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THE IMPORTANCE OF PARASITES IN THE FUNCTIONING OF WARMING ECOSYSTEMS

by

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SUMMARY

Parasites play a critical role in the structure and functioning of ecosystems, contributing to overall ecosystem stability and the provision of ecosystem services. As the global climate changes, it is of considerable importance that ecologists understand and are able to predict shifts in the relationships between parasites and their hosts. Here, I utilize a model system comprising the acanthocephalan parasite *Polymorphus minutus* and its intermediate host, *Gammarus duebeni*, in a combination of laboratory and field experiments, to explore how temperature moderates the effects of parasites on ecosystem structure and functioning. My results show that both warming and parasitic infection alter the ecological role played by host organisms. Moreover, these results reveal that the drivers of host functioning are complex and interactive, with intraspecific competition, host sex, and even the mobility status of their prey influencing host behaviour. I conclude that warming and parasitism, through altering host behaviour and modifying predator-prey interactions, could have significant and unforeseen consequences for the structure and dynamics of ecosystems.

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“In this universe we are given two gifts: the ability to love, and the ability to ask questions.”

Mary Oliver

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CHAPTER 1

GENERAL INTRODUCTION

1.1 PARASITES AND ECOSYSTEM FUNCTION

Parasites are key contributors to both the biomass and biodiversity of ecosystems throughout the globe (Dobson et al., 2008; Amundsen et al., 2009; Jorge and Poulin, 2018). Every ecosystem hosts parasites, though even recent estimates of parasite biodiversity and distribution are likely underestimates due to patchy and idiosyncratic sampling, generally low sampling intensity, complex life stages of parasites which cycle through multiple hosts, and the frequency of cryptic species (Dallas et al., 2017; Jorge and Poulin, 2018; Poulin and Jorge, 2018). Theory suggests that around forty percent of the world's species are parasitic for at least part of their life cycles (Dobson et al., 2008). Full ecosystem characterizations are consistent with this (Lafferty et al., 2006a,b; Kuris et al., 2008; Grabner, 2017) and have revealed that the biomass of parasites is equivalent to that of other dominant consumers in ecosystems, including birds and fish (Kuris et al., 2008).

In spite of their important contributions to species richness and biomass in ecosystems, there is a dearth of empirical data on the contributions of parasites to ecosystem functioning. Parasitic interactions can comprise up to 75% of all links within food webs (Sukhdeo, 2012; Dunne et al., 2013). Parasites are therefore likely of great importance to overall trophic dynamics (Hernandez and Sukhdeo, 2008; Amundsen et al., 2009), though their influence on the stability and functioning of ecosystems can be highly context-dependent (Benesh et al., 2008; Perrot-Minnot et al., 2014). Accordingly, many studies have called for empirical investigation of the impact of parasites on ecosystem function and dynamics to improve our understanding of these crucial components of ecosystems (Blasco-Costa and Poulin, 2017; Carlson et al., 2017; Vannatta and Minchella, 2018). This need is amplified even further by current global environmental change. Climate change, and its associated increased temperatures, increased frequency of disturbances, rising sea levels, and altered chemical cycling (IPCC, 2014), is predicted to have significant consequences for the structure of parasitic communities (Brooks and Hoberg, 2007; Dobson et al.,

2008), including alterations in the geographical distribution of parasites and changes in the seasonality of parasite life cycles (Lafferty, 2009). Up to thirty percent of parasitic worms are likely to go extinct in the next fifty years, due to both extinction of their hosts and range shifts (Carlson et al., 2017). Given that temperature is a major driver of within-host parasite dynamics (Kirk et al., 2018) and parasites play an important role in influencing the capacity of ecosystems to resist and recover from disturbances (Brooks and Hoberg, 2007), this has profound implications for the stability of ecosystems globally.

Rising temperatures are likely to strongly influence biotic communities in aquatic ecosystems, as the majority of species are ectothermic and have little or no capacity to regulate their body temperature. The impact of warming on parasites, both as a possible mechanism of parasite release for their host species, and as a general ecological and evolutionary question, has been received little attention outside the scope of human parasites (Scott and Nokes, 1984; Gonzalez et al., 2010). Only very recently have the intersections of parasitology and climate science in non-human, non-livestock animals begun to be explored, to-date with limited temperature ranges (Labaude et al., 2017) and a sole focus on trophic interactions (Lavery et al., 2017).

Many parasites impact their hosts directly, and behaviour-modifying parasites can have particularly strong effects on their hosts that can propagate through ecological networks (Labaude et al., 2015b). Parasite-induced changes in host behaviour can have significant consequences for habitat structure (Mouritsen and Poulin, 2005), biogeochemical cycles (Vannatta and Minchella, 2018) and energy flows (Sato et al., 2011). Parasite-induced altered flows in energy are linked to changes in the composition of the community as a whole; parasites may provide an advantage to one competitor (Hatcher et al., 2014) or alter the overall preferences of consumers (Bernot and Lamberti, 2007; Sato et al., 2011; Bunke et al., 2015), both of which lead to shifts in community structure and dynamics. These altered changes in community structure have even been linked to the persistence of top predators when the ecosystem is disturbed (Lefevre et al., 2009). The impact of behaviour-changing parasites is not always mediated trophically, as behaviour-altering parasites have been linked to altered geographic distributions of their hosts (Frick et al., 2015), and recent work suggests that behaviour changing parasites are even capable of altering the behaviour of non-hosts in ecosystems (Demandt et al., 2018). Behaviour-modifying parasites are, therefore, a highly impactful group of species with major ecological consequences. Robust understanding of the influence of temperature on parasites

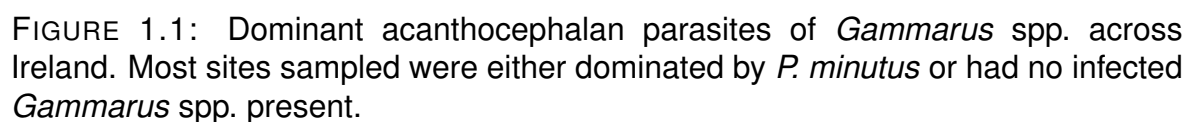
and the relationships with their host organisms is, therefore, essential to predicting how parasites may modify the dynamics and stability of ecosystems under global environmental change.

1.2 MODEL SYSTEM

In order to study the impacts of behaviour-modifying parasites and temperature on ecosystem function, I experimentally examined a model system with an acanthocephalan parasite and its intermediate amphipod host, *Gammarus duebeni*. Acanthocephalan parasites are macroparasites, meaning they can be seen with the naked eye, and infections can often be quickly identified while hosts are alive, making them an excellent model species for parasitic study. Acanthocephalan-amphipod relationships are found globally (Hynes and Nicholas, 1958; Tokeson and Holmes, 1982), and *Gammarus* are key detritivores in aquatic systems throughout the world, which speaks to their ecological relevance. Acanthocephalan parasites can impact their hosts in a broad variety of ways including: reductions of host immunocompetence (Rigaud and Moret, 2003), increases in swimming speeds (Medoc and Beisel, 2008), reductions in female fecundity (Dezfuli and Giari, 1999), castration of hosts (Bailly et al., 2017), and increased vulnerability of hosts to predation (Lagrue et al., 2007). Acanthocephalan are among the few parasites have altered host behaviours in a manner that is adaptive to the survival of the parasite (Poulin, 1995). The parasites reduce predator-avoidance of their intermediate hosts to predation by the parasites' definitive hosts (Jacquin et al., 2014). The magnitude of manipulation by acanthocephalans can be impacted by: (1) the age, sex, and size of the parasite; (2) host size and weight; and (3) parasite load, volume, and species composition (Labaude et al., 2015b). Acanthocephalan parasites can also castrate their intermediate hosts (Kakizaki et al., 2003; Bailly et al., 2017), contributing to altered behaviour, altered flow of energy within hosts, and potential changes to population structure linked to parasite prevalence. The parasite is known to have a comparably small impact on the definitive host compared to the intermediate host (Nicholas and Hynes, 1958), occasionally forming small intestinal cysts. It has been suggested that the parasite may play a role in mortality when hosts are initially of poor body condition (Itämiies et al., 1980).

The most common amphipod in Irish freshwaters is *Gammarus duebeni* var. *celticus* (Reid, 1938; MacNeil and Briffa, 2009), a known intermediate host of acan-

thocephalan parasites. The interactions between Irish amphipods and their acanthocephalan parasites have not been characterized within the last two decades outside of some specific, highly characterized, sites in the north of the country (Dick et al., 1993; Lyndon, 1996; Dunn and Dick, 1998). In order to address this dearth of information, I conducted a survey on the presence of amphipod hosts in Irish river systems and lakes in 2015 (Fig. 1.1). While *Echinorhynchus truttae*, *Polymorphus minutus*, and a single *Pomphorhynchus laevis* were found in *G. duebeni*, the most commonly identified parasite I found was *Polymorphus minutus*.



5

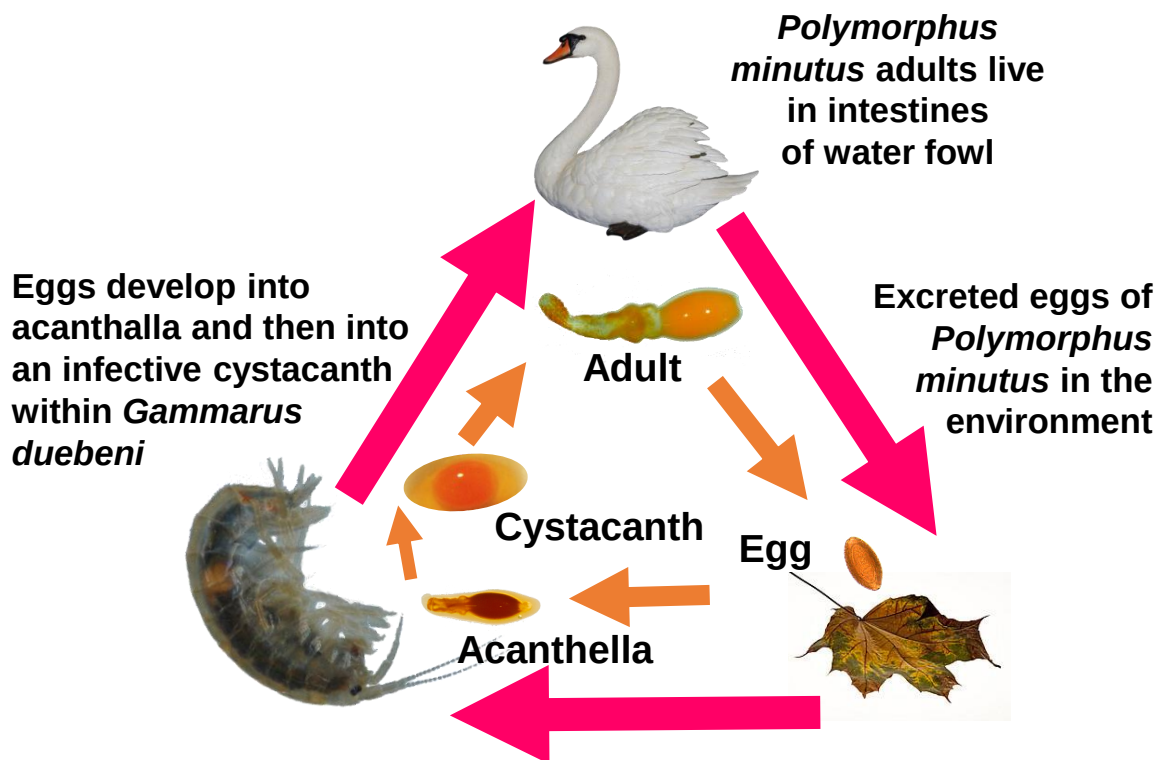


FIGURE 1.2: Life cycle of *Polymorphus minutus* in Ireland. The parasite has one intermediate host, *Gammarus duebeni*, and a definitive bird host, typically ducks or swans.

A number of studies have established that *P. minutus* manipulates the behaviour of *Gammarus* (Kaldonski et al., 2008; Perrot-Minnot et al., 2016). *P. minutus* reduces the fecundity of amphipods (Dezfuli and Giari, 1999), increases movement upwards in the water column (Perrot-Minnot et al., 2016), and reduces host activity levels (Jacquin et al., 2014). The manipulative activity of *P. minutus*, essentially the ability of the parasite to increase host risk-taking, is sensitive to environmental factors (Perrot-Minnot et al., 2016), with the oxygenation of the environment influencing the parasite's ability to alter behaviour. The ability of the parasite to alter behaviour also depends on the life-stage of the parasite, as the cystacanth stage changes behaviour but the acanthella stage of the parasite does not (Bailly et al., 2017). Few studies have addressed the crucial interaction between parasitic infection and temperature in controlling the behaviour of gammarid amphipods, especially across broad temperature ranges similar to those experienced seasonally in temperate ecosystems and those expanded temperature ranges that are predicted under current climate change models (Labaude et al., 2016, 2017). The ways in which this manipulation impacts whole-ecosystem functioning remains unknown. This thesis explores the impacts of behaviour-manipulating acanthocephalan parasites and in-

creasing temperatures on the functioning of aquatic ecosystems. By examining host physiology, trophic ecology, behavioural ecology, and even ecosystem engineering in aquatic ecosystems, this thesis will paint a fuller picture of the role of parasites in a warming world.

1.3 STRUCTURE OF THIS THESIS

The aim of this thesis is to explore the independent and combined effects of behaviour-modifying parasites and temperature on the structure and functioning of ecosystems. To this end, I conducted experiments both in the laboratory and in the field to examine the influence parasites have on their hosts at multiple temperatures on the following aspects of ecosystem and host function:

1. Host behaviour and energy flow at the individual level (Chapter 2);
2. Ecosystem engineering via bioturbation (Chapter 3);
3. Trophic ecology and host feeding preferences (Chapter 4);
4. Host feeding and ecosystem function in the field (Chapter 5).

1.3.1 Chapter 2

A thorough knowledge of the influence of parasites on their individual hosts is a crucial first step towards understanding how parasites can impact overall ecosystems, particularly in light of warming temperatures. In this chapter, I examine the impact of parasitic infection on the energy budget and behaviour of its host across a range of temperatures. My results show that a temperature increase of six degrees is enough to modify the predator avoidance behaviour of hosts to the same extent as infection with *P. minutus*. Temperature was the major driver of energy flow within individual hosts, parasitic infection reduced host respiration at low temperature, and cystacanth-stage parasitic infection did not influence feeding rates or energy assimilation. However, warming increased the movement of hosts towards light and upwards in the water column, as did parasitic infection. Parasitic infection and increasing temperature additively impacted anti-predator behaviour, increasing the hosts' vulnerability to predation. As gammarid amphipods are crucial to overall ecosystem function, this altered vulnerability to predation could lead to shifts in energy flow through the ecosystem. As infected amphipods and amphipods at higher

temperatures moved upwards in the water column, I predicted that the infected amphipods would have less interaction with bottom sediments, though this had not yet been examined experimentally.

1.3.2 Chapter 3

It has been suggested that parasites might act as ecosystem engineers as parasites can control the behaviour of animals that physically mediate habitat structure. There are a number of processes in which parasites may exert their influence within their environments. In aquatic ecosystems, one of the most critical animal-mediated processes is the process of bioturbation, in which animals dig into the sediment, releasing nutrients and aerating the bottom sediments. Gammarid amphipods are active biotubators, particularly within the surficial levels of the sediments. In this chapter, I present the first evidence that parasitism by *P. minutus* increases the rates at which hosts dig into bottom sediments. I additionally show that temperature influences rates of bioturbation. Temperature and parasitic infection combined additively, with no evidence for antagonistic or synergistic interactions found. This is the first record of a parasite increasing bioturbation activity of a host, and the first time *P. minutus* has been shown to influence this behaviour. Increased rates of bioturbation are likely to influence the concentration of soluble nutrients in the water and could potentially alter the levels of oxygenation in the sediments of the river bed, which could reduce anaerobic respiration and denitrification levels in the ecosystem.

1.3.3 Chapter 4

While there are many types of interactions between organisms, trophic interactions are by far the most studied. The temperature-dependence of the specific components of handling time and attack rates in omnivorous, ectothermic animals, such as gammarid amphipods, can reveal crucial information about both the mechanisms that underlie the structure of food webs and the relative strength of those interactions across temperature ranges. Parasites have the potential to alter the patterns of trophic interactions in ecosystems, as they alter the behaviour of their hosts. In this chapter, I demonstrate experimentally the temperature-dependence of the specific components of handling time (pursuit time, capture time, subjugation time) in gammarid amphipods and show that the status of the potential prey items (mobile or sessile) determines the pattern of the temperature dependence of feeding times.

Gammarids did not display preferences for potential prey items initially, though the amphipods were more likely to switch items between pursuit and capture when prey were mobile. These data provide a thorough and direct examination of the ability of amphipods to capture their prey linked to information about preference. As temperatures increase, we predict that we will see higher levels of scavenging and shredding in gammarid amphipods.

1.3.4 Chapter 5

The impacts of parasites and increasing temperature on the function of their ecologically important hosts were examined in the laboratory in the prior chapters. There is, however, a dearth of information on how realistically these results apply to actual ecosystems. To achieve more realistic estimates of the impact of warming and parasitism on hosts, I examine the influence of parasitic infection, group size of the host, and temperature on the feeding rates of *G. duebeni in situ* in this chapter. I set up decomposition bags with set numbers of infected or uninfected individuals. These bags were placed in experimentally warmed and ambient areas of the River Shannon, and the higher temperature treatment was provided by the thermal effluent generated by a power plant along the River Shannon. I show that *per capita* shredding rates were dependent on the size of the group of amphipods. Infection with *P. minutus* and higher temperature increased survival rates. The experiment was repeated in winter and summer, allowing us to show that most trends observed in winter were consistent over seasons. These findings show that intraspecific competition, temperature, and infection status contribute to the structure of the amphipod population in real ecosystems and the function of gammarid amphipods in their environment.

