulent kinetic energy (B) within the experimental area from a top-down perspective, generated by the commercial Computational Fluid Dynamics (CFD) software package ANSYS in Fluent (2022 R1). Maximum internal arena dimensions measure 170 cm × 98 cm. Indentation on the bottom edge of the heatmap indicates a viewing panel into the arena [from appended **Paper II**].

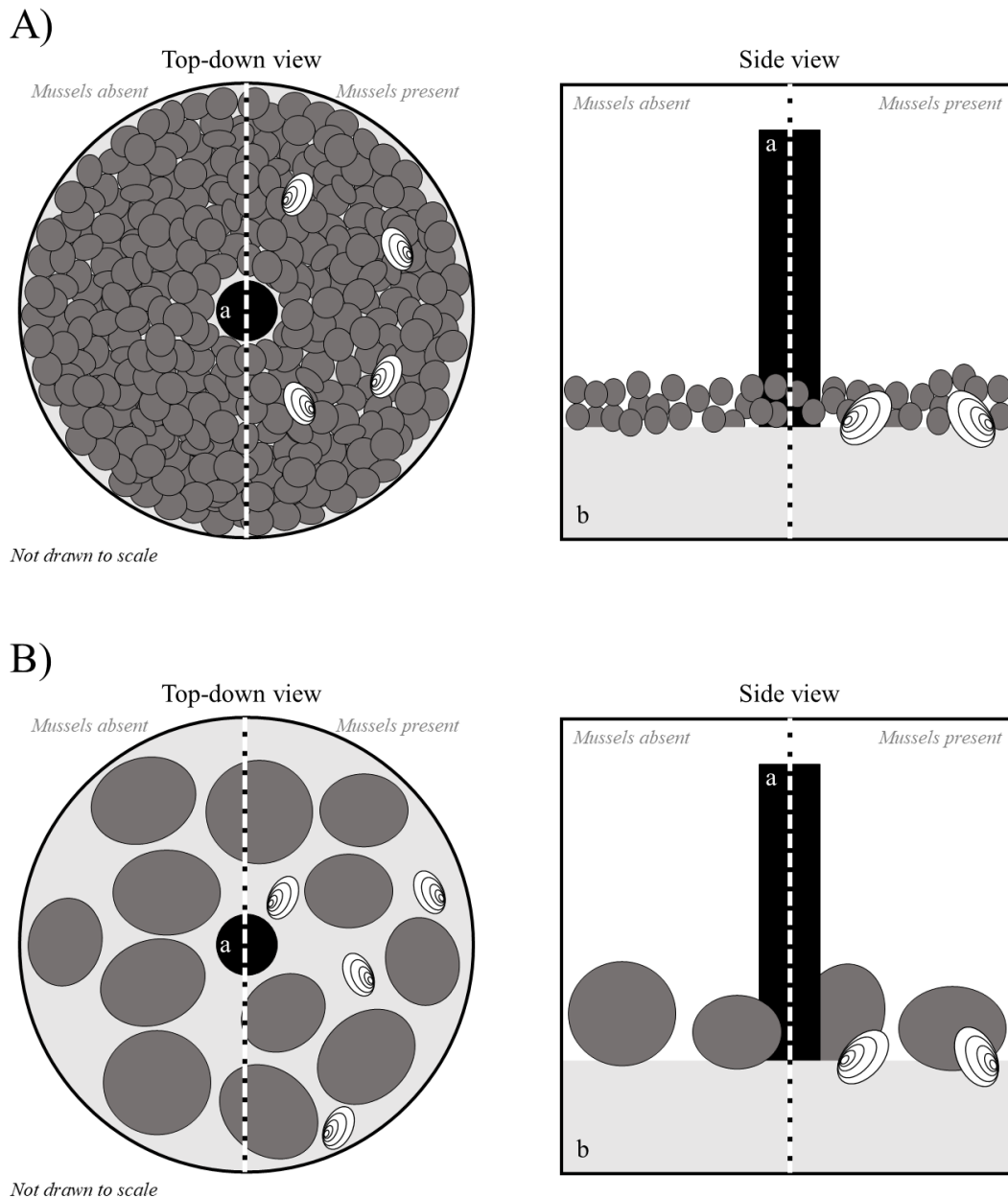
### **Paper III**

This study, initiated in May 2023, examined how glochidiosis affected the habitat preference and predatory behaviour of *C. gobio* infested with *U. crassus*. Bullhead were electrofished from the Verkeån river, near the Hallamölla waterfall whereas *U. crassus* were collected from Gärds Köpinge, Sweden; some gravid to be used for infesting the bullhead, others non-gravid to use as structure in the experimental tanks. Once the mussels released glochidia, some bullheads were infested, and housed separately from non-infested individuals. Two experiments were conducted in twelve round, recirculating plastic tanks (Fig. 7), each with an EHEIM canister filter to maintain water flow. Tanks contained either a homogenous gravel layer or a heterogeneous cobble layer on top of a sand bed (Fig. 8). Mussel density was 19 mussels/m<sup>2</sup>, considered ‘high’ in previous work (Schneider *et al.*, 2019). Experiments were conducted between 14 and 19 dpi, a period when *U. crassus* typically does not excyst (Schneider *et al.*, 2017).

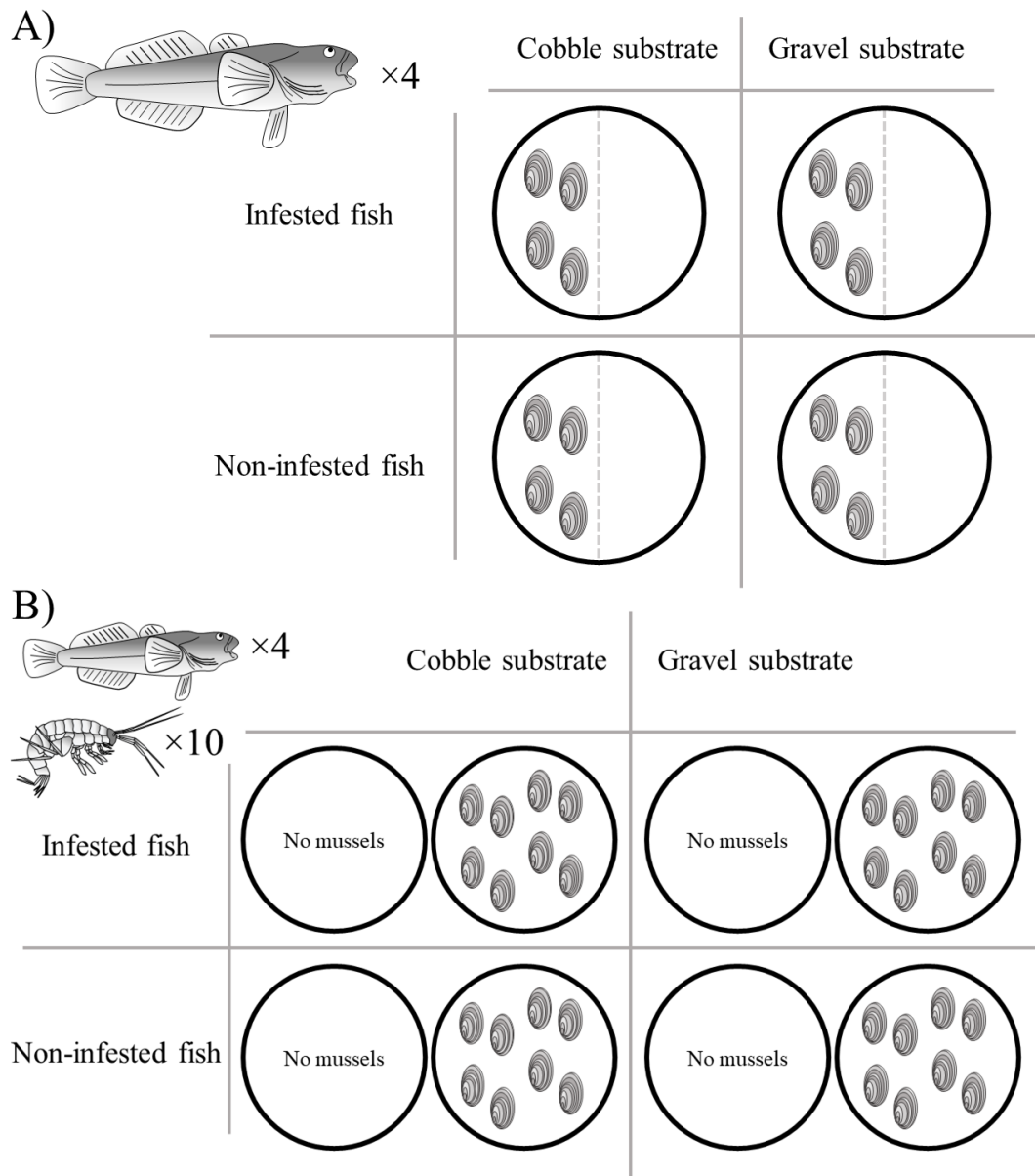
In the first experiment, bullhead habitat preference was evaluated in recirculating tanks with four mussels placed in half of the substrate, where four bullheads, either infested or not, were added (Fig. 9A). A divider was used to separate the two sections after 18 hours, and bullhead positioned in the mussel bed was recorded. In the second experiment, predation on gammarids by bullhead with and without adult mussels present in gravel or cobble substrates was assessed between 17 and 19 dpi. Eight mussels were spread across the bottom of half the tanks, and ten gammarids were introduced. After 30 minutes, four bullheads were added (Fig. 9B). As before the tanks were left overnight, the next morning, bullheads were euthanized, measured, and dissected to assess infestation success. The remaining gammarids were counted to determine predation rates.