1.3.5 Chapter 6

The final chapter of this thesis focuses on the overall consequences of warming and parasitic infection on the function of aquatic ecosystems. Here I discuss the importance of acanthocephalan parasites as potential ecosystem engineers by summarizing the results of the experiments presented in the previous chapters. I highlight the need for experimental and observational data on the impacts of increasing temperature for the host-parasite interaction and suggest how future research may continue to examine the indirect impacts of parasites in their environments.

CHAPTER 2

WARMING CAN ALTER HOST BEHAVIOUR TO THE SAME EXTENT AS BEHAVIOUR-MANIPULATING PARASITES

2.1 SUMMARY

Parasites are ubiquitous and act as key regulators of the dynamics and stability of ecosystems by modifying the physiology and behaviour of their host organisms. It is, however, as yet unclear how parasitic relationships will act to moderate or accelerate the ecological impacts of global climate. We seek to discover how warming may moderate the effects of parasites on the physiology and behaviour of their hosts and, if so, how. Utilizing a well-established aquatic host-parasite model system — the ecologically important amphipod *Gammarus duebeni* and its Acanthocephalan parasite, *Polymorphus minutus* — I constructed full energy budgets for infected and uninfected hosts across a wide range of temperatures. I also analysed the phototactic and geotactic behaviour of the hosts, both infected and uninfected, across the same temperature range. Here I show that parasites and warming both independently alter host movement in the water column and host response to light. Moreover, a few degrees of warming has the capacity to alter these critical behaviours to the same extent as infection with behaviour-manipulating parasites. By enhancing host behavioural manipulation, warming may amplify the effects of parasites on ecological dynamics, particularly given the ubiquity of parasites in nature.

2.2 INTRODUCTION

As climate change accelerates (IPCC, 2014), the importance of warming and its effects on ecosystems around the globe will continue to grow. While the direct effects of warming have been quantified for many species (Wernberg et al., 2012), relatively little is known about its indirect effects, mediated by interspecific interactions (Shaver et al., 2000; Post and Pedersen, 2008). Though the nature and magnitude of these effects are considerably more difficult to predict (Sanford, 1999; Wernberg et al., 2012), they can be at least as important as direct effects in determining

the overall impacts of warming on ecosystems (Chapin, 1983; Post and Pedersen, 2008; Donohue et al., 2017; Kordas et al., 2017). However, the complexity of ecological networks can lead to significant uncertainty in predictions, where even small changes in the abundance of a single species can determine the responses of entire communities to disturbance (Säterberg et al., 2013; Mrowicki et al., 2016). Ecological network complexity is amplified even further by the many different kinds of interactions that occur between species (Kéfi et al., 2012). Behaviour-mediated species interactions, in particular, have been shown to influence food webs (Schmitz et al., 1997). Such interactions can, however, be crucial to understanding and predicting the effects of perturbations on ecosystems (McClellan et al., 2015; Suraci et al., 2016; Donohue et al., 2017). It has been shown that the temperature dependence of species interactions can contribute to overall resistance and resilience of ecosystems, particularly in terms of the disturbances related to climate change (Kordas et al., 2011; Dell et al., 2014).

Parasites are ubiquitous (Torchin and Mitchell, 2004) and contribute significantly to diversity, biomass and energy flow in many ecosystems (Lafferty et al., 2006a; Kuris et al., 2008; Dunne et al., 2013; Grabner, 2017). Parasites increase connectance and link density within food-webs, and they can dominate trophic interactions (Lafferty et al., 2006a; Amundsen et al., 2009). Their biomass has been shown to exceed that of top predators and many other key consumer groups in some systems (Kuris et al., 2008; Preston et al., 2013). Therefore, though they remain remarkably underappreciated, parasites have the potential to play important roles in moderating the stability of ecosystems throughout the globe (Dunne et al., 2013).

In addition to their direct impacts on host physiology, parasites have long been known to impact the behaviour, metabolism, and survival of their host organisms (Burnett, 1949; Kaldonski et al., 2009; Perrot-Minnot et al., 2012; Poulin, 2013; Perrot-Minnot et al., 2014). Many parasites alter the behaviour of ecologically important organisms to make them more susceptible to predation by suppressing predator-avoidance behaviours and thus facilitating completion of the parasite's life-cycle (Dick et al., 2010; Hatcher et al., 2014; Toscano et al., 2014). Such behavioural modifications have been demonstrated across a range of parasite species, with significant indirect consequences for non-parasitised individuals (Kadoya and Ishii, 2015; Demandt et al., 2018), species interactions (Reisinger et al., 2015), and overall ecosystem function (Sato et al., 2012). However, we know little about the implica-

tions of warming for the strength, or indeed the nature, of parasitic manipulation of host behaviour. Recent experimental work suggests that parasitism and elevated temperature do not interact in moderating feeding rates of their hosts (Labaude et al., 2016), but may modify specific light-avoidance behaviour (Labaude et al., 2017). Links have yet to be drawn between the combined physiological and behavioural impacts of warming and parasitism.

Many prey species have developed behavioural strategies to avoid capture. In aquatic ecosystems, two of the most common strategies employed, both individually and together, are negative phototaxis and geotaxis (Marriott et al., 1989; Bauer et al., 2005). Phototaxis refers to an animal's movement in response to light while geotaxis is the response of an animal to gravity; in rivers and lakes the response to gravity correlates with the position of the animal in the water body, either towards the surface or the bottom. We currently have little insight into the effects of warming and parasite infection on the geotactic and phototactic responses of host organisms across the current seasonal range of temperatures experienced in aquatic environments (Kaldonski et al., 2007; Jacquin et al., 2014). It is also crucial to consider the increased temperatures these ecosystems will face in future warming scenarios, as such knowledge is needed to predict how parasites will act to moderate the functioning and stability of ecosystems in a warming world.

Here, I explore whether, and how, temperature moderates both physiological and behavioural components of host-parasite relationships, using a well-established host-parasite model system. I first explored whether temperature modifies the effects of parasites on host physiology by quantifying full energy budgets for individuals of the amphipod *G. duebeni* in the presence and absence of infection with larvae of the acanthocephalan parasite *P. minutus*. I then examined the individual and combined effects of temperature and parasitic infection on two commonly-exhibited behaviours in gammarid species that acanthocephalan parasites are known to manipulate: phototaxis and geotaxis (Bauer et al., 2005; Perrot-Minnot et al., 2012). Both behaviours are important in this species for predator avoidance as they bring the amphipods further from their predators physically and encourage innate hiding behaviours (Bethel and Holmes, 1973; Cézilly et al., 2000; Bauer et al., 2005; Jacquin et al., 2014; Perrot-Minnot et al., 2016).

The relationship between *P. minutus* and its intermediate host, *G. duebeni*, is a particularly well-suited model system for this study, as parasitised individuals can be identified *in situ* and the parasite is a known manipulator of host behaviour

(Moore and Gotelli, 1996; Fielding et al., 2003; Benesh et al., 2005; Perrot-Minnot et al., 2007; Jacquin et al., 2014). *P. minutus* infection is common in freshwater systems across Europe (Medoc et al., 2006) and Ireland (Fig. 1.1). *Gammarus* spp. are important detritus processors in freshwater ecosystems (MacNeil et al., 1997; Sutcliffe, 2000) and comprise a major component of the diets of many fish and water fowl around the globe (Mortensen, 1982; Byers et al., 2010).

The aims of our study were to (1) examine whether temperature moderates the effects of parasites on the physiology and/or behaviour of their hosts and, if so, (2) quantify the relative importance and nature of those effects. Metabolic theory suggests that temperature will increase the rates of many components of ecologically-relevant physiology (Brown et al., 2004; Kordas et al., 2011). The theory has also been shown to explain within-host parasite interactions as well as parasite impacts on host physiology (Kirk et al., 2018). I predict that temperature will impact physiology, with higher rates of respiration at higher temperatures (Halcrow and Boyd, 1967; Bulnheim, 1979), and higher feeding rates with increasing temperature (Nilsson, 1974). As parasites have been shown to depress respiration rates in normoxic conditions (Perrot-Minnot et al., 2016), I expect antagonistic influences of temperature and parasites on this component of physiology. Additionally, I predict that temperature will not directly impact behaviour, but parasitic infection will encourage movement upwards and towards light (Labaude et al., 2017). The multiple behaviours and physiological traits examined here under a wide range of temperature conditions will allow us to examine the interaction of temperature and parasitic infection in a novel way utilizing an ecologically important model species.

2.3 METHOD

2.3.1 *Physiological assays*

I calculated energy budgets (following Nilsson (1974)) for both infected and uninfected *G. duebeni* individuals at 3°C intervals between 3 and 18°C, as 3°C is the minimum temperature *G. duebeni* experience in Ireland and survival rates of *G. duebeni* fell below 25% at temperatures above 18°C. *G. duebeni* were collected via kick sample from Lough Ennell, Co. Westmeath, Ireland (53°28'13.2"N 7°23'00.2"W). Fifteen different *Gammarus* individuals were used for each infection and temperature treatment combination (i.e. 15 individuals $\times$ 2 treatments $\times$ 6 temperatures = 180 individuals in total) and were acclimated from 15°C to their experimental

temperatures with 3°C changes per day (Penk et al., 2016). Following acclimation, *G. duebeni* individuals were starved for 24 hours to ensure a clear digestive tract before the commencement of feeding trials. Individual *Gammarus* without eggs and with a fresh mass of 10-20 mg were used in the experiment, as this size range encompassed most of the naturally infected *G. duebeni* individuals in their source population.

For feeding trials, alder (*Alnus glutinosa*) leaves were cut into 2.5 cm discs that were dried at 37°C for 12 hours, weighed and then conditioned in water from Lough Ennell for three days to enhance palatability. Alder leaves were selected due to the demonstrated preference of amphipods for alder leaves over other leaf types (Agatz and Brown, 2014) and the known location of alder trees near lake margins. Leaf material was presented as the sole food source in accordance with standard methods (Agatz and Brown, 2014). *G. duebeni* individuals were housed in individual 60 ml glass jars containing 50 ml filtered aerated lake water and a clear glass pebble to allow the gammarids to express natural hiding behaviour. Individuals were presented with a leaf disc and allowed to feed for five days, over which time they were checked twice daily for molting and mortality. Five jars lacking *G. duebeni* were used as procedural controls to quantify leaf leaching, or mass loss to the water and microbial breakdown (Webster and Benfield, 1986), at each temperature. After five days, each leaf disc was removed, dried at 37°C for 12 hours and weighed to four decimal places. After a subsequent 24-hour starvation, *G. duebeni* were removed from the jars. To collect faecal matter, the water was filtered through pre-weighed Whatman glass-fibre GF/F filters, which were dried for 12 hours at 37°C. Filters and faeces were then ashed at 500°C for 4 hours and weighed to four decimal places to determine the relative amount of organic matter on the filter. Leaf consumption rates (C) were calculated as:

$$C = \frac{(M_0 - M_t) \times (1 - L_T)}{I_t} \quad (2.1)$$

where M_0 and M_t are the mass of dried leaves at the commencement and end of the experiment, respectively, L_T is the leaching correction, which corresponds to the mean proportional weight loss from leaching and handling of the leaves in procedural controls at the specific temperature (T) being tested Nilsson (1974), and I_t is the duration of the experiment (in days). C was converted to calorific values using

published values of 22.03 J mg^{-1} alder leaf (Adcock, 1982). For all physiological analyses, dry weight of the host was used to standardize measurements.

Respiration rates were determined for each *G. duebeni* individual used in the feeding experiments in sterilized, aerated lake water. Measurements were taken in a water bath in the dark to minimise stress using a YSI 53 biological oxygen monitoring system fitted with a DATAQ output tracker. Respiration chambers containing 5 ml of >90% oxygen-saturated sterile lake water were set up for each *G. duebeni* individual with a magnetic stir bar separated from the amphipod by $350\mu\text{m}$ nylon mesh. The oxygen consumption of each *G. duebeni* was calculated from the rate of change of oxygen concentrations in the closed systems over 35 minutes or until the concentration decreased by 20% (Penk et al., 2016). At the start and end of each set of respiration measurements, a sample of water was run without an amphipod present to act as a blank for the instrument. To account for instrument drift, blank samples were run every five samples throughout each set of measurements, which were consistently less than 5% of measured rates. Respiration rates were standardized to blanks by subtracting the respiration rates of blanked samples and converted into energy equivalents using a value of $450 \text{ kJ mol}^{-1} \text{ O}_2$, as determined previously for freshwater crustaceans (Gnaiger, 1983).

Growth rate was calculated as the change in wet weight before and after experimental run divided by the number of days in the experiment, which was five. Assimilation and efficiency were calculated as per Nilsson (1974).

2.3.2 Behavioural assays

I quantified phototactic behaviour as per Perrot-Minnot (2004) and geotactic behaviour as per Bauer et al. (2005) in parasitised and unparasitised *G. duebeni* individuals, at the same temperature intervals as in the physiological experiments. I measured both geotactic and phototactic behaviour for each individual at each temperature. The order of temperature exposures was randomized, as were the run orders of individuals through the experiments. All *G. duebeni* were maintained in filtered, aerated lake water at 4°C with a 12h:12h light:dark cycle prior to all experimental assays. Individuals were acclimated to each experimental temperature with changes of 3°C per day in a constant temperature room. Overall, 390 *G. duebeni*, comprising 195 infected and 195 uninfected individuals, were used in the assays, though final numbers varied across treatments due to mortality that

occurred during the trials. Infected (mean $\pm$ S.E. fresh mass: 34.4 ± 1.2 mg) and uninfected (36.7 ± 1.3 mg) *G. duebeni* individuals used in the assays had similar ($t_{385} = 1.39$, $p = 0.16$) body mass. For all assays, the water was changed between trials. Gammarids were exposed to temperatures randomly, and within temperatures amphipods were haphazardly selected for trial orders.

Phototaxis assays were conducted by placing individual amphipods into one litre of aerated filtered lake water inside a clear plastic tank. Half of the tank was fully darkened on all sides using black plastic sheeting and the other half was exposed to a light source located 15 cm from the top of the tank, similar to methods described in Perrot-Minnot (2004). *G. duebeni* individuals were given five minutes to acclimate to the set-up, after which the position of the individual, either in the light zone or the dark zone, was recorded every 30 seconds for five minutes. For each time point, a score of 0 was given if the individual was in the dark half and a score of 10 was given if the individual was in the well-lit half of the tank, leading to a minimum possible score of 0 (highly photophobic) and a maximum score of 100 (highly photophilic).

The geotactic behaviour of individuals was assessed using translucent graduated cylinders of 5 cm diameter. The inside of the cylinders was smooth, to prevent any interference from clinging behaviours. Geotaxis assays were always completed in darkness to eliminate potentially confounding responses to light. The cylinder was divided into ten zones of equal height; the bottom zone was scored 1 and the uppermost zone 10. Observations were conducted after individual *G. duebeni* were introduced to the cylinder and allowed to acclimate to the experimental set up for five minutes. The position of individuals within the water column was then noted every 30 seconds for five minutes, leading to a geotaxis score between 10 (only interacted with the benthos) and 100 (only interacted with the surface).

Upon completion of physiological and behavioural assays, all *G. duebeni* individuals were weighed and dissected to verify absence of infection in the case of uninfected individuals or remove the larval *P. minutus* from infected individuals. All individuals were checked for parasitic infections and only *G. duebeni* naturally infected with single, cystacanth stage infections were included in analyses. *G. duebeni* individuals were then dried overnight at 37°C and their dry weight was quantified. Larval parasites were placed in a solution of 0.25 mM sodium taurocholate at 37°C overnight to activate the cysts for identification purposes (Horvath, 1969) and their identity was confirmed with microscopic morphological examination using McDonald (1988).

2.3.3 Data analyses

Consumption rate, respiration rate, growth rate, assimilation and feeding efficiency (the ratio of assimilation to consumption expressed as a percentage) from the physiological assays were analysed as response variables with generalised additive models (GAMs) in `mgcv:gam` (Wood and Wood, 2016). Temperature (fixed, smoothed with thin-plate regression splines with four knots), infection status (fixed, two levels), and amphipod sex (fixed, two levels) were incorporated in all GAMs. To examine interactions between temperature and infection status, a smoothed term with 4 knots of temperature by infection status was incorporated in the GAMs. The GAMs generated were compared to generalised linear models (GLMs) with temperature, host sex, and infection status as fixed effects (Appendix Table A1). The GAMs are presented in this thesis, as they consistently had lower Akaike Information Criterion (AIC) values, though the coefficients from the linear models are presented in Appendix Table A2 for further information. Linear mixed-effects (LME) models, with temperature, infection status, and amphipod sex as fixed effects and *G. duebeni* individual as a random effect, were used to analyse data from the behavioural assays, using `lme4::lmer` (Bates et al., 2015). Likelihood ratios were used to determine *p*-values by comparing the models with and without the tested effect or interaction term between temperature and parasitism present (Crawley, 2012). All data were analysed with R version 3.4.1 (R Core Team, 2017).

2.4 RESULTS

2.4.1 Physiological assays

Respiration rates increased with increasing temperature (Fig. 2.1a), but decreased with parasitic infection (Fig. 2.1a; Table 2.1). There was a significant interaction between infection and temperature, where infection reduced respiration at lower temperatures but does not seem to impact respiration at higher temperatures as strongly (Fig. 2.1a; Table 2.1). Temperature influenced feeding efficiency (Fig. 2.1b; Table 2.1) with highest efficiencies in the middle of the temperature range. There was, however, no net effect of temperature on rates of consumption (Fig. 2.1c; Table 2.1), growth (Fig. 2.1d; Table 2.1), or assimilation (Fig. 2.1e; Table 2.1). Sex of the adult amphipod impacted only growth rates (Fig. 2.1d; Table 2.1). There was no clear pattern within survival rates in this experiment (Fig. 2.1f). There were no

main or interactive effects of parasitic infection on any of the physiological response variables I measured other than respiration rates.