**Figure 7:** Image of one experimental unit (A) and graphical representation of one experimental unit (B); water flow indicated with blue arrows. Water flows from a directionally placed outlet (a) creating a circular flow in the experimental tank (b). Water then drains from a central standpipe (c) and drains (d) into a lower sump (e). An EHEIM canister filter (Classing 500; f) then pumps water back into the experimental tank [from appended **Paper III**]



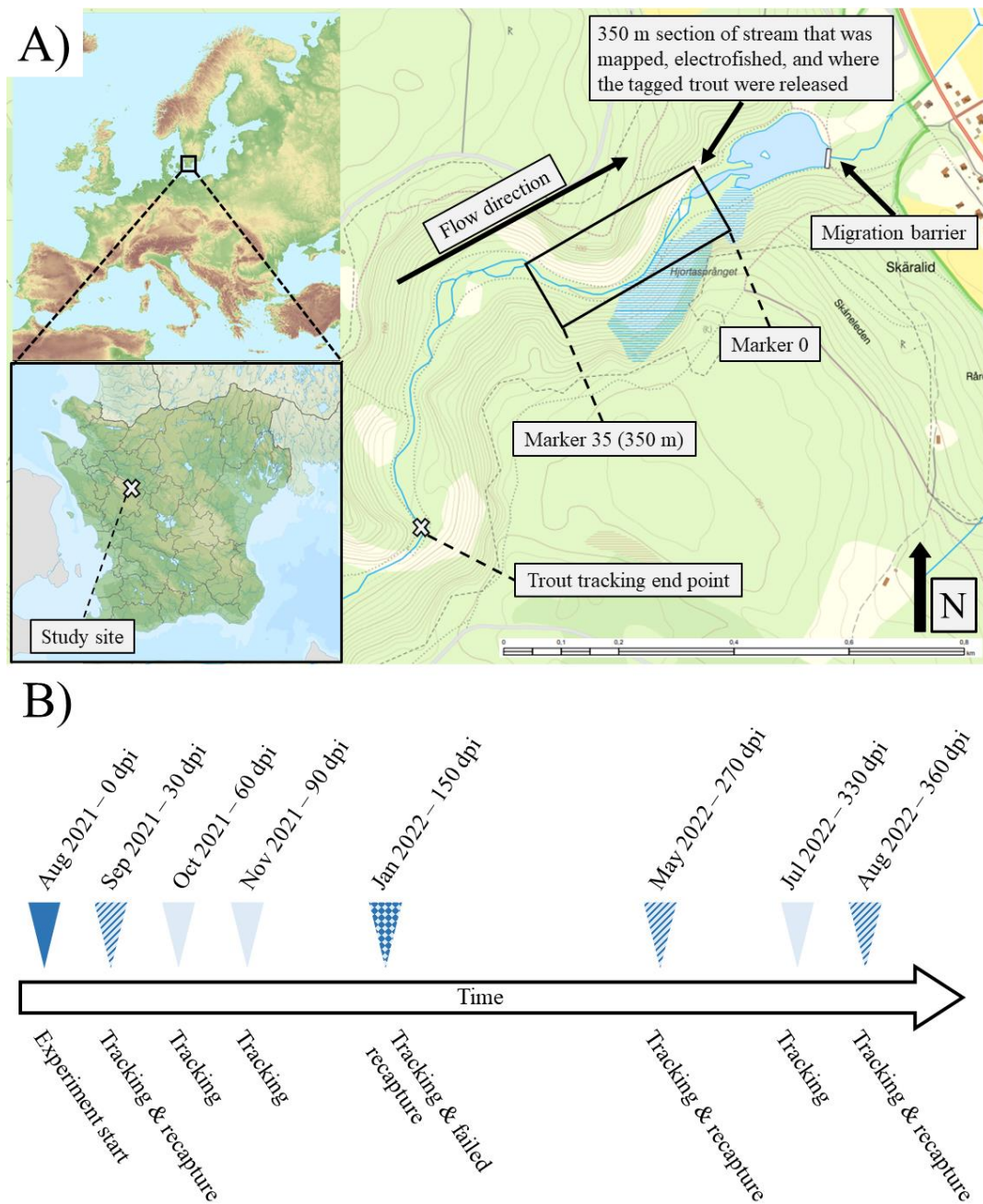
**Figure 8:** Graphical representation of the substrate treatments for the gravel-dominated substrate (A) and the cobble-dominated substrate (B). Central standpipe for the experimental unit indicated in black (a) and sandy bottom indicated in light grey (b). Dark grey ovals indicate gravel (size range 21 - 36 mm) in (A), and cobbles (size range 70 – 120 mm) in (B). Black and white dashed line separates a mussel-dominated habitat (right) from a mussel-absent habitat (left), mussels indicated with white and black ovals. Figures not drawn to scale [from appended **Paper III**]



**Figure 9:** Graphical method for **Paper III**. Experiment on habitat preference of *C. gobio* (A) and experiment on predation on *G. pulex* by *C. gobio* (B) [from appended **Paper III**].

#### **Paper IV**

This study tracked the growth, dispersal, and habitat use of infested *S. trutta* to determine if *M. margaritifera* expressed an extended phenotype and commenced in August 2021. To do this, a 350m stretch of the river Skärån, Skåne, Sweden, was electrofished, and all trout were brought into captivity. Various habitat characteristics of the same stretch of river were mapped in a similar procedure to a standard Swedish protocol (Länsstyrelsen Jönköping, 2017; Fig. 10A). Departing from the Swedish protocol, and to simplify the statistical analysis, all measured variables of habitat were collected and averaged across 10 m sections of river and analysed with a rotated PCA, which outlined three major variance axes: Rotated Component (RC)<sub>1</sub> defining primary substrate size and flow regimes, RC<sub>2</sub> defining depth, and RC<sub>3</sub> defining river width. All fish were PIT tagged, had their weight and length recorded, and some were then infested with an allopatric population of *M. margaritifera* from Klingstorpabäcken (Skåne, Sweden). The trout were later randomly released into the same stretch of river from which they were caught. I returned to the river seven times over the course of 12 months with a PIT-tag reader to follow trout dispersal beyond the mapped section. These were occasionally accompanied by electrofishing excursions to track growth and condition of the fish (Fig. 10B).



**Figure 10:** Experimental location in Söderåsen national park (A) and timeline of tracking and recapture events for **Paper IV** (B). For (B) Dark shade designates the start of the experiment, light shades designate tracking events, stripe fill indicate successful recapture events, square fill indicate unsuccessful recapture events [from appended **Paper IV**].

## **Statistical methods**

### ***Paper II***

A generalized linear mixed model (GLMM) with binominal error distribution was fitted to the shoaling presence data (Yes/No) to determine shoaling frequency, using glochidia presence (Yes/No), days post infestation (14 or 28 dpi) and their interaction as predictors; trial ID was used as a random factor. A GLMM with Poisson error distribution was fitted to the count data of isolated minnows using glochidia presence (Yes/No), days post infestation (14 or 28 dpi) and their interaction as predictors; trial ID was used as a random factor. Shoal area was analysed with a 2-way ANCOVA using glochidia presence (Yes/No), days post infestation (14 or 28 dpi) and their interaction as predictors, the average number of minnows in the shoal was included as a covariate to account for different shoal sizes. All other metrics of minnow behaviour were analysed with a 2-way ANOVA using glochidia presence (Yes/No), days post infestation (14 or 28 dpi) and their interaction as predictors (Table 1).

### ***Paper III***

To assess bullhead habitat preference, a generalized linear mixed model (LMM) was fitted to the number of bullhead counted on the mussel side of the experimental tank (*bullhead with mussels*), using substrate size (gravel/cobble), infestation (yes/no) and their interaction as fixed factors, day (of observation) was included as a random factor. Bullhead preference for mussel-dominated habitats was not statistically tested, but the 95% confidence interval of each raw mean was compared to the rate of random habitat selection (2 bullhead on the mussel side). If the 95% confidence interval did not intersect with the rate of random chance, a significant preference beyond



random chance was assumed. To assess bullhead predation on gammarids, a LMM was fitted to the number of gammarids recovered after the predation period (*gammarid survival*) using substrate size (gravel/cobble), infestation (yes/no) and mussel presence (yes/no) and all combinations of two-way and three-way interaction effects as fixed factors, day (of observation) was included as a random factor (Table 1).

#### ***Paper IV***

Effects of glochidiosis on trout survival was investigated using trout detection rates as a proxy measure for survival, and analysed with separate Fisher's exact tests for each tracking event. If the detection ratio of infested and non-infested trout was consistent through time, we assumed equal survival rates. Specific growth rate (SGR; proportional change in mass over time) was calculated as described by Crane *et al.*, (2020) and was used to assess trout growth, Fulton's condition factor (K) was used to assess the change in trout body condition over time. Changes to both SGR and K were calculated in relation to mass and length at initial release. Distance moved (DM) was measured in 10 m increments relative to the initial release location and was calculated by subtracting the release section number from that of each re-capture section. Positive values correspond to upstream movement and negative values to downstream movement. Trout habitat preference was analysed by comparing the regression factor scores (RFS) of the stream sections trout were found in along the first three rotated components (RC). Differences in SGR, K, DM, RFS<sub>1</sub>, RFS<sub>2</sub> and RFS<sub>3</sub> were analysed with separate LMMs using infestation (yes/no), dpi, and their interaction as predictors. Post-hoc pairwise comparisons for all LMMs were performed using the least significant difference (Table 1).

**Table 1:** Statistical analysis, corresponding figures and tables for different response variables reported in the papers included in this dissertation.