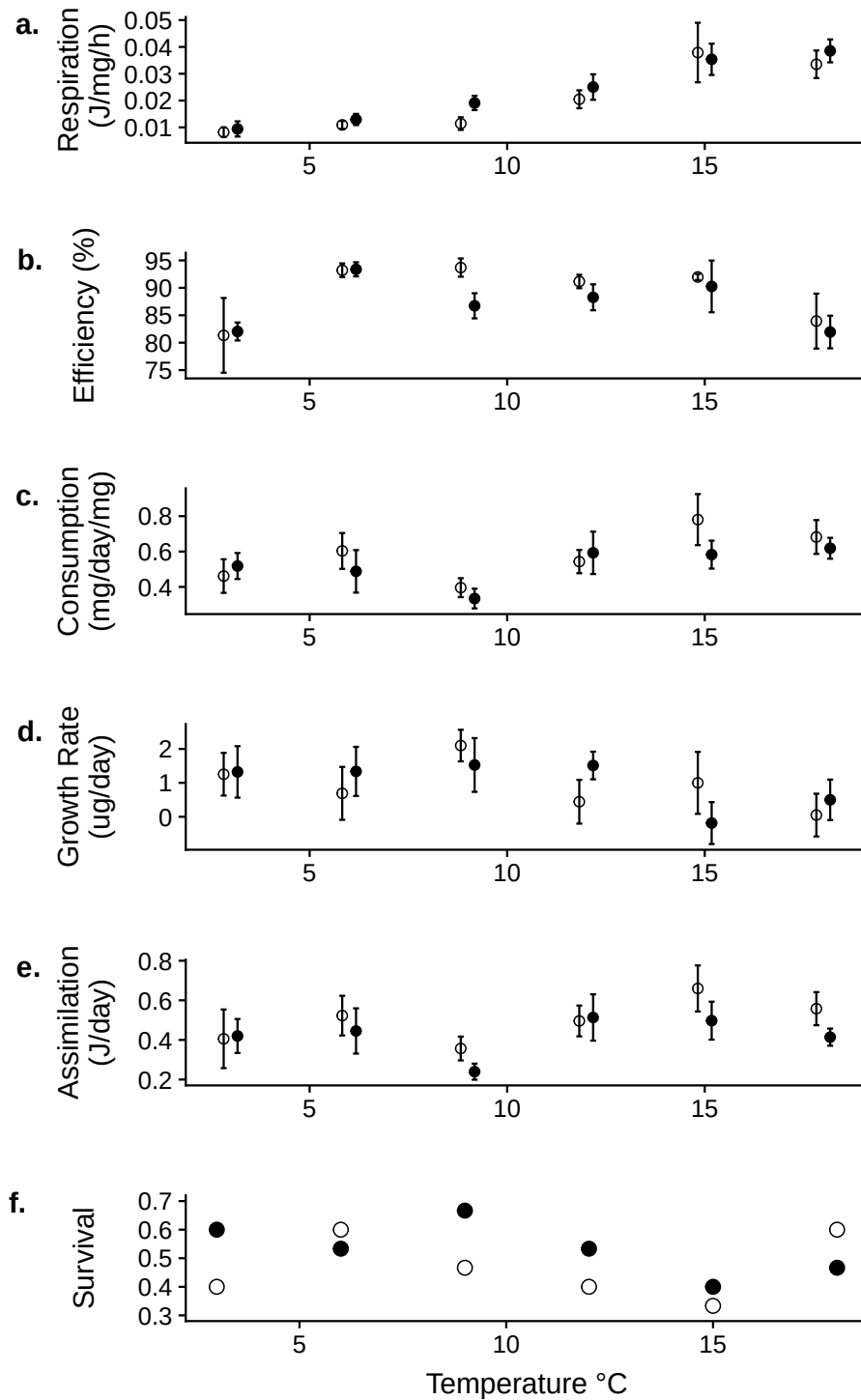


FIGURE 2.1: Variation in rates (mean $\pm$ S.E.) of (a) respiration, (b) efficiency, (c) consumption, (d) growth rate, (e) assimilation, and (f) survival of *G. duebeni* individuals infected (open circles) and uninfected (closed circles) with *P. minutus*.

TABLE 2.1: Results of generalized additive models testing the effects of temperature, parasitic infection, and host sex on various components of host physiology. Significant terms are listed in bold.

Response	Temperature		Infection		Host Sex		Temperature × Infection (Infected)		Temperature × Infection (Uninfected)	
	F	P	F	P	F	P	F	P	F	P
Respiration	110.56	<0.01	0.51	0.02	<0.01	0.97	8.63	0.02	12.32	<0.01
Efficiency	9.52	<0.01	1.03	0.31	0	0.99	0.92	0.44	0.27	0.67
Consumption	3.48	0.09	1.04	0.31	0.8	0.37	1.84	0.27	0.08	0.82
Growth	2.22	0.24	0.35	0.56	4.17	0.04	0.39	0.61	0.13	0.77
Assimilation	1.72	0.15	1.16	0.29	0.03	0.87	0.01	0.94	3.98	0.11

2.4.2 Behavioural assays

Parasitism altered both the phototactic and geotactic behaviour of *G. duebeni* (Fig. 2.2; Table 2.2), with infected individuals displaying significantly greater preference for light and upward movement in the water column (Fig. 2.2). Further, these effects were not modified by temperature (i.e. there were no interactions between temperature and parasitism; Fig. 2.2). However, I found that temperature influenced geotaxis (Fig. 2.2b; Table 2.2) in *G. duebeni* independently, yet in a similar manner to parasitism; *G. duebeni* individuals displayed significantly increased preference to move up into the water column as temperatures increased (Fig. 2.2b).

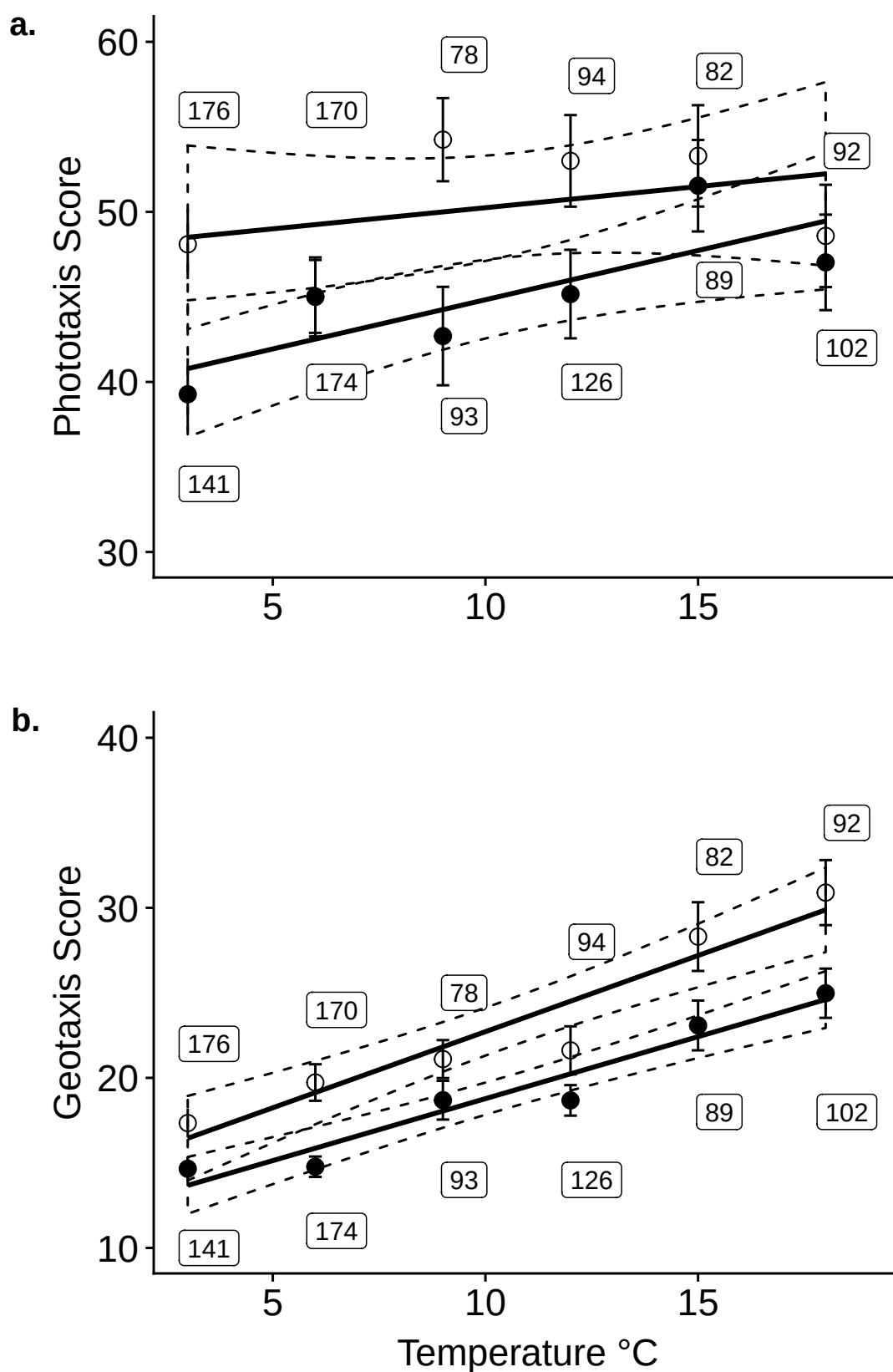


FIGURE 2.2: Variation in (mean $\pm$ S.E.) the (a) phototactic and (b) geotactic behaviour of *G. duebeni* individuals infected (open circles, dotted lines) and uninfected (closed circles, solid lines) with *P. minutus*. Relationships are shown as least-squares regression $\pm$ 95% C.I. Points are labeled with sample size.

TABLE 2.2: Results of chi-squared analysis of linear mixed-effects models testing the impact of temperature, parasitic infection, and host sex on the geotactic and phototactic behaviour of *G. duebeni*. Significant terms are listed in bold.

Response	Temperature		Infection		Host Sex		Temperature × Infection	
	χ^2	P	χ^2	P	χ^2	P	χ^2	P
Phototaxis	0.97	0.32	5.19	0.02	0.55	0.46	0.09	0.77
Geotaxis	92.33	<0.01	25.49	<0.01	<0.01	0.95	0.77	0.38

2.5 DISCUSSION

My results demonstrate that temperature and parasites both significantly influence key components of predator-avoidance behaviour in gammarid amphipods. A key finding of my study was that just a few degrees of warming has the capacity to suppress predator-avoidance behaviour to the same extent as infection with behavioural manipulating parasites, as a temperature increase of six degrees increased movement upward in the water column as much as parasitic infection. Warming encouraged movement upwards in the water column, reducing the use of benthic refugia. As temperature increases, ectothermic hosts become more capable of movement, likely allowing the movement upwards and toward light away from the benthos (Pawar et al., 2016; Abram et al., 2017). The altered movements not only increase the vulnerability of the arthropod to predators (Perrot-Minnot et al., 2012) but also may simultaneously alter the time hosts spend foraging and predating, as they more frequently move away from benthic detritus and invertebrates towards surficial refugia or open water. The temperature-dependence of both trophic (Uszko et al., 2017) and non-trophic (Kordas et al., 2017) interactions between species comprises a key determinant of the response of whole communities to warming. My analysis of the temperature dependence of predator-avoidance behaviour reveals a previously underappreciated impact of warming that could be critical to predicting its impacts in many ecosystems

I found that warming and parasitism additively influenced the predator-avoidance behaviour of *G. duebeni* and that these effects were consistent across a broad temperature range. Geotactic behaviour, associated with the use of benthic refugia, responded especially strongly and monotonically to warming. Such behavioural

change, particularly in relatively common and functionally important species such as our focal host organism, has the capacity to modify the structure and dynamics of ecosystems, though future work is necessary to determine the degree to which our results impact *in-situ* communities (Kéfi et al., 2015, 2016; Suraci et al., 2016; Donohue et al., 2017). This novel and important finding was not recorded in previous studies of amphipod behaviour (e.g. Labaude et al. (2017)), possibly because a more limited range of temperatures studied prevented the broad trend I found from being detected. By examining the full 15°C range experienced by *G. duebeni*, I was able to see the equivalence of the impacts of infection and 6°C of warming. There is also specificity in host-parasite interactions, due to tightly coupled co-evolution, which might explain the differential observations between this study and prior work (O'Mahony et al., 2004; Westram et al., 2011).

With recent findings on the complexity of *P. minutus* lineages (Zittel et al., 2018), it will be necessary to determine the generalisability of our findings by examining data from multiple strains of the parasite and multiple hosts. Future work to determine the commonality of these findings would shed light on the specificity of behaviour manipulation and potentially yield exciting findings for both ecology and parasitology. As relatively minor changes in temperature of only a few degrees – well within the range of seasonal temperature variability in northern temperate climates – altered geotaxis to the same extent as parasitic infection, the importance of examining the hosts' entire realistic temperature range is clearly apparent.

There is potential for the altered behaviour of the intermediate hosts under warmer conditions to increase the rate of completion of the parasite's life cycle (Tierney et al., 1993; Strepparava et al., 2017). The specific impacts of temperature on the development of the parasite within the definitive host need to be examined, as responses of species to temperature can be asymmetric (Dell et al., 2014; Goedknecht et al., 2015) and the rate of parasite development is crucial to understanding how temperature may influence the speed at which the parasites are transmitted. Given the significant role that parasites can play in moderating the dynamics of entire communities (Dunne et al., 2013), these findings have implications for both the functioning and stability of ecosystems in a warming world, though a thorough assessment of the dynamics of the parasite in its definitive hosts would be necessary to confirm the prediction.

The effects of both parasitism and warming on predator-avoidance behaviour found in my study contrast with the comparatively minor effects of my focal para-

sites on host physiology in everything other than respiration rates. At the lowest temperatures, infection with the parasite suppressed respiration of the host, a finding in line with prior studies on acanthocephalan parasites (Rumpus and Kennedy, 1974), though at higher temperatures there were no significant differences between infected and uninfected individuals. The mechanisms behind oxygen use in acanthocephalan and amphipod relationships is of particular interest as hypoxia and anaerobic metabolism have been implicated as potential mechanisms by which *P. minutus* alters host behaviour (Perrot-Minnot et al., 2016). The suppression of respiration seen in this study provides support to the theory that the parasite reduces host aerobic metabolism and provides some support to the theory that anaerobic metabolism may be involved in parasitic manipulation at temperatures below 15°C.

Much importance has been placed on the trophic interactions between parasites and their hosts (Van Veen et al., 2008; Chen et al., 2011; Benesh et al., 2014). However, I found no effects of parasitism on feeding rates, growth rates, rates of assimilation, or feeding efficiency measured within individual gammarids. Previous studies of the influence of parasites on amphipod feeding rates is equivocal, with some demonstrating significant impacts of acanthocephalan parasitism (Labaude et al., 2016; Lavery et al., 2017) and others showing no effect (Fielding et al., 2003). The specificity of host-parasite interactions may explain this ambiguity and may explain why I did not see an impact of parasitic infection on feeding rate, a finding consistent with feeding rates determined *in situ* in Chapter 5. The small impact of the parasite on energy flow is consistent with the assertion that parasite infection may not in itself be as energetically costly to host organisms as thought previously (Labaude et al., 2015a), a realisation with important implications for energy flow and models for future ecosystem management.

Our study focused on a single —though important and well-established—model system. While this limits somewhat the capacity to generalise our findings, this limitation is mitigated somewhat by the almost global presence of gammarid amphipods (Karaman and Pinkster, 1977; Westram et al., 2011), and their dominance of animal biomass in many communities (Mortensen, 1982), where they process detritus, act as predators, and act as key energy conduits to higher trophic levels (MacNeil et al., 1997; Little and Altermatt, 2018). Further work on the interactions between temperature and parasitic infection in additional model systems, particularly those that involve behaviour-modification in intermediate hosts, are needed to examine the generality of our results and explore further the potential impacts of warming

on predator-prey interactions mediated by behaviour. Specifically, meta-analyses of the impact of acanthocephalans on the behaviour of their intermediate hosts across multiple host populations could reveal the generality of these findings. Additional experiments tracking intermediate host behaviour in the field would also determine the overall importance of this altered behaviour in real ecosystems.

By altering behaviour and therefore modifying predator-prey interactions, our results indicate an additional mechanism through which warming could have unforeseen consequences for the structure and dynamics of communities. These findings highlight the need for holistic knowledge of interaction networks, incorporating both direct and indirect trophic and non-trophic interactions (Kéfi et al., 2016), to predict the effects of warming on the dynamics and stability of ecosystems (Kordas et al., 2017). There remains a critical need for experiments in natural communities to test the generality of these predictions in a variety of ecological contexts and help us understand and anticipate how ecosystems will change in a warming world.

CHAPTER 3

INFECTION WITH BEHAVIOUR-MANIPULATING PARASITES ENHANCES BIOTURBATION BY KEY AQUATIC DETRITIVORES

3.1 SUMMARY

The ubiquity of parasites within their ecosystems and their potential impacts on host behaviour has led to the suggestion that parasites may act as ecosystem engineers, structuring their environment and physical habitats. Climate change may alter the relationships between hosts and parasites, potentially changing the rates at which hosts interact with their larger environment. Gammarid amphipods contribute to ecosystem function in aquatic environments by bioturbating, or digging into sediments, with consequences for sediment and water oxygenation and nutrient cycling within rivers and lakes. In this study, I test how temperature and infection with acanthocephalan parasites alters the rates at which *Gammarus duebeni* rework surface sediments. I show that higher temperatures and parasitic infection additively increase rates of amphipod bioturbation. These increases in bioturbation will have knock-on effects for overall ecosystem functioning in a warming world. In terms of benthic habitat structure, parasites do seem to act as ecosystem engineers and future ecosystem management strategies should account for parasitic infection when predicting the impacts of increasing temperature.

3.2 INTRODUCTION

Parasites are found in all ecosystems throughout the globe (Jorge and Poulin, 2018). They comprise up to 40% of all described species (Dobson et al., 2008), feature in up to 70% of the links within food webs (Dunne et al., 2013), and contribute significantly to the biomass of many ecosystems (Kuris et al., 2008). Their presence has, therefore, important — though still remarkably underappreciated — implications for the structure, functioning and dynamics of entire ecosystems (Amundsen et al., 2009; Dunne et al., 2013). However, their influence on how ecosystems respond to environmental change, particularly a warming climate (Kutz et al., 2005; Hoberg and

Brooks, 2007), remains largely unknown. Climate warming will likely modify rates of parasite transmission (Mouritsen and Jensen, 1997) and infectivity (Studer et al., 2010). Moreover, temperature also moderates host behaviour (Issartel et al., 2005; Abram et al., 2017), which can influence host susceptibility to parasites (Morley and Lewis, 2014) and overall host functioning in the ecosystem (O’Gorman et al., 2012).