<b>Paper</b>	<b>Response variable</b>	<b>Statistical analysis</b>	<b>Figure (in kappa)</b>	<b>Table (in paper)</b>
<b>I</b>	Publication characteristics	n.a.	Fig. 11	Supplement 1
	Shoaling frequency	GLMM	Fig. 12A	Table 1
	Loner count	GLMM	Fig. 12B	Table 1
	Average minnow area	2-way ANCOVA	Fig. 12C	Table 1
	Average minnow NND	2-way ANOVA	Fig. 12D	Table 1
<b>II</b>	Shoal area	2-way ANOVA	Fig. 12E	Table 1
	Shoal NND	2-way ANOVA	Fig. 12F	Table 1
	Average minnow flow velocity	2-way ANOVA	Fig. 13A	Table 2
	Average minnow TKE	2-way ANOVA	Fig. 13B	Table 2
	Shoal flow velocity	2-way ANOVA	Fig. 13C	Table 2
	Shoal TKE	2-way ANOVA	Fig. 13D	Table 2
<b>III</b>	Bullhead habitat preference	LMM	Fig. 14A	Table 1
	Gammarid survival	LMM	Fig. 14B	Table 1
	Trout survival	Fisher's Exact	n.a.	Table 3
	Trout SGR	LMM	Fig. 15a	Table 2
	Trout K	LMM	Fig. 15B	Table 2
<b>IV</b>	Trout DM	LMM	Fig. 16	Table 2
	Trout RFS1	LMM	Fig. 17A	Table 2
	Trout RFS2	LMM	Fig. 17B	Table 2
	Trout RFS3	LMM	Fig. 17C	Table 2

## Result Summary

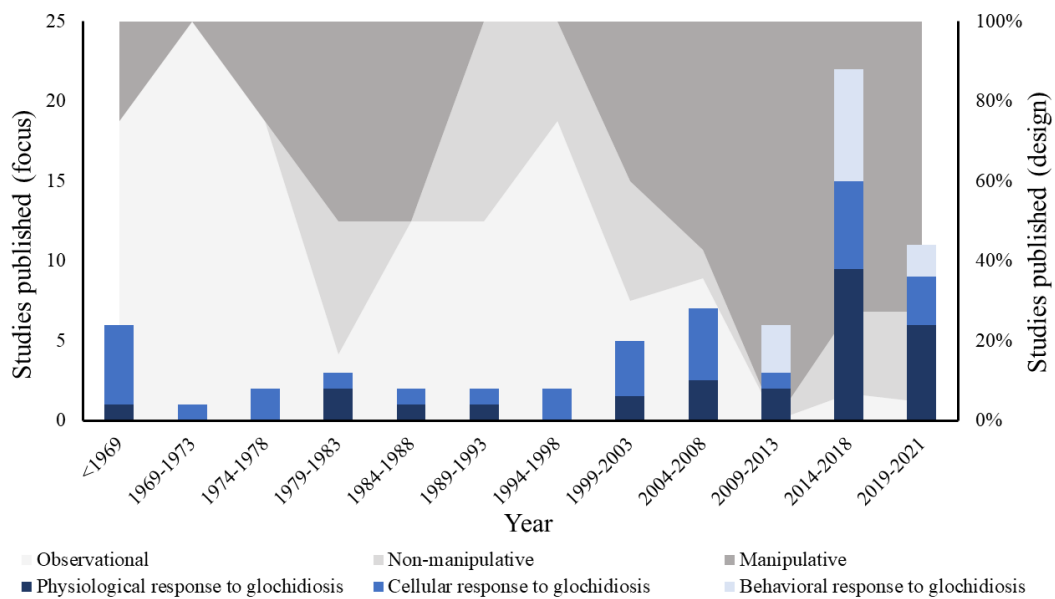
### Paper I

Studies on the effects of glochidiosis on host fish have predominantly gained attention in the last 15 years, with more manipulative studies improving research quality compared to the previous dominance of observational and non-manipulative study designs (Fig. 11). However, most studies focus on *M. margaritifera* and salmonid hosts, which are poor models for general unionid-host interactions as the species is evolutionarily distinct, highly host specific and has a longer than typical encystment period.

Upon host contact, glochidia 'bite' into host tissue, typically the gills, causing trauma. Despite epithelial damage, underlying structural tissue is rarely affected, though blood flow can be restricted. In rare cases, initial attachment leads to haemorrhaging and host mortality. Once attached, glochidia can disrupt blood flow and gas exchange, leading to asphyxia, additionally multiple lesions exacerbate general osmotic and immune stress. Host tissue responds by forming cysts, which can occur as quickly as 2 hours after attachment, although environmental factors, host species and glochidia species influence cyst growth (Fig. 12). Host tissue exhibits common histopathological responses such as hyperplasia, hypertrophy, spongiosis, and sloughing. In long-term infestations, host tissue may show reduced hypertrophy and hyperplasia after two weeks (Rock & Townsend, 2025). Though glochidia lack structures for nutrient extraction, stable isotope analysis suggests some nutrient transfer, possibly through passive absorption or digestion of host tissue.

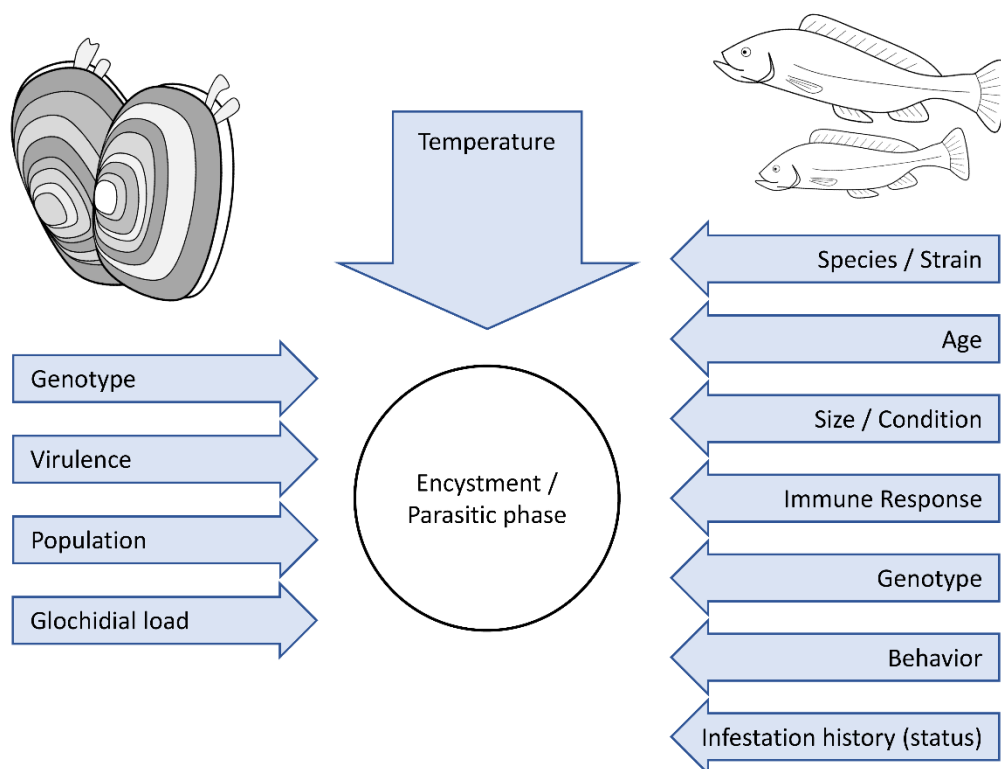
Host immune responses are categorized into innate and adaptive immunity. Innate immunity acts quickly and non-specifically, leading to the removal of all glochidia in incompatible hosts. In suitable

hosts, the immune system can eliminate many glochidia within weeks. Adaptive immunity, developed after repeated exposure to glochidiosis, improves host response, with "hard immunity" leading to a more effective immune response and "soft immunity" resulting in longer sloughing of dead glochidia.



**Figure 11:** *Distribution histogram of the publication dates of papers investigating the impact glochidiosis has on behaviour and physiology of host fishes. Specific paper focus is represented in blue within the histogram bars (dark blue: cellular, mid blue: physiological, light blue: behavioural). The proportional usage of different study designs through time are represented with a shaded background (light grey: observational, mid grey: non manipulative, dark grey: manipulative). Papers with multiple foci, or using multiple designs were recorded with 0.5 or 0.33 in their respective counts to result in a total sum of one per paper. Six papers published between 1919 and 1942 were grouped into one year range labelled <1969 [caption and figure modified from appended Paper I].*

The effects of glochidiosis are dependent on encystment rates, for example, *S. trutta* infested with ~5000 glochidia showed reduced growth within the first year (Chowdhury *et al.*, 2019). In contrast, a study with fewer glochidia (~200 glochidia) found no significant growth effects (Marwaha *et al.*, 2019). This discrepancy suggests that glochidia load is crucial in determining the severity of effects, with higher loads generally causing more harm. Mussels with shorter encystment periods tend to cause more damage, particularly at high infestation levels.



**Figure 12:** Host, parasite and environmental factors that can have an influence on the Unionida–fish host–parasite interaction [caption and figure from appended **Paper I**]

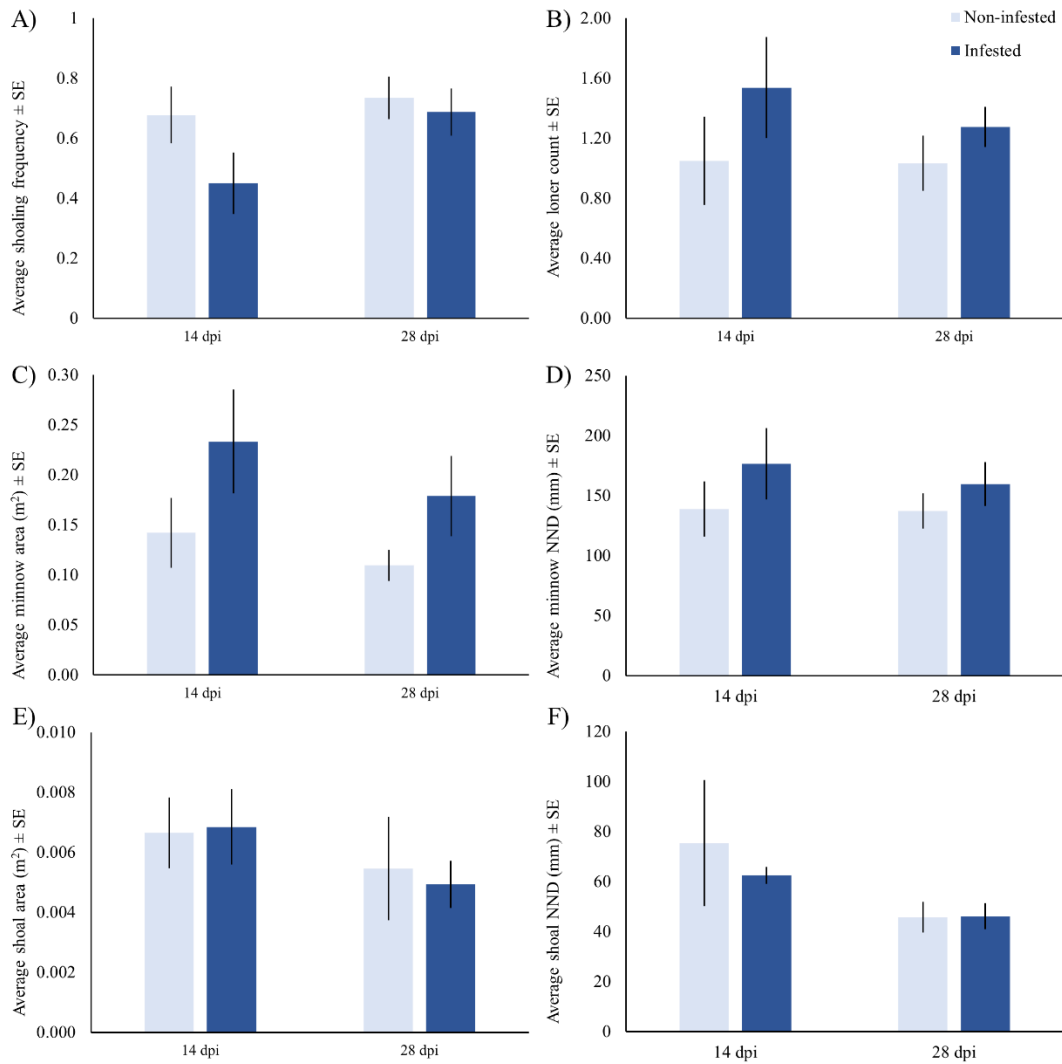
Infestation typically affects host metabolic rate. Trout infested with *M. margaritifera* showed an increased ventilation rate positively correlated with infestation intensity. Such observations suggest that glochidiosis-induced stress may initially increase metabolic demand but could lead to compensatory adjustments. Studies on some mussel species like *Sinanodonta woodiana* and *Hyriopsis cumingii* show glochidiosis can alter osmotic balance, liver function, and cortisol levels, indicating chronic stress that affects metabolism and immune function. Some host species like *Pelteobagrus fulvidraco* and *Oreochromis nilotica* show reduced amino acid and lipid concentrations, likely due to prolonged stress after glochidia dislodge (Wen *et al.*, 2009; Ma *et al.*, 2018).

Studies on host activity levels show no clear impact on *S. trutta* from *M. margaritifera* infestations. However, some studies indicate a negative correlation between infestation rate and activity (Taeubert & Geist, 2013; Filipsson *et al.*, 2016). The effect of glochidiosis on activity is generally temporary (Horký *et al.*, 2014; Slavik *et al.*, 2017). The effects of different mussel species on host behavior may vary, as shown by a study on the host fish *Etheostoma caeruleum*, which reacted differently to infestations by *Ptychobranchus occidentalis* and *Venustaconcha pleasii* (Crane *et al.*, 2011). Infestation does not significantly affect feeding behaviour in early stages but can reduce feeding at later stages (Österling *et al.*, 2014; Filipsson *et al.*, 2016). In contrast, *E. caeruleum* showed no significant feeding changes when infested with *P. occidentalis* or *V. pleasii* (Crane *et al.*, 2011). Some changes in habitat use, such as altered thermoregulation, have been observed (Horký *et al.*, 2014, 2019).

## Paper II

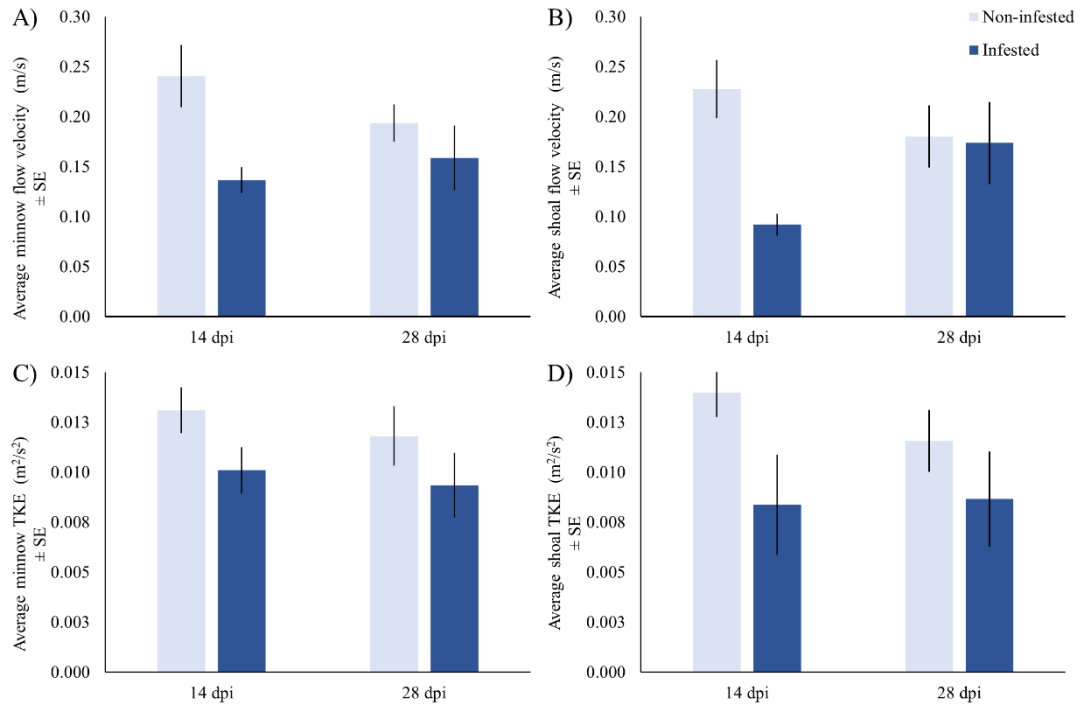
Infested minnows shoaled significantly less frequently than their non-infested counterparts (Fig. 13A) and had significantly more isolated individuals (loner count; Fig. 13B), which resulted in a significantly increased average minnow area (Fig. 13C). Despite these differences, the average infested minnow NND did not differ from that of non-infested minnows (Fig. 13D). Infested minnow shoal area and shoal NND did not differ significantly from those of non-infested minnows (Fig. 13E, F; Table 1 of **Paper II**).

Infested minnows demonstrated a preference for significantly slower-flowing water compared to their non-infested counterparts, a difference which did not vary significantly over time (Fig. 14A). Similarly, shoals of infested minnows demonstrated a preference for significantly slower-flowing water at 14 dpi, but did not differ from their non-infested counterparts at 28 dpi (Fig. 14B). Infested minnows demonstrated a near-significant preference for less turbulent water on average and a significant preference for less turbulent water when shoaling (Fig. 14C, D; Table 2 of **Paper II**).



**Figure 13:** Measures qualifying shoaling behaviour of infested and non-infested *P. phoxinus* at two points during the infestation. Average shoaling frequency (A), average loner count (B), average minnow area (C) average minnow NND (D), average shoal area (E) and average shoal NND (F) [from appended **Paper II**].