Bioturbation, the mixing of sediment by mobile organisms, is an important ecosystem function that occurs in both terrestrial and aquatic environments. Bioturbation comprises a key non-trophic mechanism through which organisms physically, chemically, and biologically structure ecosystems (Grant and Daborn, 1994; Jones et al., 1996; Baranov et al., 2016; Wohlgemuth et al., 2017). In aquatic ecosystems, bioturbation influences the flow of nutrients (Mermillod-Blondin et al., 2004), oxygenation of sediments (Baranov et al., 2016), the turbidity of the water (Croel and Kneitel, 2011), and sediment erosion rates (Grant and Daborn, 1994). Moreover, the rate of bioturbation in has also shown to increase with warming (Baranov et al., 2016). There is, however, little known about the influence of parasites on rates of bioturbation (Vannatta and Minchella, 2018). While parasitism has been shown to modify burrowing behaviour in intertidal cockles (Mouritsen and Poulin, 2005), by reducing their digging into the sediments, there have been no cases where the presence of parasites increases bioturbation rates of their hosts.

Gammarid amphipods contribute significantly to the bioturbation in aquatic ecosystems globally (Mermillod-Blondin et al., 2004; Hunting et al., 2012; De Nadaï-Monoury et al., 2013; Vadher et al., 2015) by reworking the uppermost layer (i.e. 2-3 cm) of sediment. In freshwaters, gammarids are also frequently infected with an acanthocephalan parasite, *P. minutus*, which alters host movement in the water column and the rates at which they shred detritus (Bauer et al., 2005; Labaude et al., 2016). Two life-stages of the acanthocephalan, the acanthella and the cystacanth, utilize the amphipod intermediate host. The cystacanth is the life-stage associated most strongly with behavioural changes (Bailly et al., 2017), as it is the stage at which the parasite is infective to its definitive, or final host.

I examined bioturbation activity of *G. duebeni* var. *celticus* experimentally in the laboratory across a range of temperatures encountered in their native range to determine whether (1) parasitic infection and temperature, individually or in combination, modify rates of sediment surface reworking (our measure of bioturbation) by *G. duebeni*, and (2) the combined effects of parasitic infection and temperature on bioturbation are additive, antagonistic, or synergistic. *Gammarus* are used fre-

quently as a model system to examine the impacts of parasites on intermediate host behaviour (Agatz and Brown, 2014; Perrot-Minnot et al., 2014; Perrot-Minnot et al., 2016) and *G. duebeni* comprise important components of the benthic community throughout Ireland (Reid, 1938; MacNeil and Briffa, 2009), playing a crucial role in ecosystem functioning by processing of detritus (Kelly et al., 2002). As the amphipods are ectothermic (Baranov et al., 2016), I expect temperature to increase rates of bioturbation. I also predict that parasitic infection will reduce rates of bioturbation due to reduced interaction between the gammarids and the benthos as gammarid hosts infected with *P. minutus* display enhanced phototaxis and are more likely to move upward in the water column (Perrot-Minnot et al., 2016, Chapter 2).

3.3 METHOD

3.3.1 *Experimental design*

I quantified the rate of sediment surface re-working by adult *G. duebeni* at two levels of infection (i.e. infected or uninfected by *P. minutus* cystacanths) and at four temperatures (4°C, 9°C, 14°C, and 19°C), encompassing the majority of the temperature range experienced by *G. duebeni* in their native range in Ireland, in a full-factorial experiment. Each experimental treatment combination was replicated 20 times.

Amphipods, benthic lake sediments and lake water used in the experiment were collected from Lough Lene, Co. Westmeath, Ireland (53.6625°N, 7.234°W) on 22 January 2018. Surficial (i.e. less than 3 cm depth) benthic lake sediments were collected, homogenized, passed through a 1 mm sieve to remove macrofauna and rocks, and allowed to settle in lake water for a day before use.

Bioturbation was quantified based upon methods developed by De Nadaï-Monoury et al. (2013) and Wohlgemuth et al. (2017). Eight 10 L buckets were filled with lake sediments to a depth of 5 cm. Sterile centrifuge tubes (85 mm long with an internal diameter of 2.7 cm) with their tops and bottoms removed were placed into the buckets (25 pipes per bucket). Tracer sand (pink luminophores < 125 µm; Brianclegg Ltd., UK) was added to a depth of 0.2 cm within each tube. Filtered, aerated lake water was then added to the bucket to a depth of 13 cm above the sediment. A single *G. duebeni* adult (> 0.02 g fresh weight) was added to individual tubes which were then covered with mesh (hole diameter 1mm) to maintain the organisms within the tubes

while allowing the circulation of aerated water. Each 8 L bucket contained ten tubes containing infected *G. duebeni*, ten tubes with uninfected *G. duebeni*, and five tubes containing no *G. duebeni*, which acted as procedural controls. Fresh mass of *G. duebeni* individuals at the commencement of the experiment were similar across all experimental treatment combinations (ANOVA; $F_{7,135} = 1.696$, $p = 0.115$). Turnover rates in the controls were negligible, and did not vary with temperature (Appendix A2; Figure A.2.1.). Two 8 L buckets were kept at each of the four temperatures analysed. The buckets were aerated continually and kept in a 12h:12h light:dark cycle. After 28 days, *G. duebeni* were removed and dissected to ensure infection status. Only organisms with single, cystacanth-stage infections were designated as infected, any hosts with multiple-infections or acanthellae-stage infections were omitted from analyses. Parasites were then examined microscopically to confirm their identity morphologically (following McDonald (1988)) after cystacanths were first placed in a 0.25 mM solution of sodium taurocholate, a type of bile salt which encourages extension of the proboscis, and left overnight at 37°C.

3.3.2 Data analyses

Photographs of the sediment surface of each experimental tube were taken with a Canon EOS 550D (Aperture: f/4.5; Pixels: 5184×3456) and saved as RGB coloured JPEGs. Images were captured under UV light (395 nm wavelength, UV LED Flashlight, LightingEVER, Las Vegas, USA) to optimize fluorophore detection. Images were then processed using ImageJ version 1.43u (US National Institutes of Health, <https://imagej.nih.gov/ij/>). Images were cropped to appropriate areas using an elliptical cropping shape, then split into red, green and blue colour channels. The red channel was then selected, as it allowed for clearest distinction between the pink fluorophores and the black Lough Lene sediments. Images were thresholded in order to colour the fluorescent particles white and the sediment particles black. The photo was then analysed and the proportion of black pixels, representing the Lough Lene sand brought up from underneath the fluorophores, recorded. The total area of surface sediment reworked was then quantified in cm² (Fig. 3.1).

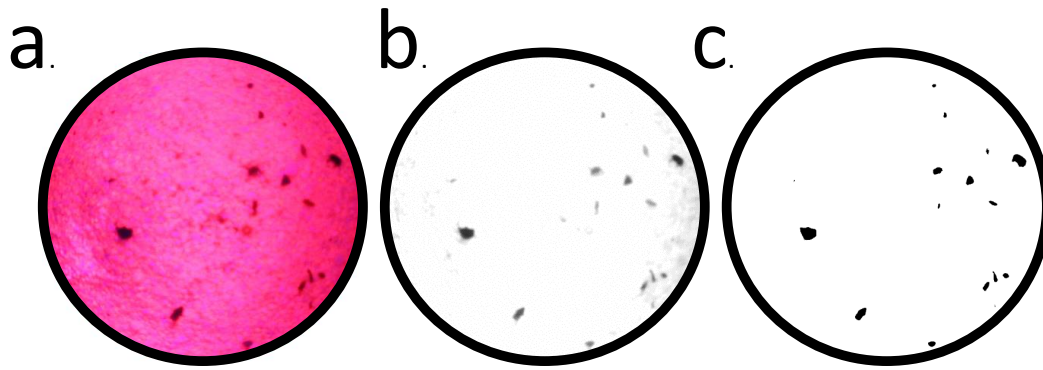


FIGURE 3.1: The image processing workflow: (a) the image is selected from its background, then (b) the red channel has been selected after splitting the image, and finally (c) the image is thresholded, with only black pixels (representing the sediment brought up by the amphipod) and white pixels (representing the fluorophores) remaining.

Data were analysed in R version 3.4.1 (R Core Team, 2017). The extent of sediment surface reworking was $\log_{10}$ -transformed prior to analyses to meet assumptions of normality and homoscedasticity. A linear mixed-effects model was constructed using `lme4::lmer` (Bates et al., 2015), with the $\log_{10}$ -transformed area reworked as the response variable, bucket as a random effect, and temperature and infection status as fixed effects. Model selection with `model.sel:MuMIn` (Barton and Barton, 2018) was conducted and the influence of fixed effects on the model with the lowest AIC is presented.

3.4 RESULTS

Infected individuals consistently reworked significantly more sediment surface area than uninfected individuals (linear mixed-effects model, $F_{1,137} = 7.38$, $p < 0.01$; Fig. 3.2a). Rates of sediment reworking also increased significantly with temperature (linear mixed-effects model, $F_{8,137} = 5.30$, $p = 0.05$; Fig. 3.2a). Combined effects of parasitic infection and warming were, however, additive, as temperature did not interact with parasitic infection in moderating bioturbation, and the magnitude of the effect of parasitism was consistent across the range of temperatures examined (Fig. 3.2b).

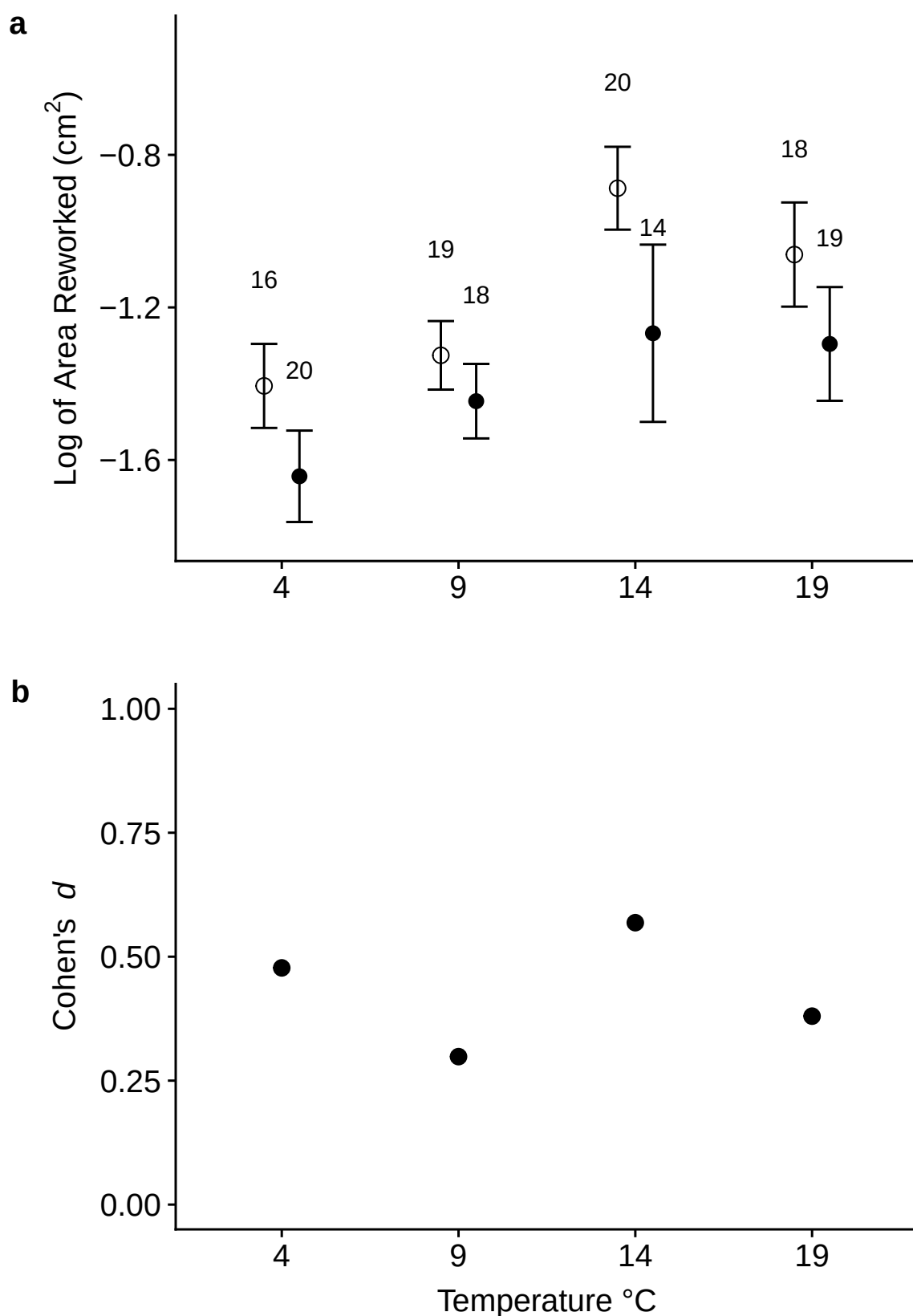


FIGURE 3.2: (a) Rates of bioturbation (mean $\pm$ SE) by *G. duebeni* infected (open circles) and uninfected (closed circles) with *P. minutus* across the temperature range. Bioturbation was measured as the area of benthic surface sediments in our experimental microcosms that were reworked over the course of the experiment. Final sample size is indicated above each datapoint. (b) Effect size of *P. minutus* infection on bioturbation rates across the range of temperatures examined.

3.5 DISCUSSION

I found that both temperature and parasitic infection impacted the rates at which *G. duebeni* reworked the upper sediment in our experimental microcosms. Moreover, infection and temperature did not interact and moderated bioturbation additively. This comprises the first evidence of which we are aware of parasites enhancing the bioturbation activity of their hosts. Given the importance of gammarid amphipods as key drivers of detritivory and bioturbation in freshwater ecosystems (Hunting et al., 2012), coupled with predicted increases in the prevalence of parasites in a warmer world (Galaktionov, 2017), this finding has important implications for the functioning of freshwater ecosystems under global change.

The enhanced bioturbation caused by infection with *P. minutus* contrasts with my *a priori* predictions. As infection with *P. minutus* increases movement upwards in the water column (Jacquin et al., 2014; Perrot-Minnot et al., 2016; Bailly et al., 2017), I expected that infected hosts would interact less with the benthos, leading to a decrease in the rates of surface sediment reworking. However, parasites often do not have fine-scale control when manipulating their hosts. The manipulation of crickets by nematomorph worms provides a clear example. The worms alter the behaviour of crickets to increase their chances of entering the water. However, the manipulation is not a specific push towards the water, but rather results in an increase in erratic jumping (Thomas et al., 2002). It has been suggested previously that the behavioural manipulation by *P. minutus* is non-specific and does not drive the intermediate host directly to the exact, preferred definitive host (Jacquin et al., 2014). The mechanism of manipulation by the parasite is likely to be similar to that of the closely-related parasite *Pomphorhynchus laevis*, which alters the levels of serotonin in the brain of *Gammarus* in order to control the amphipod and increase its potential for transmission (Kaldonski et al., 2007; Perrot-Minnot et al., 2014). The increased digging I observed in infected *G. duebeni* may therefore reflect a generalized reduction in risk-aversion behaviour and consequent increase in movement, rather than a mechanism for directly increasing transmission of the parasite to its definitive host. However, further work is needed to determine whether or not enhanced bioturbation activity is adaptive for the parasite, and could be completed using experimental mesocosms which have predator mimics such as those designed by (Demandt et al., 2018).

A wide range of animal behaviours exhibit thermal dependence, many of which can be explained by metabolic theory (Kordas et al., 2011; Dell et al., 2014). Higher temperatures have been linked previously to enhanced bioturbation rates in non-amphipod aquatic species (Ouellette et al., 2004), though the extent to which temperature enhances or suppresses bioturbation likely varies across species (Maire et al., 2010). My results are consistent with those from previous studies (Labaude et al., 2016), and work in this thesis (Chapter 2) which found additive, and not interactive, effects of temperature and parasitic infection on a range of behaviours in *Gammarus*. As the climate continues to warm, alterations in the prevalence of parasites and associated shifts in the behaviour and functioning of *Gammarus* have the potential to moderate the impact of many of the stressors of aquatic systems associated with global environmental change (Baranov et al., 2016).

Our results demonstrate a significant influence of parasites on the key ecosystem function that is bioturbation (Vannatta and Minchella, 2018). Bioturbation has, for example, been linked to the rates of community respiration, sediment transport, nutrient availability (Ouellette et al., 2004; Wohlgemuth et al., 2017) and overall community structure (Grant and Daborn, 1994; Croel and Kneitel, 2011; Baranov et al., 2016). Therefore, irrespective of whether or not the altered behaviour we found is adaptive in terms of the parasite's fitness, our findings have important implications for our understanding of the roles played by parasites in the structure and functioning of entire aquatic systems.

CHAPTER 4

THE TEMPERATURE-DEPENDENCE AND INFLUENCE OF PREY MOBILITY ON MULTIPLE COMPONENTS OF HANDLING TIME

4.1 SUMMARY

Species are known to respond asymmetrically to warming, potentially altering the links between parasites and their hosts as the global climate warms. The ability of omnivores to capture and process their food can be altered by both parasitic infection and changes in temperature, though the combined impacts of these drivers have yet to be fully examined empirically. Here, I divide handling time into its components (time in pursuit, time to capture, and time to subjugate potential prey) to determine whether each handling time process, and the potential prey chosen at each point, respond similarly to temperature changes and whether parasites and the mobility status of prey could alter those thermal dependencies. I found that each component of handling time had unique temperature-dependencies, though the overall propensity of amphipods to eat was increased at higher temperatures. The mobility of potential prey had significant impacts on the time it took gammarids to capture and subjugate their food. Parasites only influenced the time it took predators to capture prey, suggesting that the impact of larval acanthocephalans is limited to a very specific process within predation. These results highlight the complexity of the interactions between predators and prey, whereby each process within the interaction is controlled by different drivers and thus is likely subject to different limitations. As temperature increases and the movement behaviour of prey species change, these findings highlight the need to consider the multiple distinct components of predator-prey interactions when predicting shifts in energy flow and ecosystem stability under climate warming.