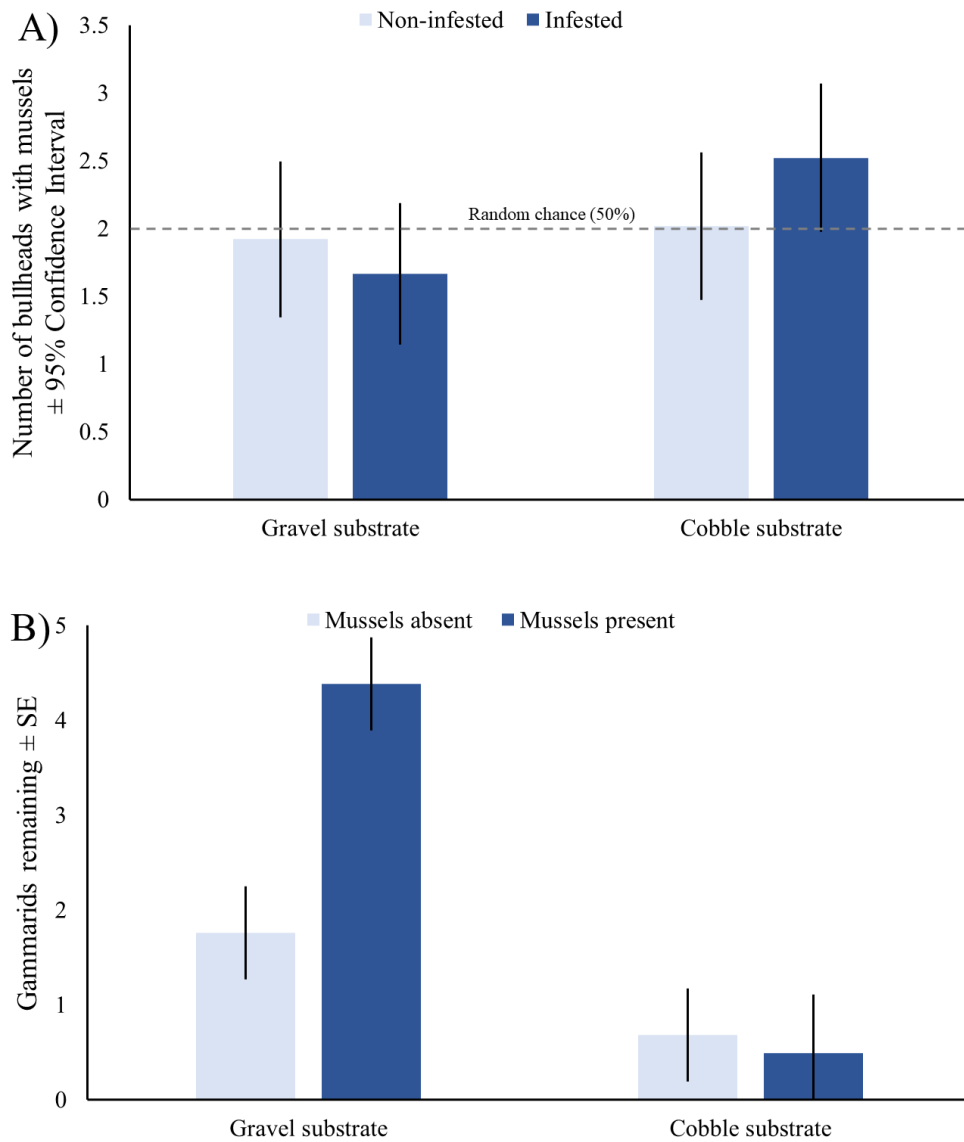


**Figure 14:** Measures qualifying habitat preference of infested and non-infested *P. phoxinus* at two points during the infestation. Average minnow flow velocity (A), average shoal flow velocity (B), average minnow TKE (C), and average shoal TKE (D) [from appended **Paper II**].

### **Paper III**

Infested bullhead did not differ significantly from non-infested bullhead in their preference for mussel-dominated habitats (Fig. 15A). Neither substrate size nor the interaction term significantly impacted bullhead habitat preference. In the gravel substrate, infested bullhead were recovered in mussel-dominated habitats at a rate that was near significantly different from random chance (lower boundary of 95% CI = 1.976). Bullhead habitat preference was significantly different between days but did not show a temporal trend; I therefore assume the effect of infestation on bullhead predation rates remained consistent over time (Table 1 of **Paper III**).

Gammarid survival was three times higher in the gravel substrate compared to the cobble substrate in the absence of mussels. When mussels were present in the gravel substrate, survival was additionally increased approximately threefold (Fig. 15B). Gammarid survival under bullhead predation was significantly impacted by substrate size, mussel presence, and the interaction between the two. The interaction of infestation with the other factors did not significantly impact gammarid survival; day did not have a significant effect on predation rates, I therefore assume the effect of infestation on bullhead predation rates did not change over time (Table 1 of **Paper III**).



**Figure 15:** A) Mean number of bullhead (*C. gobio*) with mussels (*U. crassus*) in different habitat types. Bullhead did not differ in their preference for mussel habitats between substrate sizes or when infested with glochidia from *U. crassus*. Infested bullhead had a near significant preference for mussel habitats when infested with glochidia from *U. crassus* when in the cobble-dominated substrate. Dashed line indicates threshold for random chance (2 bullhead on the mussel side; 50%). B) Number of gammarids (*G. pulex*) remaining after a period of predation by bullhead (*C. gobio*) when infested with glochidia from (*U. crassus*) in different habitat conditions when adult *U. crassus* were present or absent [from appended **Paper III**].

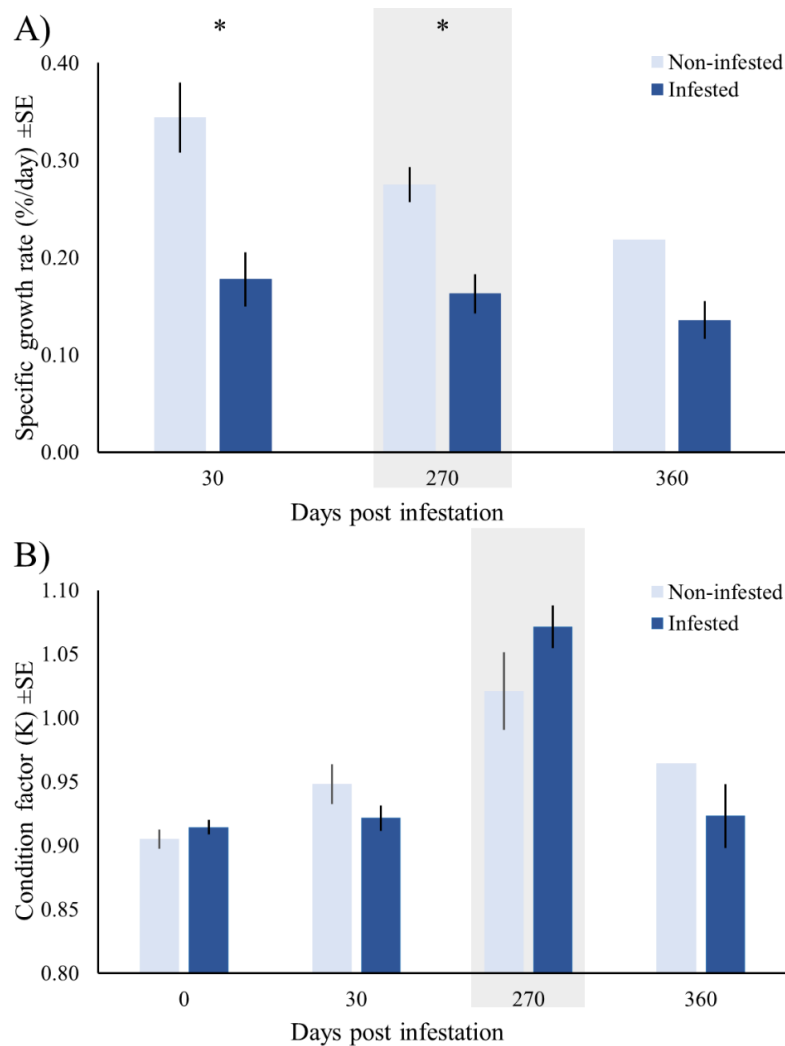
## **Paper IV**

There was no significant difference in detection rates between infested and non-infested trout for all tracking events (separate Fisher's exact tests;  $p > 0.05$ ; Table 3 of **Paper IV**), indicating that infestation did not influence survival over the investigation period. Infested trout had significantly lower growth than the non-infested trout, gaining half as much mass during the first 30 dpi (Fig. 16A). This difference in SGR remained relatively consistent for the duration of the investigation period. The difference in SGR did not result in a difference in condition factor between infested and non-infested trout (Fig. 16B, Table 2 of **Paper IV**).

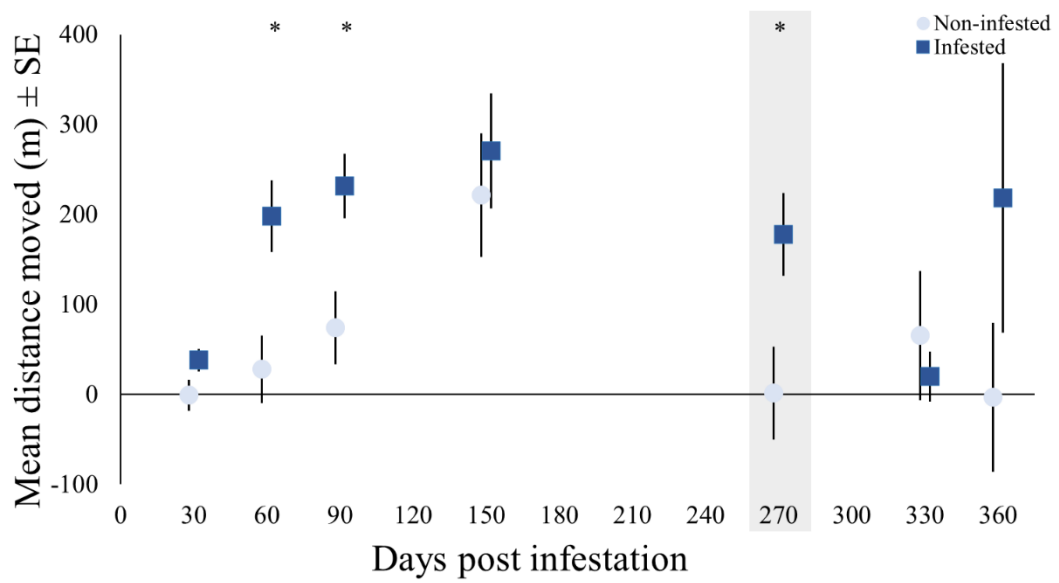
Infested trout moved significantly farther and earlier than the non-infested trout (Fig. 17; Table 2 of **Paper IV**). At 30 dpi, infested trout had moved upstream by almost 40 m, whereas non-infested trout did not relocate. By 60 dpi, infested trout had moved almost 200 m upstream whereas the non-infested trout had moved less than 30 m upstream. At 90 dpi, both trout groups moved upstream an additional 160 m, maintaining their original difference in dispersal. During the period of mussel excystment – 270 dpi – non-infested trout had returned to their original release location, whereas the infested trout remained almost 180 m upstream from their original release location.