4.2 INTRODUCTION

The nature and strength of trophic interactions are a key determinant of the stability of ecosystems (May, 1974; Pimm, 1984; O’Gorman and Emmerson, 2009;

Allesina and Tang, 2012; Donohue et al., 2016, 2017; DeLong et al., 2018). The consequences of a warming climate for consumer-resource interactions depend to a large extent upon the thermal optima of individual species, with some species gaining advantages over others due to asymmetries in performance (Dell et al., 2014; Penk et al., 2016). Climate warming is predicted to have particularly profound consequences for ectothermic animals, as it will increase the metabolic demand of organisms in general, likely resulting in significant shifts in both intra- and interspecific interactions and altered habitat use (Kordas et al., 2011; Abram et al., 2017; Vander Vorste et al., 2017).

The metabolic theory of ecology (MTE) (Brown et al., 2004) posits that ecological dynamics across all levels of organisation are broadly controlled by the temperature-dependence of metabolism. The theory has been used both to understand how ecosystems function (Ohlund et al., 2015; Sentis et al., 2015; O’Gorman et al., 2017) and predict how they will change as temperatures increase (O’Connor et al., 2009; Petchey et al., 2010). Linking trophic relationships into the MTE framework is challenging, however, due to the existence of threshold temperatures below which consumers are inactive (Ohlund et al., 2015), the importance of spatial and temporal scale (Kordas et al., 2011), and the relative advantage of prey items at lower temperatures due to smaller size (Dell et al., 2011).

Handling time — the time it takes for predators to chase, capture, process, and digest their prey (Jeschke et al., 2002) — plays a critical role within the MTE, by providing valuable information for predicting predator behaviour and interpreting the behavioural response of both predators and their prey (Rall et al., 2012; Reuman et al., 2014). The many steps that make up handling time can, however, each be subject to different drivers and respond to elevated temperatures in different ways (Sentis et al., 2013), as animals are more likely to expend energy on certain tasks over others (Dell et al., 2011). Explicit quantification of these various components, such as attack rates (Ohlund et al., 2015), digestion (Sentis et al., 2013) and excretion rates (Rall et al., 2010; Englund et al., 2011), has helped to explain the deviation of many observed measurements from those predicted by theory. Mechanistic understanding of the thermal-dependence of the distinct steps that make up handling time is, therefore, critical for the prediction of shifts in trophic interactions under global climate change.

Aside from its moderation of handling times, temperature may also influence the feeding choices of predators (Ferrari et al., 2015), particularly when they are

omnivorous (Boersma et al., 2016). At higher temperatures, predators tend to become more selective, aiming for higher quality food (Gordon et al., 2018). Though this has potentially profound implications for energy transfer and the stability of food webs (O’Gorman et al., 2016), no empirical studies have examined the influence of temperature on both consumer food choice and the various components of prey handling times simultaneously.

Here, I examine experimentally the thermal-dependence of the specific components of handling time and food choice of *Gammarus*, a key omnivorous ectotherm in aquatic ecosystems. Infection with parasites is known to influence the feeding preferences of *Gammarus* (Bunke et al., 2015) and the rate at which they process food material (Labaude et al., 2016). Given parasites’ ubiquity and ecological importance in ecosystems globally (Poulin and Jorge, 2018), I examined whether, and how, (1) temperature and parasitism, in isolation or in combination, influence the various components of handling time and / or feeding preferences of *Gammarus* and (2) predatory and scavenging behaviour are moderated similarly by temperature and / or parasitic infection.

To address these questions, I utilize an established model system, the amphipod *G. duebeni celticus* and its acanthocephalan parasite *P. minutus*. *G. duebeni* is a dominant benthic macroinvertebrate in many freshwater ecosystems (Mortensen, 1982; Kelly et al., 2006), as it plays an important role in ecosystem functioning (MacNeil et al., 1997; Sutcliffe, 2000). The parasite *P. minutus* is relatively well-studied (Dezfuli and Giari, 1999; Bailly et al., 2017), and the cystacanth-stage larvae of the parasite is a known manipulator of host behaviour (Jacquin et al., 2014), is easily identified in live hosts, and is common across Europe and North America (VanCleave and Rausch, 1951).

4.3 METHOD

4.3.1 *Organism collection and preparation*

Adult *G. duebeni* used in the experiment were collected from Lough Lene, Co. Westmeath, Ireland (53°39’37.1"N 7°11’41.1"W) along with juvenile *G. duebeni* individuals that were used as potential prey. *Asellus aquaticus* were collected simultaneously from nearby Lough Ennell, Co. Westmeath, Ireland (53°28’13.2"N 7°23’00.2"W). *P. minutus*-infected and uninfected adult *G. duebeni* were placed in individual housings and maintained at 15°C with a 12h:12h light:dark cycle. For

all trials, *G. duebeni* were acclimated to the experimental temperatures with 3°C temperature changes per day (Penk et al., 2016).

Three items were selected for feeding preference trials. Alder leaves (*Alnus glutinosa*) were selected due to the demonstrated preference of amphipods for alder leaves over other leaf types (Agatz and Brown 2014) as well as their use in standard methodologies (Little and Altermatt, 2018). Alder leaves were cut into 0.7 mm discs and conditioned for 72 hours in Lough Lene water to improve palatability. *A. aquaticus* were selected as a potential prey item, as it has been shown that isopods are important prey for amphipods in lake ecosystems (MacNeil et al., 1997). Finally, juvenile amphipods were presented as a food item, as cannibalism is known to be commonplace in gammarid amphipods (Dick et al., 1993). Potential prey items — *A. aquaticus* and juvenile *G. duebeni* — were weighed individually before being presented live for predation trials. For scavenging trials, prey items were euthanized by freezing and were defrosted fully before use.

4.3.2 Trial apparatus

Trials were conducted in a purpose-built experimental chamber (Fig. 4.1). The main body of the chamber is a petri dish, which was darkened with a black marker on the outside of the dish in order to reduce the stress of the experimental animals. In the centre of the dish, a “pizza saver” was used to provide a refuge. This refuge allows the experimental individual to hide, in order to separate leaf-feeding behaviour from the tendency of the animals to use leaves as a refuge. From each of the three points of the pizza saver, a glass slide cover was used to divide the petri dish into three areas, each of which the adult *G. duebeni* could access. For trials, one of the three potential prey items was placed in each chamber. Observations confirmed that prey items did not leave their chamber or interact with the other prey options. Water in the dish was changed between trials and the location of each prey item was varied haphazardly among trials.

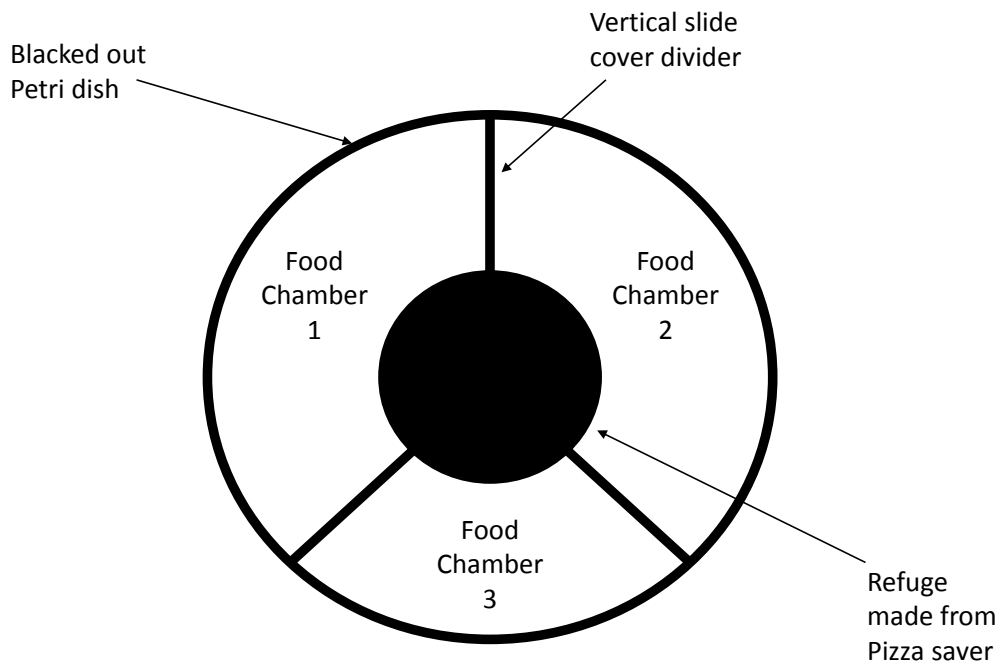


FIGURE 4.1: The design of the three chamber apparatus for *G. duebeni* feeding preference trials with the refuge in the centre.

4.3.3 Experimental design

Trials were run at 3°C intervals for temperatures between 6°C and 21°C, as this encompasses both the majority of the typical temperature range of lakes in Ireland and includes a temperature based on future climate change scenarios in Irish lakes (21°C; IPCC (2014)). Adult mortality at temperatures exceeding 21°C was greater than 50% and thus we limited trials to a maximum of 21°C. Gammarids were exposed to temperatures randomly, and within temperatures amphipods were haphazardly selected for trial orders.

Adult *G. duebeni* were allowed five minutes to acclimate to the experimental housing, which was filled with clean, oxygenated water at the same temperature as the animals' housing. After acclimation, the amphipod was encouraged into the hide, and then presented with a leaf disc, juvenile *G. duebeni* and *A. aquaticus* in each of the three food chambers. The latter two organisms were presented live in predation trials and dead in scavenging trials. The identity and time of the adult's first touch of a prey item, the time and item of first capture, where the adult grasped hold of a prey item, and the time and item of the adult's first bite were all recorded. Trials ended after 10 minutes of observation. The time taken for an adult to touch an item was

characterized as the pursuit time, the time between touch and capture as capture time, and the time between capture and first bite as subjugation time.

Following trials, adult *G. duebeni* were weighed and dissected to ensure infection status as per methods in Chapter 2. For all analyses, only adult *G. duebeni* infected with single cystacanth-stage infections of *P. minutus* were included in analyses as infected and only *G. duebeni* adults with no acanthocephalan infection were included as uninfected.

4.3.4 Data analyses

The time predators spent in pursuit, time it took for predators to capture prey, and time predators spent subjugating prey were analysed using generalized linear mixed models (GLMMs) with Gamma distributions and an inverse link using lme4::glmer (Bates et al., 2015). In these analyses, time (in seconds) was the response variable, gammarid individual was a random effect, temperature, infection status, and feeding mode (i.e. availability of live or dead prey) were fixed effects. All possible interaction terms were included in initial analyses. The items touched, captured, and bitten were analysed as GLMMs using MCMCglmm (Hadfield, 2010) with multinomial distributions. For each of these analyses, temperature, infection status, and prey status were fixed effects, gammarid individual was random, and prey item (i.e. juvenile *G. duebeni*, *A. aquaticus*, leaf, no response) was the response variable. The proportion of adults eating, defined as whether or not an adult bit an item, was analysed using a GLMM with a binomial distribution modelled with the lme4 package. In these analyses, whether or not the individual ate was a binary response variable, gammarid individual was random, and infection status, prey status, and temperature were fixed effects. Finally, the number of adult *G. duebeni* that switched items between initial touching and biting was analysed with a GLMM with a binomial distribution with lme4::glmer and gammarid individual as a random effect, and with infection status, prey status, and temperature as fixed effects. All data analyses were performed in R version 3.4.1 (R Core Team, 2017).

4.4 RESULTS

The effect of temperature on the likelihood of *G. duebeni* feeding varied depending upon the status of their prey (i.e. there was a significant interaction between temperature and whether their potential prey were dead or alive; Table 4.1a; Fig. 4.2). The

likelihood of feeding increased significantly with temperature when available prey were dead, whereas temperature had no effect on the likelihood of feeding when live prey items were present (Fig. 4.2).

TABLE 4.1: Effects of temperature, infection and prey status on *G. duebeni* feeding behaviour. Significant ($P < 0.05$) effects are highlighted in bold.

Response		Temperature		Infection		Prey Status		Temp× Infection		Temp Prey Status		Infection× PreyStatus		Temp×Infection ×Prey Status	
		<i>t/z</i>	<i>p</i>	<i>t/z</i>	<i>p</i>	<i>t/z</i>	<i>p</i>	<i>t/z</i>	<i>p</i>	<i>t/z</i>	<i>p</i>	<i>t/z</i>	<i>p</i>	<i>t/z</i>	<i>p</i>
a	Number Eating	4.61	<0.01	-1.20	0.26	0.34	0.73	-0.93	0.35	-2.53	0.01	0.62	0.54	0.89	0.38
b	Pursuit Time	2.08	0.04	-0.90	0.37	-0.48	0.63	0.69	0.49	-0.44	0.66	1.36	0.17	-0.63	0.53
c	Capture Time	0.40	0.53	0.01	0.93	8.91	<0.01	2.11	0.15	0.13	0.72	1.77	0.18	6.32	0.01
d	Subjugation Time	<0.01	0.99	0.22	0.64	4.08	0.04	0.22	0.64	0.07	0.80	0.05	0.82	0.22	0.64
e	Pursuit Item		0.40		0.17		0.20		0.20		0.47		0.72		0.44
f	Capture Item		0.49		0.12		<0.01		0.26		0.56		0.49		0.44
g	Subjugation Item		0.60		0.18		<0.01		0.31		0.59		0.94		0.80
h	Switch Item	-0.38	0.70	1.53	0.13	-2.70	<0.01	-1.50	0.13	0.12	0.90	-1.13	0.26	1.36	0.17

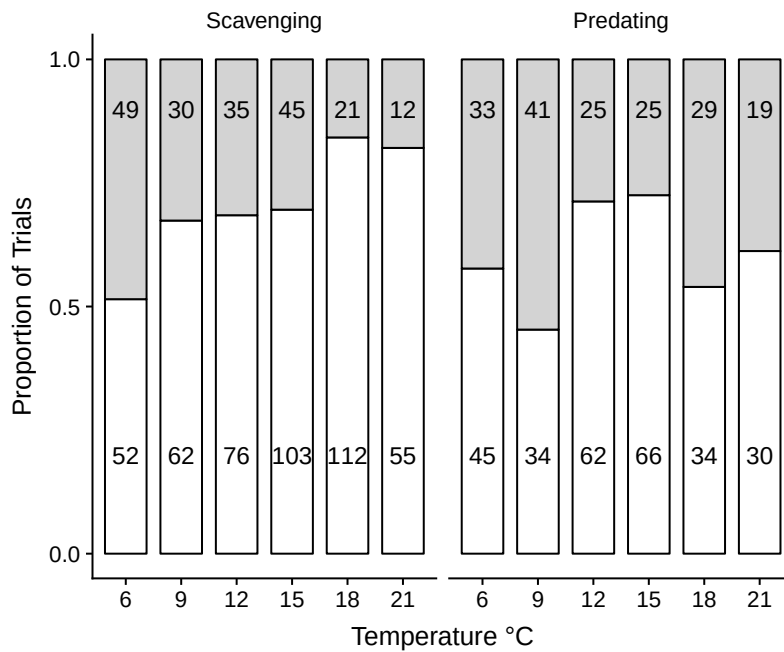


FIGURE 4.2: Proportion of trials at each temperature where *G. duebeni* individuals ate (white) or did not eat (grey) when amphipods were pursuing dead (scavenging) and live prey (predating).

4.4.1 Components of handling time

The specific components of handling time varied significantly in their response to temperature and prey status (Table 4.1b-d). Temperature was the only driver of amphipod pursuit time (Table 4.1b; Fig. 4.3a), with pursuit times decreasing as temperatures increased regardless of the prey being pursued (Fig. 4.3a). Time to capture prey was determined by a three-way interaction among temperature, parasitic infection, and potential prey status (Table 4.1c; Fig. 4.3b). Parasitic infection increased capture times when amphipods were actively predating and at lower temperatures when amphipods were scavenging, though the effect of parasitic infection was not seen when adults were scavenging at higher temperatures (Fig. 4.3b). In contrast, temperature had no effect on the time adults spent subjugating their prey (Table 4.1d; Fig. 4.3c). There was, however, a significant difference in subjugation time between when potential prey was alive or dead, with the amphipods spending significantly longer subjugating live compared with dead prey (Table 4.1d; Fig. 4.3c). Parasitic infection had no effect on pursuit or subjugation times of the amphipods used in the experiment (Table 4.1).