Infested trout generally utilized habitats with significantly lower flow velocities and smaller substrate sizes (RFS1), but did not differ in habitat use at the time of mussel excystment (Fig. 18A). Generally, trout utilized habitats with significantly deeper water as they aged and gained mass. Infested and non-infested trout did not generally differ in their usage of different habitats, but did demonstrate a noteworthy difference in usage of shallower stream sections at the period of mussel excystment (Fig. 18B). Likewise, infested trout

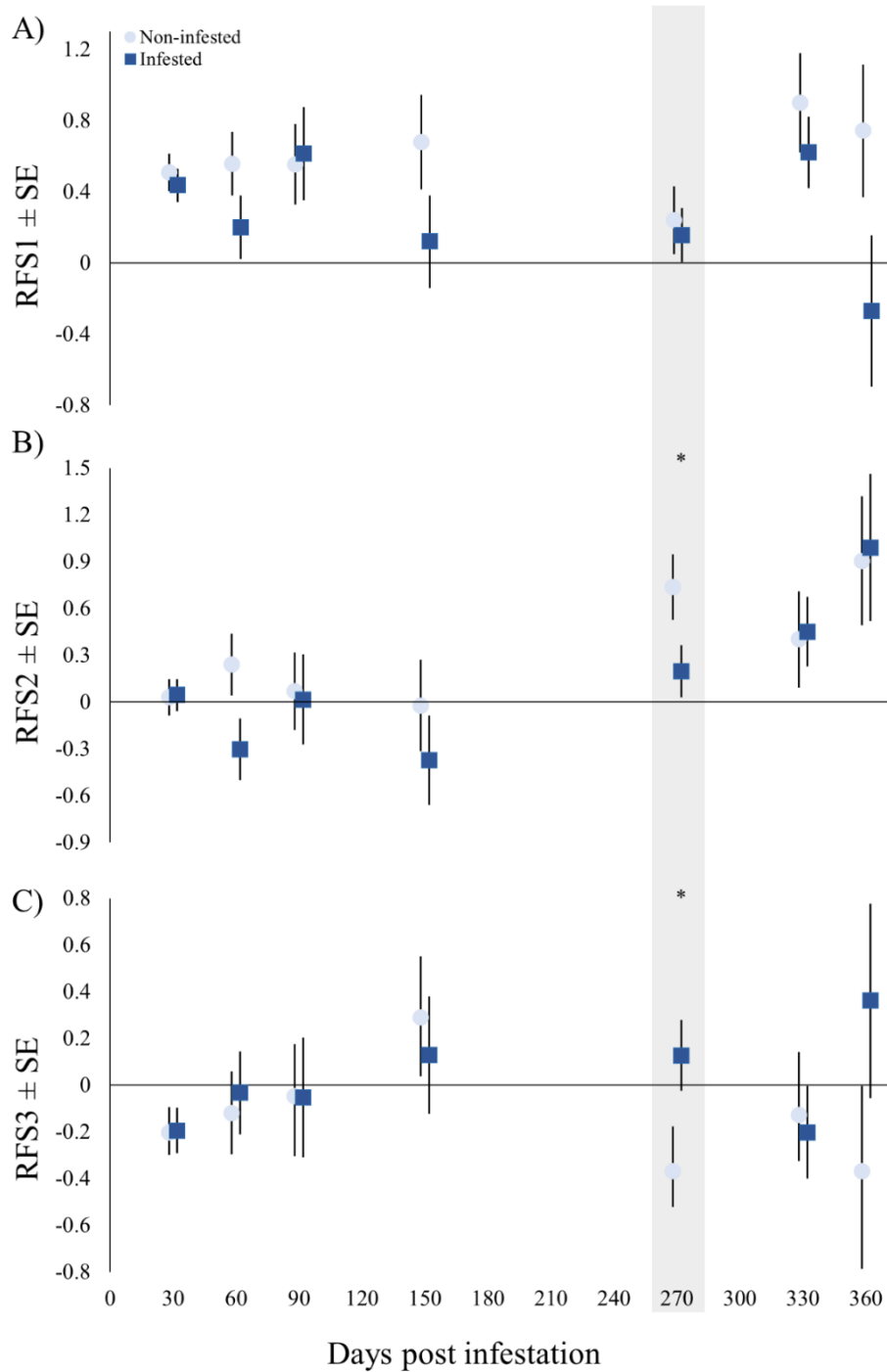
utilized stream sections with similar width as non-infested trout, with a noteworthy difference in usage of wider stream sections at the period of mussel excystment (Fig. 18C; Table 2 of **Paper IV**).



**Figure 16:** Specific growth rate (A) and Fulton's condition factor (K; B) of infested and non-infested one-summer old (1+) *S. trutta* over time. Asterisk indicates significant differences between treatments groups at  $p < 0.05$ , shaded section indicates excystment period, sample sizes indicated within each bar [modified from appended **Paper IV**].



**Figure 17:** Distance moved by infested and non-infested one-summer old (1+) *S. trutta* over one year. Asterisk indicates significant differences between treatments groups at  $p < 0.05$ , shaded section indicates



**Figure 18:** Average regression factor score (RFS) of habitats used by infested and non-infested one-summer old (1+) *S. trutta* over time for rotated components (RC) 1, 2 and 3. A) RPC1, flow condition and primary substrate. B) RPC2, water depth. C) RPC3, section width. Asterisk indicates significant differences between treatments groups at  $p < 0.05$ , shaded section indicates excystment [modified from appended **Paper IV**].

## Discussion and conclusions

Unionid-fish interactions follow similar effect patterns to other parasite-host interactions. Infested fish can be negatively impacted by infestation, an effect that is highly dependent on infestation intensity and specific host-parasite compatibility. However, as it is not a fitness advantage for glochidia to exhibit an overly exaggerated effect on the hosts, the negative effects reported are often minimal and may induce patterns of host behaviour beneficial to the excysting juvenile mussels. I provide some evidence for this argument and expand the general knowledge base on the impacts of glochidiosis on their host fishes. Such information is essential as conservationists move towards broader unionid reintroduction as it allows them to better predict the downstream ecological effects of increasing freshwater mussel populations.

### Paper II

The results presented in **Paper II** demonstrate that glochidiosis affects minnows in ways similar to other parasitic infections, reducing shoaling frequency and altering habitat preferences, likely as part of a generalized anti-parasite response (Barber *et al.*, 2000; Kasumyan & Pavlov, 2023). These findings align with previous studies showing that glochidiosis reduces host swimming ability, which I suggest caused infested minnows to prefer slower and less turbulent flows where they could more easily maintain shoal cohesion (Garner, 1997; Horký *et al.*, 2014; Slavík *et al.*, 2017; De Bie *et al.*, 2020). As a result of their reduced swimming efficiency, infested minnows were more likely to be isolated from the shoal, placing them at greater risk of predation, potentially reducing unionid recruitment.



Nevertheless, glochidiosis did not impact the area or NND of minnow shoals, which might be advantageous for mussels, as decreased shoal cohesion could increase predation risk. Moreover, the preference of infested minnows for calmer water may be an additional advantage to unionid mussels (as in **Paper III, IV**), as recently excysted juveniles unionids are less likely to be swept downriver after excystment. Parasites can manipulate host behaviour to enhance transmission success through either direct or indirect effects. In this case, the effects of glochidiosis may influence host minnow behaviour such that it advantages the next life stage.

### **Paper III**

The results presented in **Paper III** demonstrate that both the adult and parasitic life stages of freshwater mussels can alter host behaviour and the surrounding benthic interactions. Aligned with our expectations, adult mussels influenced the habitat preferences of infested bullheads, attracting them to mussel beds. This indicates that mussel beds not only enhance biodiversity but also facilitate predator-prey interactions. Contrary to expectations, bullheads did not show a general preference for mussel habitats. As glochidiosis typically reduces host swimming performance (Horký *et al.*, 2014; Slavík *et al.*, 2017), and adult mussels increase habitat complexity (Gutiérrez *et al.*, 2003; Bódis *et al.*, 2014), I suggest that the preference infested bullheads have for mussel habitats may be beneficial to juvenile mussels, indicating an instance of host manipulation. By providing refuge for the hosts of their larvae, adult mussels may increase their own reproductive success, as these same mussel beds provide refuge areas from high flow, allowing recently excysted juvenile mussels to settle in suitable habitats (as in **Paper II, IV**).

While not directly observed, I suggest that bullheads may occasionally feed directly on mussel pseudofeces, contributing to their altered behaviour. I support this, as gammarid survival in the gravel habitats - where gammarids had more refuge opportunity - was significantly improved by the presence of adults, an effect which I did not observe in the cobble habitat where gammarids had fewer refuge opportunities. Overall, the results presented here provide evidence that freshwater mussels can significantly impact ecosystem dynamics, both as adults and parasitic larvae, and highlight the need for further research into their role in community interactions, particularly in the face of ongoing population declines.

#### **Paper IV**

The results presented in **Paper IV** demonstrate that freshwater mussels likely express an extended phenotype and manipulate host behaviour. Trout infested with glochidia gain less mass over time and were significantly smaller than their non-infested counterparts; nevertheless, they displayed a similar body condition and mortality to their non-infested counterparts. This reduced growth is likely related to the increased metabolic rate typically observed in infested fish (Thomas *et al.*, 2014; Filipsson *et al.*, 2017), which I observe here as a general preference for slower-flowing stream sections (as in **Paper II, III**), where trout would need to expend less energy to maintain their position. Moreover, infested trout swim further upriver to habitats where adult mussels are typically found, specifically during the period of juvenile mussel excystment.

This general upstream movement of infested trout is beneficial to the infested mussels, as their broadcast reproductive behaviour inherently brings subsequent generations downstream, and adults have limited upstream movement (Schwalb *et al.*, 2010, 2012).

The preference of infested trout for shallow, slow-flowing stream sections is additionally beneficial, as the newly excysted juvenile mussels can receive a temperature cue to excyst in a suitable area for them to bury into the sediment without being washed downstream (Jung *et al.*, 2013; Scheder *et al.*, 2014; Eybe *et al.*, 2015).