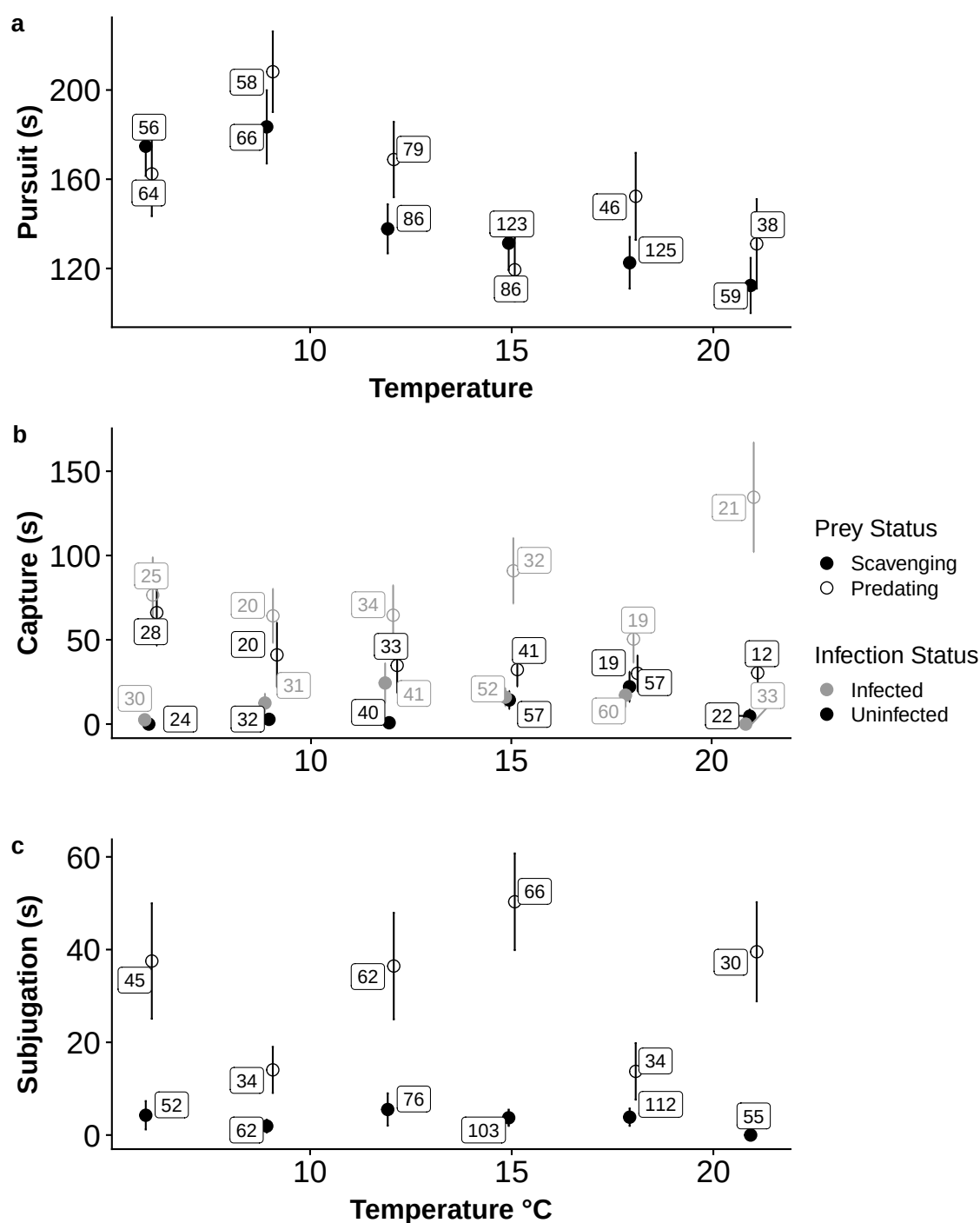


FIGURE 4.3: Thermal dependence of individual components of handling time when potential prey were either alive (predating) or dead (scavenging). (a) Pursuit time, (b) time to capture, and (c) time to subjugation. All times are shown in seconds and points are mean $\pm$ S.E. Labels indicate the number of samples in each datapoint.

4.4.2 Feeding preferences

Amphipods did not show a preference for any of the available food items during their initial pursuit, regardless of host infection, temperature, or whether potential prey was alive or dead (Table 4.1e; Fig. 4.4a). However, the status of their potential prey

as dead or alive determined its likelihood of capture (Table 4.1f; Fig. 4.4b). When only dead or inactive prey were available, adults were equally likely to capture and subjugate any of the food items present. However, when predation was possible, amphipods were significantly more likely to capture and subjugate leaf matter than either of potential live prey available (Table 4.1f,g; Fig. 4.4). Finally, the proportion of individuals switching prey items between initial pursuit and actual capture was also influenced by the status of the potential prey, with significantly more adults switching items when potential prey were alive than when they were not (Table 4.1f). The majority of amphipods presented with live prey switched from initially pursuing isopods or juveniles before capturing and subjugating leaf material. Neither temperature nor parasitic infection had any effect on choice of prey.

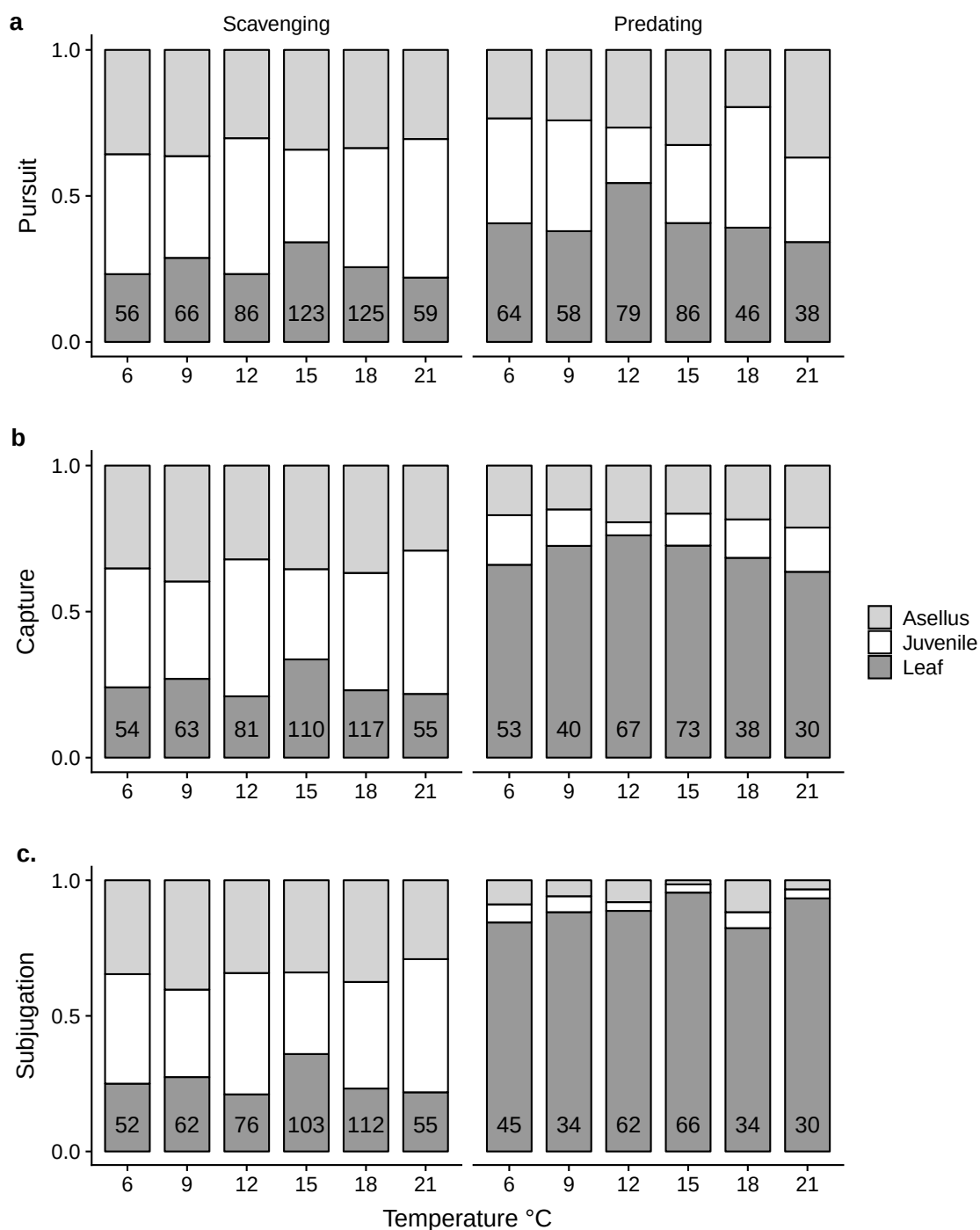


FIGURE 4.4: Proportional predator preferences while potential prey items were alive (predating) or dead (scavenging). The proportion of times each potential prey item was initially (a) pursued, (b) captured, and (c) subjugated by amphipod individuals. Numbers within bars are the number of individual trials represented by each bar.

4.5 DISCUSSION

My results demonstrate clearly that the various components of handling time differ significantly in their responses to temperature and, moreover, that these patterns can vary depending upon whether potential prey were alive or dead. In con-

trast, food choice was not influenced by temperature, though amphipods generally avoided capturing and subjugating moving prey at all temperatures, while infection with behaviour-manipulating parasites had a somewhat surprisingly minor influence on handling time. These findings highlight the significant challenges associated with predicting how predator-prey interactions, and thus the stability of ecosystems, will change as the global climate warms.

Handling time is often quantified effectively as a one-dimensional process (Jeschke et al., 2002). My results, in concert with previous studies (Jeschke et al., 2002; Sentis et al., 2013), challenge the assumptions made when grouping multiple behaviours, with different regulating factors, into a single metric (Englund et al., 2011; Sentis et al., 2013). By parsing handling time into its constituent components, I show that pursuit, capture, and subjugation do not respond uniformly to warming. The presence of mobile live prey led to significantly longer capture and subjugation times compared to when they were dead or inactive. When prey were sessile, time in pursuit was faster at higher temperatures. However, in the presence of active potential prey, pursuit times were not affected by temperature, at least across the range of temperatures I examined. This is likely due to asymmetries in the performance of the comparably larger predators and their smaller prey (Dell et al., 2014).

The thermal responses of an organism can vary significantly among its physiological and ecological traits (Dell et al., 2011). The thermal dependence of the propensity of gammarid amphipods to feed differed in the presence of live and mobile potential prey compared to dead, sessile prey. When prey were sessile and predators were scavenging, the proportion of *Gammarus* that were feeding increased with temperature, as would be expected with increasing metabolic rates (Brown et al., 2004; Schmidlin et al., 2015; Labaude et al., 2016). In contrast, temperature did not affect the propensity to feed in the presence of motile prey. The dynamics of predators and their prey often do not scale linearly when both species are mobile (Dell et al., 2014) and, though I did expect to find a difference between the temperature dependence of handling time components when prey were motile compared to when they were sessile, I found no interactions between temperature and prey status in any of the components of handling time we examined.

Prior work on ectotherms from arctic ecosystems has found thresholds in the feeding behaviour of some predators, where they would not attack below specific temperatures (Ohlund et al., 2015). I found no evidence of the existence of such

thresholds, possibly due to the fact that this study focused on organisms from seasonal temperate ecosystems. Nonetheless, these results highlight the difficulties associated with predicting the effects of warming on predator-prey dynamics, particularly as the effects of temperature are context-specific and exhibit considerable variation across systems (Englund et al., 2011; Ohlund et al., 2015).

Gammarids did not display a preference for the item they first pursued, and were equally likely to initially pursue juvenile conspecifics, other invertebrate prey, or leaf matter. However, capture and subjugation of live prey proved difficult, with gammarids showing a strong preference across all temperatures to capture and subjugate leaf matter in the presence of mobile prey. Many gammarids initially pursued live prey items before actually capturing and biting the leaf matter presented. This contributed to the increased times to capture in the treatments that included active prey. Research on preferences of aquatic macroinvertebrates in the field has found higher selectivity of some animals at higher temperatures, though the trend is species-specific (Boersma et al., 2016; O’Gorman et al., 2016). The gammarids in my study did not, however, demonstrate a shift in preference at higher temperatures, and are consistent with the overall classification of gammarid amphipods primarily as shredders (Cummins and Klug, 1979; MacNeil et al., 1997), with a secondary role as omnivorous scavengers.

Surprisingly, the only component of feeding behaviour in my study that was influenced by infection with *P. minutus* parasites was capture time. As previous work has found that parasitic infection can impact host functional response curves (Toscano et al., 2014) and host feeding preferences (Bunke et al., 2015), I expected to find a significant role of parasitic infection in most of the response variables we examined. However, the role of parasites in the handling time of hosts was limited to generally increasing capture time, suggesting that the impact of infection with larval acanthocephalans is quite specific. Host-parasite interactions can exhibit a high level of specificity (Hynes and Nicholas, 1958; Zittel et al., 2018), and further experimental work exploring the generality of the impact of parasites on handling time and feeding preference is needed. Additional tracking studies on parasitised and non-parasitised omnivores would help determine the specificity of these findings. Functional feeding curves constructed with the potential prey items used in this study could also reveal the generality of the conclusions.

Temperature plays an important role in the feeding behaviour of many ectothermic species and, as animals attempt to cope with increasing temperatures, there

are a number of ways organisms can mediate the impact of temperature by altering their behaviour (Barnes et al., 2015; Vander Vorste et al., 2017). Moreover, the response of organisms to warming is both behaviour- and species-specific (Dell et al., 2011; Englund et al., 2011; Ohlund et al., 2015; Kenna et al., 2017). Even though gammarid amphipods are globally distributed (Karaman and Pinkster, 1977) and ecologically important (Little and Altermatt, 2018), our study was limited to a single model system. Nonetheless, by splitting feeding behaviour into its individual components, our findings demonstrate how the specific components of handling time exhibit different thermal dependencies and drivers. Temperature, potential prey status, and parasitic infection impacted specific feeding behaviours, but frequently not additively. As climate warms, increasing temperatures have the potential to alter predator-prey dynamics significantly, and our findings highlight the need to consider the multiple distinct components of predator-prey interactions when predicting shifts in energy flow and ecosystem stability under climate warming.

CHAPTER 5

INDIVIDUAL AND COMBINED EFFECTS OF WARMING, INTRASPECIFIC COMPETITION AND PARASITIC INFECTION ON DETRITUS PROCESSING RATES IN SITU.

5.1 SUMMARY

One of the greatest challenges facing ecologists is how to detect and predict the impact of parasites on their hosts in warming ecosystems as hosts face biotic pressures. Here, I examine the individual and combined effects of warming, intraspecific competition and parasitic infection on feeding behaviour of an important aquatic ectotherm, *G. duebeni*, in the field. I found that *per capita* rates of detritus processing by *G. duebeni* decreased with population density. In addition, high *per capita* processing rates at low densities enabled a few individuals to process as much leaf litter as groups of up to ten-fold greater densities. Further, both moderate warming (2°C) and infection with acanthocephalan parasites increased survival rates of *G. duebeni*. The increased survival of infected hosts *in situ* should be considered in future attempts to analyse the transmission rates of larval acanthocephalans, particularly as the behavioural changes associated with these parasites may counterbalance the increased survival. Overall, these results demonstrate the important, and often underappreciated, roles of intraspecific competition and parasitic infection in moderating ecosystem functioning and highlight the need for their inclusion in models predicting the consequences of global environmental change.

5.2 INTRODUCTION

Global climate change is expected to have significant impacts on the structure and function of aquatic ecosystems (Carpenter et al., 2011; O’Gorman et al., 2012). As the climate warms, the nature and strength of biotic interactions are likely to change. Intraspecific competition is a particularly important determinant of the overall functioning and stability of ecosystems (Barabas et al., 2016), and of the persistence of species in variable climates (Pilfold et al., 2014; Stenseth et al., 2015).

Though there is some theoretical understanding of how temperature could moderate intraspecific competition (Amarasekare and Coutinho, 2014), empirical evidence is lacking. Metabolic scaling theory suggests that greater activity levels at higher temperatures should increase *per capita* acquisition of resources, and thus reduce carrying capacity (Savage et al., 2004). Alternatively, intraspecific competition may be greatest at the thermal optimum for reproduction due to a peak in demand for resources. Empirical quantification of the individual and combined influence of intraspecific competition and temperature on the species' functioning is needed to improve the predictive power of theoretical models and support more robust management of vulnerable ecosystems.

Parasites play keystone roles in ecosystems (Hatcher et al., 2008), and influence the intensity of both intra- and interspecific competition (Yan and Stevens, 1995; MacNeil et al., 2003). The close coevolution of parasites and their hosts places parasites at particular risk to stress from climate change (Carlson et al., 2017). Increasing temperatures have, therefore, the potential to decouple host-parasite relationships (Goedknecht et al., 2015; Strepparova et al., 2017). However, the influence of climate warming on host-parasite relationships under differential levels of intraspecific competition has not yet been examined.

Here, I examine whether warming and parasitic infection interact to moderate the density dependence of a key ecosystem function in aquatic ecosystems, the rate of detritivory. I tested this in the field using the model host-parasite system of *G. duebeni* and its acanthocephalan parasite *P. minutus*. I used thermal effluents from a power plant to provide *in situ* warming. Though many detritivorous species contribute to overall leaf litter breakdown in aquatic ecosystems (Tonin et al., 2018), amphipods in particular dominate many benthic macroinvertebrate assemblages and contribute significantly to detritus processing (Kenna et al., 2017; Little and Altermatt, 2018). *Gammarus* species are ectothermic amphipods that are widespread geographically and account for up to three quarters of leaf litter degradation in European freshwater systems (Piscart et al., 2011). *Gammarus duebeni* var. *celticus* is the most abundant amphipod in Irish lakes and rivers (Reid, 1938), acting as an omnivorous shredder and a valuable food source to higher trophic levels (Kelly et al., 2002). Gammarid amphipods are a particularly suitable model for the questions we seek to address, as infection with parasites has been shown to alter the feeding rates of gammarid species in laboratory experiments in the literature (Bunke et al., 2015; Labaude et al., 2016; Lavery et al., 2017) and

in this thesis (Chapter 4). Moreover, the larval cystacanth of *P. minutus* is found frequently in amphipods in many Irish waters (Chapter 1), and this infective stage reduces the fecundity of its hosts and alters their behaviour (Bailly et al., 2017).

Thermal effluents are an often overlooked source of increased temperatures for warming experiments in natural communities in the field. Power plants often intake water from sources near their location and dispel warmed coolant water into local water systems, where the alteration in temperature creates microclimates within larger water bodies (Aho et al., 1982; Höglund and Thulin, 1990), providing realistic complex systems for the study of climate warming effects (Raptis et al., 2016).

I hypothesized that warming would cancel out any reductions in shredding rates caused by infection (Labaude et al., 2016), and group size would significantly reduce per capita shredding rates due to increased intra-specific competition at high density (Vander Vorste et al., 2017).

5.3 METHOD

5.3.1 *Study site*

The Lough Ree power station in Lanesborough, Co. Longford (53°40'29.8"N, 7°59'30.3"W), has been discharging warmed effluent water into the River Shannon since 1958. The thermal effluent is raised up to 10°C above ambient conditions. We utilized two 100 m reaches (Fig. 5.1) within the River Shannon as experimental locations, with the thermal effluent entering one reach but not the other. The two reaches are separated by a barrier island that prevents water mixing. The reaches are ideal for temperature-based experiments, as the warmed (effluent) reach has similar characteristics to those in the main river. The average dissolved oxygen in the main channel was 8.87 ± 0.23 (mean $\pm$ SD) and 7.57 ± 0.06 . Depth in the main channel experimental area averages $93 \text{ cm} \pm 28.6 \text{ cm}$ and $89.4 \text{ cm} \pm 21 \text{ cm}$. Velocity in the ambient reach averaged 0.25 ± 0.12 cubic meters per second and 0.22 ± 0.11 cubic meters per second in the warmed reach.