The mechanism by which this manipulation occurs cannot be definitively described by this study; however, I propose that the encysted mussels can hijack the natural responses of the fish to parasitism, including their preference for warmer, slower-moving waters, to facilitate the mussels' transport and settlement (MacNab & Barber 2012; Mohammed *et al.*, 2016; Rakus *et al.*, 2017; Boltana *et al.*, 2018; Horký *et al.*, 2019). Moreover, juvenile mussel excystment has been demonstrated to be more damaging to the gill tissue than the initial encystment of the larvae (Rock & Townsend, 2025), further supporting this proposal of behavioural thermoregulation-mediated manipulation.

This study highlights the complex relationship between parasitic mussels and their hosts, and is particularly valuable as trout naïve to glochidiosis could behave in their natural environment without interference and the possible confounding effects of the adult life stage. The observations presented here challenge currently held assumptions that freshwater mussels do not manipulate host behaviour beyond the use of lure mechanisms by adults.

## Conclusions

Summarizing the conclusions from **Paper I**: research into the impacts of glochidiosis is sparse and requires further investigation. The lack of genetic and molecular data on the impacts of glochidiosis means most conclusions are drawn from the ultimate observed effects, rather than the proximate causes. While ecologically less relevant, studies on the genetic and molecular aspects of glochidiosis provide crucial information on the underlying mechanisms surrounding glochidiosis, which, given the diversity of effects observed, are likely equally diverse. The interaction between *M. margaritifera* and its salmonid hosts is the most well-studied but least generalizable, as *M. margaritifera* is taxonomically distinct, highly specialized, and particularly long-infesting. From this limited and skewed knowledge base, three major conclusions can be drawn:

- a.** Glochidiosis causes minor, but observable, impacts on host fishes, which can become particularly apparent in the presence of other stressors.
- b.** A variety of behavioural and metabolic effects are observed early in the infestation period but generally decrease over time (seen in **Paper II, IV**). A noteworthy exception may be made for higher glochidia loads and during the period of juvenile mussel encystment, which may cause more tissue damage than initial encystment, leading to greater changes in host behaviour (**Paper IV**).
- c.** *M. margaritifera* has a much lower proportion of negative effects to neutral and positive effects, suggesting it may not harm host fish as much as other mussel species.

Among the most ecologically significant effects of glochidiosis are the changes observed in host behaviour. As glochidiosis reduces swimming performance, infested hosts typically prefer slower-flowing water (**Paper II, IV**) and habitat with higher substrate heterogeneity (**Paper III**) which can provide refuge from higher flows. As unionids utilize hosts as a dispersal vector, juvenile mussel dispersal is likely biased toward habitats with slower-flowing water (**Paper II, IV**) and more heterogeneous habitats (**Paper III**). Free-living mussels often prefer habitats with slower flows as they allow juveniles to burry themselves more effectively, and heterogeneous substrates as the sediment is more stable, allowing adults to maintain their position and feed more efficiently. Infested hosts also appear to disperse further upriver (**Paper IV**), a significant fitness benefit to unionid mussels, as their reproductive strategy inherently flushes gametes and larvae downriver.

Adult mussels can increase habitat heterogeneity, drawing infested hosts to existing mussel beds, areas we may assume to be suitable habitat for juvenile mussels (**Paper III**). I did not demonstrate that glochidiosis significantly decreased feeding rates in my investigation (**Paper III**), but such results have been demonstrated previously. As such, mussel beds may not only provide ideal habitat for infested hosts to find refuge from higher flows but also prove to be good feeding grounds for those same individuals as mussel beds are known biodiversity hotspots.

Together, the impacts of glochidiosis on host behaviour and the effects of adult mussels on surrounding benthic structure and community composition suggest that unionid mussels may express an extended phenotype and manipulate host behaviour through a combination of direct effects on their hosts as parasites and indirect effects on their hosts as habitat.

## Further considerations

From the results and discussion above, I suggest that future research take the following considerations into account:

1. Most studies on the impacts of glochidiosis are biased toward *M. margaritifera*. As such, future studies should investigate a more generalizable model genus. I suggest the genus *Unio*, given its global distribution and broad host usage.
2. Very few true comparative studies have been performed on the impact of one mussel species on multiple fish species, or of multiple mussel species on one host. As such, additional work should investigate the variability of effects glochidiosis can produce on a singular host or how various hosts respond to glochidiosis from one mussel species.
3. Very few studies outside of this dissertation investigate the social behaviour of fish infested with glochidia or the interaction of infested host behaviour with other environmental elements, such as adult mussels themselves. Additional work in these directions would provide a greater ecological understanding of the effects of glochidiosis.
4. Multiple studies in this dissertation suggest that unionid mussels may express an extended phenotype on their hosts, though none can provide a definitive mechanism for this effect, which is a necessary piece of evidence to make the claim of its existence. As adult mussels have well-described host manipulation behaviours, further work should be conducted to determine whether larval unionids can, in fact, manipulate host behaviour in a manner beneficial to future life stages, and provide a definitive mechanism.

5. The findings from this dissertation provide further evidence that mussel conservation efforts should not rely entirely on reintroduction projects, but should be paired with efforts to restore habitat for not only the mussels, but also for their hosts. Without some focus on fish, we do not support the complete mussel life cycle. Moreover, as adult mussels can support fish populations, comprehensive conservation projects which co-manage multiple taxa (such as the funding project for the dissertation, LIFE Connects) may prove to be more effective than projects which target single taxa.

## Acknowledgements

Taxonomic keys are often used by biologists to identify species from physiological characteristics. Similarly, this acknowledgements key, modified from Nilsson (2000; as cited in Schneider, 2017), can help someone find why I'd like to acknowledge them at the end of my dissertation. For non-biologists, go the next page and start at **1**), follow the numbers of each subcategory until you find your name. I apologize for not being able to include everyone here, I've tried my best to include as many as possible.



**Figure 19:** Participants of the FMCS 2024 field excursion, pictured by the Karlstad mussel statue.



- 1) How were we originally connected?
- Professionally (as biologists).....2
  - Personally.....19
  - Family.....24
- 2) In what capacity were we originally professionally connected?
- Involved with PhD supervision.....3
  - Co-worker at Karlstad University.....5
  - Through LIFE Connects.....10
  - Other.....13
- 3) It's all thanks to you that I was able to make it as far as I could.
- If you were a supervisor.....4
  - Lutz, thank you for looking out for me when planning all the dates of my defence, making sure I was planning my courses correctly and, more importantly still, approving some of my less-than-orthodox credit awarding activities.
- 4) If you were a supervisor...
- Martin, it was a by chance alone that I found the advertisement for the PhD position that I eventually took, and chance alone that I decided to take the offer when you gave it. I can honestly say that coming here to work with you has been the best decision of my life. Learning from you has been an absolute blast! Sorry for being a bit of a stubborn, slow learner. I'd also like to apologize for running the budget dry, but, since our adventures together seem like they will continue for another few years, I can't have been all that bad, right?
  - Anders, it was not on my bingo card to first meet my supervisor at his front door, to be invited in for some beers and later a bed to rest in. Thank you for all the help you've offered me in the field and the tools

you've let me use out of your garage in the evenings as I tinkered with PIT-tag reader.

→ Johan, when we first met you gave me a tour of some of the university buildings and kept going on about a song by some band with the words "the egg man" (I think, I still don't know what that song is). Chatting about music and aquariums with you has been loads of fun! Thank you for all the patience you've had with my highly mediocre statistical abilities.

→ Olle, I believe we first met at Ander's place when you showed up several hours late following some difficult boat issues (if I recall correctly). You've been the least involved of my supervisors, which is very understandable as four supervisors is a lot to have. Regardless, you've helped a great deal with writing papers, traveling around and generally injecting energy into the daily comings and goings of the department. Thank you for the kayak and the cherries that one summer. I won't be needing the cherries anymore, but perhaps I'll inquire again soon about the kayak.

5) There's a lot of people in this university, and I won't be able to list my thanks to everyone individually here, otherwise this acknowledgements list will be as long as the dissertation itself. However, I would like to make some honourable mentions, after some further categorization.

- Were/are you a PhD?..... **6**
- Are you a technician?..... **7**
- Did you already have a PhD when we met?..... **8**
- Other..... **9**

6) I can't talk about all of you, but my favourites have been...

- Jacqueline, you've been a great friend and drinking buddy. More importantly, thank you for all the help you've been proofing this thesis for me. I'll be missing the company while chatting about the goings on of the department. I wish you the best of Germany, but expect to see you around quite often, so perhaps the chatting and drinking can continue.
- Emil, I can't thank you enough for all the help you've been looking after my pets while I've been away and for being a general wealth of knowledge. It's been a pleasure to mess around with work-adjacent distractions with you. I'm sure that we'll get a publication out of one eventually.
- Raviv, my loyal long-haired mussel companion, I do not miss your puns. The fika room will have far fewer aquarium-related discussions now that you're moving on. Make sure to keep me in the loop when you develop your animal room!
- Mikael, we didn't have enough whisky tasting sessions, perhaps we can change that in future? I wish you and your young family stay in the best of health!
- Sam, my fellow LIFE connects PhD, it's a shame we never collaborated on research during my tenure here as a PhD, I hope that the socio-economy report will not be our only collaboration.
- Dennis, you've been a great addition to the morning crew. It's a shame you stopped. I hope it's a trend that continues for several years to come!
- Veli and Florian, if I were to have used the time spent chatting with you two around the department working on papers, I'd probably have a few more associated publications. I don't regret the way it turned out and am happy to continue further discussions on complicated spex plans (Veli) or whatever we usually talked about (Florian).

7) To the reliable lab technicians without which the department would fall into chaos.

→ Niklas, thank you for all the help you've offered in the basement and the field, you've always offered help when I asked for it. I'm looking forward to further developing the basement into a super high-tech facility!

→ Geni, thank you for all the help you've given me while looking for little things around the labs, arranging chemical deliveries and helping with our well-organized collaborator from Cambridge.

8) As with the PhDs, I apologize for not listing all of you. You've collectively had a transformative effect on me during my stay here as a biologist.

→ Miguelín, you've been significantly more than a simple co-worker, as a matter of fact you're now a neighbour! I hope the meat fests continue for a long time, perhaps we could make apple juice a staple addition?

→ Magnus, It's a shame you decided to make your way back to Gothenburg as quickly as you did, you were loads of fun to have in the department and a great addition to the mussel team!

→ Ann, it's been a pleasure working alongside you through the struggles of our well-organized collaborator from Cambridge. Hopefully any future collaborations we share don't require us to stay in the lab as late.

→ Daniel, you've done wonders as head of department! Thank you for entertaining Emil and I when we asked to set an aquarium up in the fika room, perhaps we can add some more glass boxes filled with life in the future?

→ Hanna, we didn't enjoy too many afterworks before your priorities changed, I'm sure you'll eventually get some free time soon. In the meantime, good luck with the twins!

→ Joshka, we talked a lot about fishing before the winter came. We should talk some more and plan an excursion. I'm looking forward to seeing

your mighty vessel and smoking some fish (literally and metaphorically)!

→ Jan, with all the talks we've had about metal, we haven't been to a show together yet. Since I'm sticking around for a little longer, we should change that!

→ Stefanos and Jan-Olov, I think I've chatted with you more at bars than in the office, and they've always been a great way to get my mind off work.

→ Bianca (and Viktor), you've been a great addition to the department and in the social circles. As with Jan, we should go to some more shows!

9) It takes a lot of people to keep a department, and university on a broader scale, running and not everyone is an academic. For example...

→ Kristina, thank you for everything you've done managing the back end, it's because of all the work you've done that my PhD went as smoothly as it did.

→ Åsa and the communications department, when you offered me the opportunity to do an Instagram take-over, I barely knew the university had an account dedicated to research. It was an honour and a pleasure to have fun with it for a week.

→ Maria and the university library, thank you for taking the time to proof my dissertation and sorting out the mini errors I was too busy to find on my own without your help.

→ Elizabeth, Rikard, Magnus & Tryckeriet, thank you for helping me put together and format the final print of my dissertation, it wouldn't look as good without your help!

**10)** My PhD was funded by LIFE connects, a project I was only a small part of which involved a great many people. For example...

→ Länsstyrelsen Skåne.....**11**

→ Sportfiskarna.....**12**

**11)** Länsstyrelsen Skåne was the primary organizer of LIFE connects and many people work there, like...

→ Ivan and Karin, thank you for actually starting and running this project. It's been an honour to be a part of the team, I hope the work I've done so far is up to standards.

→ Vibeke, thank you for helping me get the MusselLAB up and running and sharing your honey with me, it was very tasty and didn't last long.

**12)** Several people at Sportfiskarna have helped me in multiple different contexts, particularly...

→ Niklas, thank you for all the tips and tricks you've taught me about working with mussels. I hope your recovery goes well and you can get back to full working order soon.

→ Ebbe and Julius, thank you for taking the time to help me electrofish different parts of various rivers. Your efforts were really appreciated when I had no one else to turn too.

→ Anders, I know that you're not really a part of Sportfiskarna, but you work with them a lot and I've always met you with that crowd. Thank you also for first showing me how to electrofish!

**13)** I've met lots of people while doing research over the course of my PhD, some involved with the papers included here, others not.

→ Field assistants.....**14**

→ Collaborators in PhD papers.....**15**

→ Other.....**16**

**14) You're a reason for the success of my PhD!**

- Anna, on top of being an excellent field assistant, your master's thesis is included as a paper in my PhD! Thank you so much for all the help you've been and for the eggs you've given me, they were extremely tasty!
- Marie, your master's thesis was originally supposed to be a part of my PhD, unfortunately it didn't turn out that way, I'll work on getting published eventually. Thank for you your help in the field, it was truly indispensable!

**15) You're a reason **Paper II** got to where it did!**

- Fabio, while your visit here in Karlstad was short, it was quite productive. Thank you for the models, every time I had a question your replies were always fast and thorough.
- Madeleine, Paper II is actually an evolution of your bachelor's thesis, it's a great achievement! You worked tirelessly on the image analysis and provide some great data. Thank you!

**16) Some other people I've originally met in a professional capacity.**

- Published collaborations ..... **17**
- Other ..... **18**

**17) We've published a paper together!**

- John, it seems an eternity ago when I first asked you why some of the flatworms I collected were different colours. I never could have guessed that would eventually turn into a publication. You were the first to give me a chance to do real research. Thank you for all the help through the years!

- Zowi, you've been team flatworm through and through, still doesn't feel real we got to publish that paper! Thanks for hosting me when I visited Finland, I hope I get to return the favour!
- Christian, the first paper I published was actually with you. You gave me all sorts of autonomy that allowed me to develop into the researcher I am today, thank you!
- Victor, it seems like now you've published with two generations of Rocks! Thank you for teaching me all your SEM techniques, I hope to put them to use in future.

18) A lot of the people I met while doing research I simply learned a lot from, others I actually did research with. While I haven't published with anyone in this list yet, I hope that will eventually.

- Dan, when Martin first asked me if I had some time to set up the lab for a study with a fellow PhD from Cambridge, I was excited to participate in a fun *short* study. I did not expect what happened next. Between the countless 3 am lab days, trips to different countries and several different publications in process, every time I meet you it's an absolute typhoon. I'm so glad I said yes to working with you and, despite the sleepless nights, I hope we can do more of it.
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- Rebecca, Paulo and Vanessa, I'm not sure if any of the work we did together will ever result in a publication, but I was glad to be a part of your STSM and learned a lot from all of you.



- Katerina, I hope all goes well with the data analysis and that we can turn it into something. Thank you for teaching me how to use the equipment you left. I'm looking forward to using it for future research! I hope to visit Czech at some point soon and see what you do, where you do it in person!
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- SS and GS, I would like to specifically acknowledge how difficult the two of you have to work with. Had I not been as competent as I otherwise have been, you two would have given me significantly greater issues than you otherwise have. The only interaction I wish to have with you again is the minimal necessary to publish the manuscript we've worked on together.

I didn't spend all my time doing research, I've done other stuff too.

→ In Sweden.....20

→ In The Netherlands.....23

19) While not in the office I've spent time...

→ Drinking.....21

→ Going to the gym.....22

20) I'm already bad with names and faces, and copious beers don't help, however some people have become regulars.

→ Jonnie, you legend. It's been a pleasure letting you raid my collection over and over again. I can forgive your fruity nature given the amount of 96 you've had over the years.

→ Suraj, you've not been the heaviest drinker, but perhaps the messiest. Beyond that, the food we've made over the years has been a wonder to enjoy, we should keep making more!

→ Frey, remembering your Chernobyl moment always brings a smile to my face. I hope you have a list of all the things in your collection that we've started watching but never finished, we've got a lot of things to wrap up.

→ Ibbe, I still need to perfect the bread your taught me to make, I still can't figure it out. Looking forward to getting some good grilling done at my new place.

→ Filip and Frederick, it's been great going to shows with you two, it's a shame you no longer live in Karlstad. We need to go to more in various cities!

→ Dinos, three words man, not four.

21) Going to the gym is a great way to burn off steam and keep the brain working as it should.

→ Niklas, our treadmill chats are regularly some of the best parts of my mornings. Your love for candy truly knows no limits, though your other meals could get spruced up a little, I hope to help you change that in future.

→ Sven, Robin and Hugo, working out with you guys around is great. Though sometimes I chat too much and ruin my timeline, it's great catching on the daily and trading stories.

22) My Dutch crew. I love you guys. Specifically...

→ Mila, thank you for making such a nice cover for my dissertation. I knew you'd pull through for me and you certainly knocked it out of the park! Perhaps I should do something for your dissertation cover in return, my artistic skills know no bounds.

→ The rest of you, I can't write what I'd like to thank you for all here while still being within semi-professional limits. You know who you are and what I like about you. If you don't, ask me. What I will write here is I'm thankful we're all friends and have stayed close. Between trips to various countries, concerts, festivals, road and fishing trips, the past years have built a beyond significant amount of lore for the ages. Thank you.

23) To my family, I love all of you!

- Nonna, vorrei dedicare questa tesi a te. Nonostante tu ci abbia lasciati solo pochi mesi fa, posso ancora sentire il tuo abbraccio e la stessa domanda che mi ponevi sempre. Spero che, dovunque tu sia, tu abbia gli occhi per vedere dove andrò.
- Mamma e Papà, grazie per tutto l'aiuto, supporto ed ispirazione che mi avete dato, sia per la durata del mio dottorato e durante la mia vita in generale. Non sarei potuto arrivare fino a questo punto senza di voi.
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- Susanna, words alone cannot describe the joy you have brought and continue to bring to my life, so I won't write any more. I love you.



**Figure 20:** *A very loyal guard dog ensuring a safe working environment while in the field.*

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## Glochidiosis and behaviour

Unionid mussels are a unique order of bivalves characterised by the presence of a parasitic larval life stage, known as a glochidium. In this dissertation, I explore the behavioural effects of glochidiosis (the condition of bearing glochidia) on common hosts of Europe's most endangered unionids. The dissertation includes a general review of the effects of glochidiosis, two laboratory studies, and a year-long field study. The results presented here demonstrate that glochidia induce effects on their host fish similar to those caused by other parasites, including reduced growth, decreased swimming performance, and a general preference for calmer water and more structurally complex habitats. Together, the behavioural alterations induced by glochidiosis may benefit unionid recruitment, as infested host fish may transport excysting juvenile mussels to habitats favourable for later development. This provides evidence for the presence of an extended phenotype in unionids.

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