5.3.2 *Experiments*

I used Onset UA002 HOBO temperature loggers to track water temperature every 10 minutes within the experimental reaches. Because river flows modified the temperature differential between the warmed and ambient reaches (Fig. 5.2a), I ran

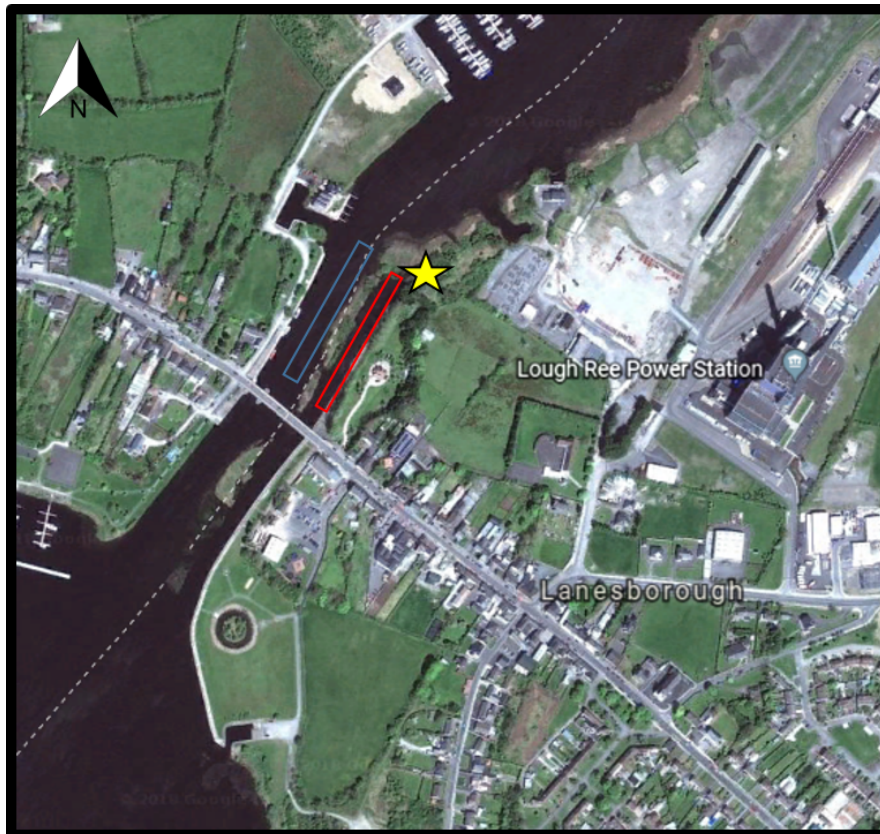


FIGURE 5.1: The location of the warmed (red) and ambient (blue) reaches used in my experiments. The Lough Ree power station thermal discharge is indicated with a yellow star.

my experiment twice: once during high flows in October 2017 (Winter Experiment) and then again during low flows in June 2018 (Summer Experiment). In winter, high water levels, with flow rates in the top 5% of flow rates measured annually, diluted the thermal effluent more than anticipated (Office of Public Works, 2018). The high flows reduced the temperature differential between the heated and ambient reaches, though a temperature differential of between 0 and 2.4°C was recorded (Fig. 5.2a,b). During summer, high air temperatures and very low rainfall generated high ambient water temperatures (Fig. 5.2a). As the warmed treatment is heated above ambient temperatures, the heated treatment reached temperatures in excess of 30°C in summer, with the temperature differential between ambient and heated reaches exceeding 8°C (Fig. 5.2b).

Amphipods used in the experiments were collected from Lough Lene (53°39'37.6"N 7°11'41.7"W) in October 2017 and June 2018. Only adult amphipods were used in experimental trials. I quantified rates of *Gammarus* detritivory using leaf litter decomposition bags (Benfield, 2006). These were constructed using double-layered mesh (20 cm×30 cm, aperture 1 mm), each containing 7 g of dried horse chestnut (*Aesculus hippocastanum*) leaves (Agatz and Brown, 2014). Horse chestnut leaves were selected due to the abundance of horse chestnut trees near the site and the known palatability of horse chestnut leaves to amphipods (Agatz and Brown, 2014). Background rates of microbial decomposition were quantified using 0.5 g of dried horse chestnut leaves placed within a smaller double-layered, sealed mesh bag that was inaccessible to amphipods. Litter bags were conditioned in aerated lake water for 24 hours to increase palatability (Graça et al., 1993; Agatz and Brown, 2014), after which amphipods were added to the larger bags in numbers appropriate to experimental treatments. There were three levels of amphipod density: 10 individuals (low density), 25 individuals (intermediate density), and 100 individuals (high density). As there were insufficient numbers of infected gammarids to explore the effects of parasitic infection at the highest level of *Gammarus* density, parasite infection was crossed with just two levels of amphipod density (i.e. low and intermediate density). Each experimental treatment combination was replicated five times.

Decomposition bags were placed in the river attached to cinderblocks to maintain their position at the experimental site. The bags were deployed over four weeks in winter (16 November 2018 - 14 December 2018) and three weeks in summer (4 July 2018 - 25 July 2018). I shortened the duration of the Summer Experiment

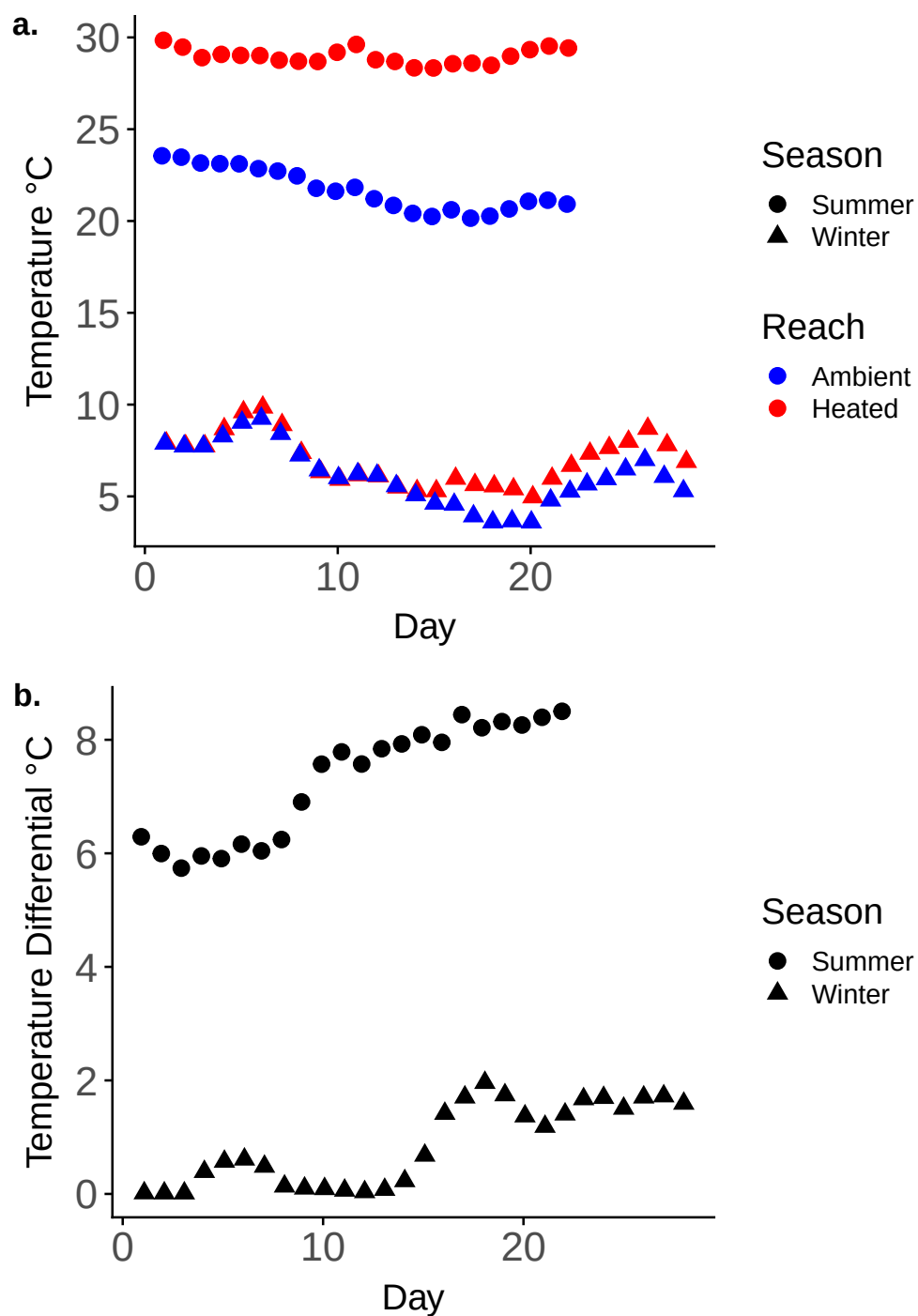


FIGURE 5.2: Temperature (a) and temperature differential (b) of warmed and ambient reaches during the two experimental runs. Day refers to day number within the experimental run.

due to high rates of mortality, which resulted in the death of all amphipods in the experimentally warmed reach. At the end of the experiments, bags were returned to the laboratory and leaf litter, gammarid amphipods, and control bags were separated from each other. Leaves were dried at 60°C for 48 hours and weighed. All *G. duebeni* individuals used in the experiment were dissected to confirm infection status. Larval cystacanths were dissected out of hosts and placed in a 0.25 mM solution of sodium taurocholate. Cystacanths were incubated in the sodium taurocholate at 37°C for 12 hours to encourage the extrusion of the hooked proboscis. Cystacanths were examined microscopically to confirm their identity, following McDonald (1988).

The absolute mass of leaf litter decomposed was calculated as the difference between the dry mass of leaves before and after the experiment. This was then standardized to account for microbial degradation and leaching, the two major sources of leaf litter loss not due to shredding (Cummins and Klug, 1979), using the small bag controls which were included within each replicate bag. A microbial degradation factor was determined for each bag as the difference between the dry weights of the small bag leaves before and after the experiment as a proportion of the initial dry weight of the small bag leaves. The corrected amount of leaves shredded was the change in leaf weight minus the product of the initial leaf weight and the microbial degradation factor (Benfield, 2006). The corrected shredding amount was then divided by the mean number of *G. duebeni* in the bag over time and the number of days the bag was immersed *in situ*. I therefore quantified three main response variables: the shredding rate per individual amphipod per day (after accounting for microbial degradation), the absolute shredding rate (after accounting for microbial degradation), and the survival rate of amphipods.

5.3.3 Data analyses

All data analyses were done using R (R Core Team, 2017). Within the Winter Experiment, I used linear models to determine how temperature, parasitic infection, and intraspecific competition separately and collectively influence the overall shredding and survival rates of gammarids. The *per capita* shredding rate during the Winter was analysed using a generalized linear model with a Gamma distribution and an inverse link function to account for non-normality of the data. Given the full mortality of gammarids in the warmed river reach, data from the summer experiment were omitted from these analyses. In addition, I explored whether the individual

and combined effects of density dependence and parasite infection on *Gammarus* detritivory and survival varied over the year within the ambient reach. I generated linear models for both the total amount shredded and survival and a generalized linear model with an inverse Gaussian distribution for *per capita* detritivory. Season (i.e. summer or winter) was incorporated as a fixed effect in these analyses.

5.4 RESULTS

Even though the total amount of leaf litter processed did not vary with the density of *G. duebeni*, warming, or infection (Table 5.1, Fig. 5.3a), *per capita* shredding rates varied significantly with *Gammarus* density (Table 5.1), with the highest rates of individual shredding in lowest density groups (Fig. 5.3b). Neither infection with *P. minutus* nor warming influenced shredding rates, and there were no interactions between group size, warming, and infection status, indicating that warming and infection did not modify the density-dependence of feeding rates (Table 5.1, Fig. 5.3b).

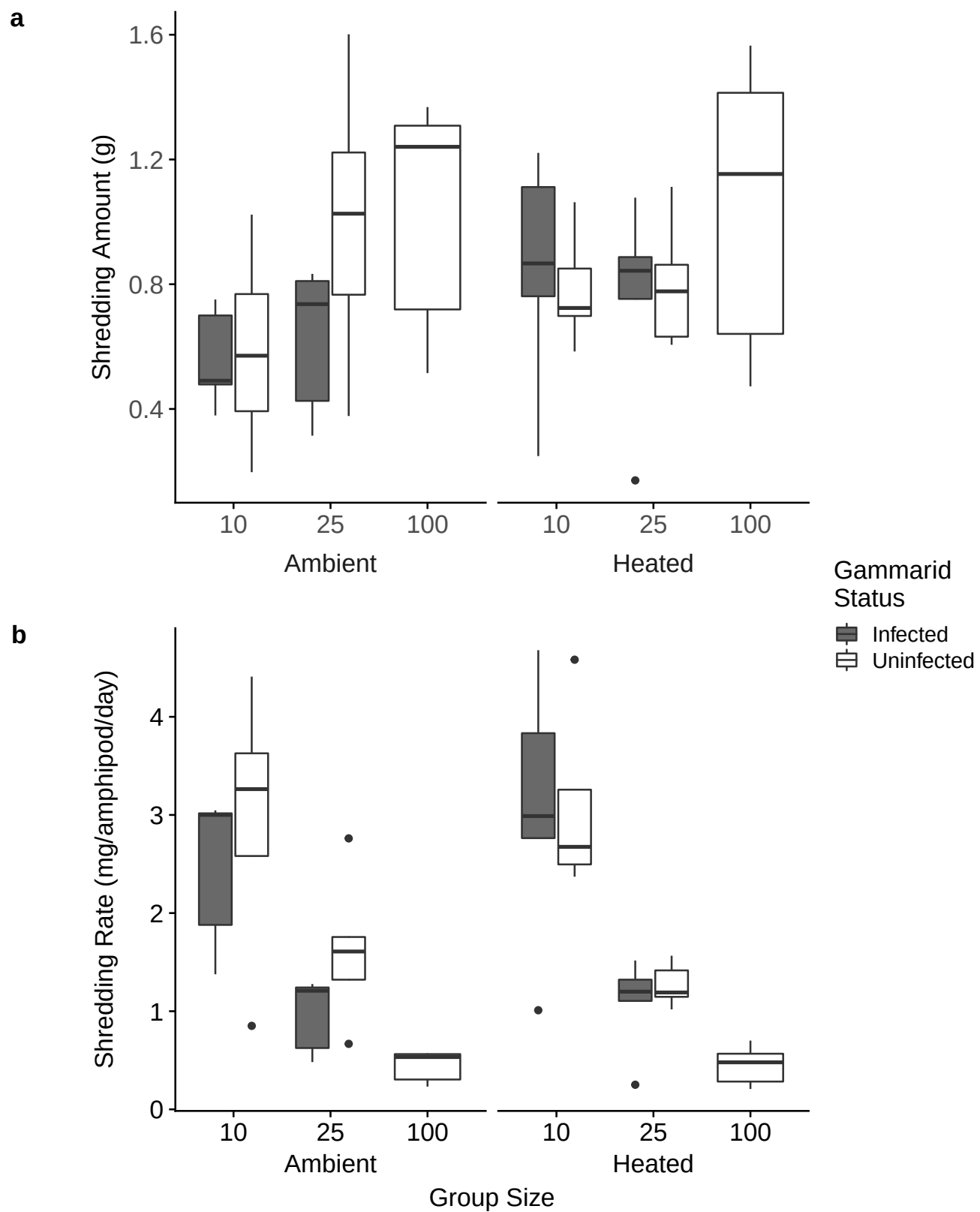


FIGURE 5.3: The total amount shredded (a) and *per capita* shredding rates (b) at each *Gammarus* density (10, 25 and 100 individuals) are shown for infected and uninfected individuals.

TABLE 5.1: Individual and combined effects of group size, parasite infection and warming on rates of detritivory and survival of *G. duebeni*. Statistically significant effects are shown in bold.

Response variable	Density		Infection		Warming		Density× Infection		Infection× Warming		Warming× Density		Warming× Infection × Density	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Daily shredding per capita	64.19	0.00	2.32	0.14	0.16	0.69	2.55	0.12	0.81	0.37	0.25	0.78	0.43	0.52
Shredding total amount	3.86	0.06	1.97	0.15	0.66	0.42	1.05	0.31	1.11	0.30	0.81	0.45	0.30	0.59
Survival	2.07	0.16	5.11	0.03	10.26	0.00	0.05	0.82	0.04	0.84	3.92	0.06	0.30	0.59

TABLE 5.2: Results of analysis of interannual variation in rates of shredding and survival of *G. duebeni*. Statistically significant effects are shown in bold.

Response variable	Density		Season		Infection		Density× Infection		Infection × Season		Season× Density		Season× Infection × Density	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Daily shredding per capita	30.53	<0.01	0.28	0.6	2.36	0.13	0.82	0.37	0.58	0.45	2.79	0.01	1.89	0.18
Shredding total amount	8.23	0.001	0.23	0.63	4.88	0.03	0.48	0.49	0.45	0.51	1.98	0.15	0.95	0.34
Survival	2.46	0.13	2.15	0.15	6.56	0.02	0.62	0.44	0.36	0.55	2.56	0.12	1.14	0.29

Both infection with *P. minutus* and warming increased survival rates of *Gammarus* significantly, though group size had no effect (Table 5.1, Fig. 5.4).

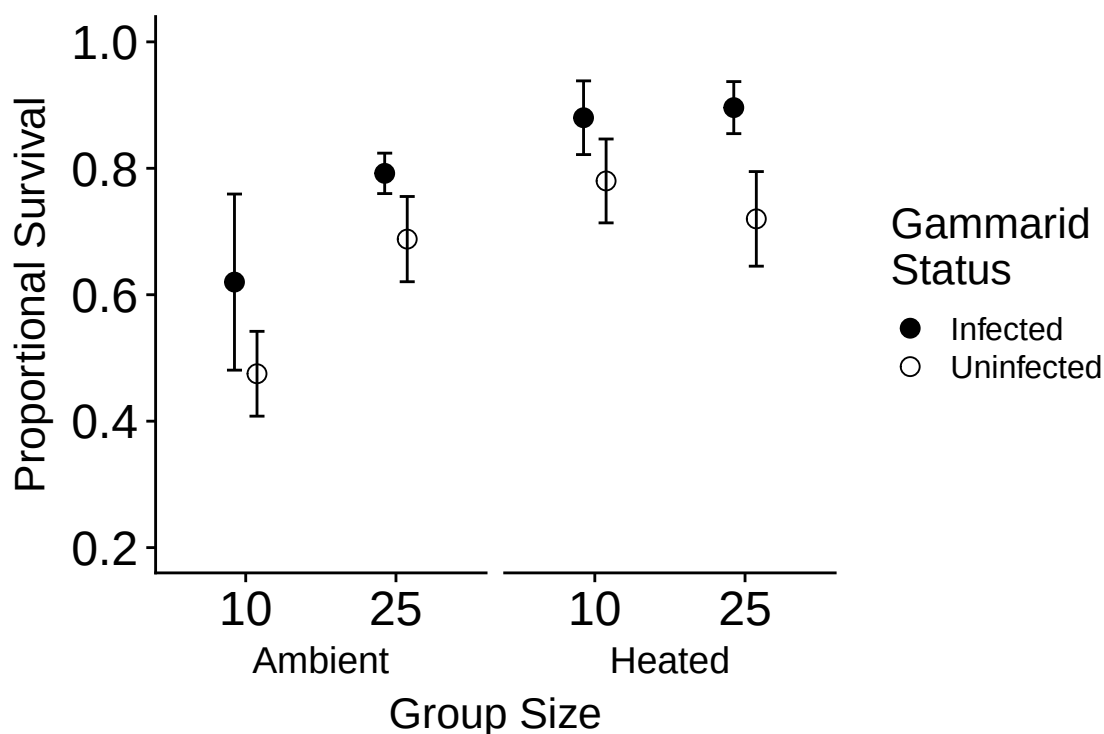


FIGURE 5.4: Proportion of infected and uninfected *G. duebeni* surviving in ambient and heated reaches at low (10 individuals) and intermediate (25 individuals) densities during the winter experiment.

The density dependence of *per capita* shredding rates varied significantly between the winter and summer experiments (Table 5.2), with a significantly stronger effect of *Gammarus* densities in winter (Fig. 5.5). This suggests that the key role of intraspecific competition on gammarid shredding rates varies over the year.

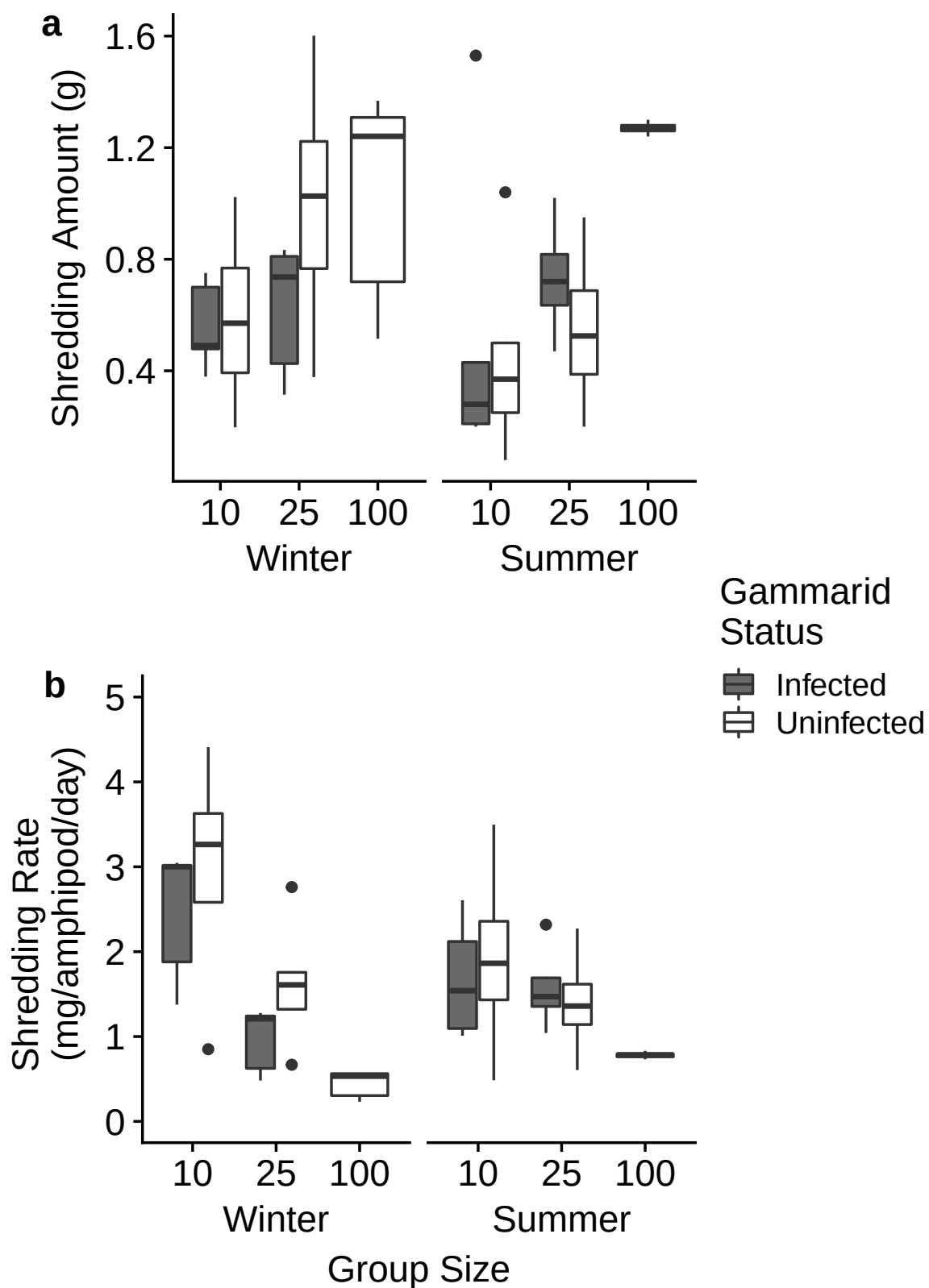


FIGURE 5.5: The total amount shredded (a) and *per capita* shredding rates (b) at each Gammarus density (10, 25, and, 100 amphipods) are shown for infected and uninfected individuals.

5.5 DISCUSSION

My results demonstrate the importance of intraspecific competition in moderating a key ecosystem function, rates of detritivory, in aquatic ecosystems. Moreover, these effects also appear to vary seasonally, being stronger in winter than in summer. Intraspecific competition for resources is a key driver of amphipod feeding behaviour even when food resources are relatively abundant, a finding which is in concurrence with laboratory studies on amphipod feeding behaviour (Mancinelli, 2012; Labaude et al., 2016; Vander Vorste et al., 2017). The sex, body size, mouthpart shape, physiology, and behaviour of amphipods have all been found to moderate shredding rates in the laboratory (Rota et al., 2018). Our findings indicate that the density-dependence of shredding rates should be considered in future estimates of amphipod leaf litter shredding. Given that allochthonous detritus contributes significantly to the overall carbon available in aquatic ecosystems (Wallace et al., 1997), these findings have important implications for energy transfer and food-web stability in aquatic ecosystems in general.

I found no effect of warming on rates of detritivory. Though this was an unexpected finding in light of previous research (Labaude et al., 2016; Pellan et al., 2016; Kenna et al., 2017; Lavery et al., 2017, Chapter 4), it may be a consequence of the relatively small temperature differential observed between the ambient and warmed reaches in winter. Nonetheless, temperatures in the warmed reach were approximately 2°C higher than ambient conditions over at least fifteen days towards the end of the experimental period. Given the results of my previous experiments, particularly those described in Chapters 2 and 4, such a temperature differential would have been expected to have caused some detectable shifts in gammarid feeding behaviour. Unfortunately, the attempt to examine the influence of warming in summer was confounded by exceedingly high temperatures in the heated reach which caused mortality of all experimental animals. I recommend that future work in this system should focus on experiments in the autumn and spring, when ambient temperatures are generally mild and temperature differentials will be higher than in winter.

High *per capita* shredding rates of *Gammarus* at low densities in winter enabled a few (10) individuals to process as much leaf litter as groups of up to ten-fold greater densities. Given the importance of shredders in low order aquatic ecosystems (Vannote et al., 1980), and the significant role of shredders in leaf litter

processing globally (Petersen and Cummins, 1974), these findings have important implications for overall ecosystem function and nutrient flow. Moreover, infection with *P. minutus* reduced the *per capita* shredding of amphipods when examined across seasons. Laboratory examination of the impact of acanthocephalan parasitism on the shredding rates of gammarid amphipods has found that infection either reduces (Agatz and Brown, 2014; Labaude et al., 2016) or does not affect shredding rates (Fielding et al., 2003, Chapter 2). These disparities are perhaps due to the varied temperatures at which these rates are measured and potential influences of the multiple source populations of hosts and parasites examined. The impact of acanthocephalans on the feeding behaviour of their hosts may also be species-specific and context-dependent.

I found that infection with *P. minutus* parasites increased survival of *G. duebeni* significantly. Some laboratory experiments have found higher mortality rates of amphipod hosts when infected with larval acanthocephalans (Brown and Pascoe, 1989; Labaude et al., 2015a), while others have found no effect on survival (Chen et al., 2015), or that acanthocephalan infection even confers some advantages to hosts, such as increased salinity tolerance (Piscart et al., 2007). Survival of the intermediate host is beneficial to *P. minutus*, which relies on the amphipod's survival for transmission, and it seems a complex and realistic environment provides the context in which parasitic infection confers a survival advantage.

Warming enhanced gammarid survival in winter, though the high levels of warming in summer caused 100% mortality in our experimental populations, likely due to increased metabolic demand (Galic and Forbes, 2017). Temperature within the warmed reach in winter was well within the annual range experienced by amphipods in their native range, which may explain the higher survival levels, as ambient temperatures at the time were close to their annual minimum.

As temperatures continue to increase, it is crucial for future management of economically and ecologically valuable ecosystems to understand how multiple stressors interact in realistic field studies (O'Gorman et al., 2014; Jackson et al., 2016). My results show that intraspecific competition was the key driver of shredding behaviour of ecologically important detritivores, a finding with implications for ecosystem functioning and for any future predictions of ecosystem structure and function.

6.1 THE IMPORTANCE OF PARASITES IN THE FUNCTIONING OF WARMING ECOSYSTEMS

One of the greatest challenges currently facing ecologists is the prediction and mitigation of climate change impacts on the stability and functioning of ecological communities (Holling, 1973; Walther et al., 2002; Donohue et al., 2013; Mouquet et al., 2015; Hewitt et al., 2016; Ullah et al., 2018). The factors that contribute to ecosystem functionality have been hotly debated (Grime, 1997), though many agree that ecosystem function is likely to be reduced by climate change through reductions in biodiversity (Traill et al., 2010). While numerous species face threats from changing climates (Thomas et al., 2004), parasites are particularly vulnerable to the impacts of global warming (Carlson et al., 2017), and alterations to the relationships between parasites and their hosts are expected as temperatures increase (Hoberg and Brooks, 2007). It has been suggested that parasites may play a greater role in ecosystem functioning than other groups (Hatcher et al., 2012), due to the critical roles that parasites play in the regulation of nutrient cycling and energy flow (Sato et al., 2012; Buck and Ripple, 2017; Vannatta and Minchella, 2018), in contributing to biodiversity and community composition (Wood et al., 2007; Grabner, 2017), and in the health and behaviour of their hosts (Cable et al., 2017). Changes in climate will impact host-parasite interactions, as seen in the interactive effects of temperature and parasites on host respiration (Chapter 2) and the time it took hosts to capture prey (Chapter 4), with potentially significant consequences for overall ecosystem function.

Recent estimates of ecosystem function have focused on ecosystem multifunctionality, the ability of ecosystems to provide multiple functions and services simultaneously (Manning et al., 2018). Though there is disagreement about the definition, measurement, and application of the ecosystem multifunctionality concept (Gamfeldt and Roger, 2017; Manning et al., 2018; Meyer et al., 2018), it is likely that multifunctional assessments of ecosystems could provide insight into the fundamental

drivers of ecosystem functioning by accounting for the impact of biotic communities on ecosystem-level functional processes (Manning et al., 2018) and by revealing the impacts of climate change on these processes (Traill et al., 2010). Much research has focused on biodiversity as a key driver of the multifunctionality of ecosystems (Gamfeldt and Roger, 2017; Meyer et al., 2018), though there remains a lack of data and insight into the contribution of individual species to multifunctionality. As parasites have multidimensional impacts on their hosts (Thomas et al., 2010; Cézilly et al., 2013), it is likely that the multiple consequences of parasitic infection have effects on many aspects of host, and potentially ecosystem, function. As shown in Chapter 2 and Chapter 3, increasing temperature acts additively with parasitic infection to alter host behaviour, increasing movement upwards in the water column and increasing the rates at which hosts dig into sediments. These findings have significant implications for the contribution of host organisms to ecosystem function, as this increased movement upwards in the water column increases their vulnerability to predation (Jacquin et al., 2014) with potential consequences for energy flows through ecosystems (Buck and Ripple, 2017). Additionally, increased host movement into benthic sediments has important consequences for nutrient flow and oxygenation levels of aquatic ecosystems (Baranov et al., 2016; Wohlgemuth et al., 2017). These multiple impacts of parasites on the multiple functions of hosts within ecosystems suggest likely alterations to ecosystem multifunctionality. Further work, at both the community and whole ecosystem level, to examine the generality of these findings will yield important insights into the role parasites play in maintaining ecosystem functioning in a warming world.

By thoroughly examining one model system, the acanthocephalan *P. minutus* and its intermediate host, *G. duebeni*, I am able to show that the drivers of host function within ecosystems are diverse and often specific to the function examined, whether it is the additive influence of parasitic infection and temperature on host bioturbation rates (Chapter 3) or the impact of intraspecific competition on host shredding rates (Chapter 5). However, there are limits to the generality of the findings presented in this thesis. The influence of temperature and *P. minutus* on behaviour of the host may vary among different intermediate hosts. For example, behavioural manipulations shown in Chapter 2 with *G. duebeni* as an intermediate host were not found in studies with the intermediate host *Gammarus fossarum* (Labaude et al., 2017). Recent work has suggested that parasites typically classified as *P. minutus* may actually be three cryptic species, each of which exhibits some

level of host specificity (Zittel et al., 2018), making generalisation across host range and across host species considerably more difficult. However, functionally similar behavioural manipulations have been shown to arise from different mechanisms, as similar changes in geotaxis and phototaxis of host amphipods have been linked to different mechanisms among different parasite species, with *P. minutus* likely causing changes by increasing anaerobic metabolites (Perrot-Minnot et al., 2016) and *Pomphorhynchus laevis* altering serotonin concentrations (Perrot-Minnot et al., 2014). While the mechanism of manipulation may differ among parasite species, the consequences for ecosystem functioning may be identical. Additionally, due to the fact that *P. minutus* utilizes avian definitive hosts, I was unable to either experimentally infect intermediate hosts or determine the consequences of infection on the function of the definitive host within these ecosystems. Finally, amphipods may not function identically across their native and invasive ranges, which has consequences for the generality of the findings described in this thesis (Little and Altermatt, 2018; Tonin et al., 2018). These limitations, however, are somewhat counterbalanced by the pervasiveness of *P. minutus* and *G. duebeni* in Irish ecosystems (Chapter 1) and the nearly global distribution of amphipods and acanthocephalans.

Throughout this thesis, I highlight the joint impacts of temperature and parasites on their hosts within the context of the ecosystems in which they are found, as each impacts specific components of host function. By integrating studies from the laboratory and the field into a single framework, I show that findings from the laboratory scale to the field and that *in situ* experimental systems may provide the most accurate estimates of the influence of temperature and parasites on host function. Focusing only on trophic or non-trophic components of interactions between hosts and parasites likely underestimates their impact on ecosystem function (Buck et al., 2018). The data presented here emphasize the need for a holistic approach to ecosystem-level ecology that is built upon a strong understanding of the populations that persist and the biotic interactions within ecosystems.

6.2 FUTURE PROSPECTS

6.2.1 *Community Dynamics*

Ecological communities are complex systems and the impacts of global climate change at the community level are likely to be both significant and difficult to predict (Kordas et al., 2011; Hewitt et al., 2016). Prior work has shown that variability in

a single species can have impacts on whole community responses to disturbance (McClellan et al., 2015; Mrowicki et al., 2016), suggesting that the joint effects of parasitism and warming on host populations described in this thesis may have broader consequences for community dynamics. As parasite ecology is increasingly informed by community ecology to predict the impacts of parasites outside of their host organisms (Johnson et al., 2015), the need for empirical data focused on the community-level impacts of parasites grows exponentially (Poulin, 2018).

P. minutus has a multi-host lifecycle, cycling between eggs in the environment, larvae in amphipods, and adult stages in water fowl. As such, *P. minutus* parasites have impacts on hosts across multiple trophic levels within the biological community, as well as potentially altering the competitive balances between species within the same guild (MacNeil et al., 2003). Multiple hosts and parasites interact to contribute to ecosystem multifunctionality, increasing the potential for the impacts of parasites on ecologically important hosts to be either magnified or reduced. The impact of parasites on host function can be altered by host-community dynamics. For example, the influence of parasites on the feeding ecology of predatory hosts can be altered by the presence of predators (Reisinger and Lodge, 2016) and competitors (Paterson et al., 2014). These community-level dynamics, particularly interspecific competition, have been shown to moderate the impact of parasites on their hosts and their ecosystems with consequences for ecosystem function (Kordas et al., 2011). Moreover, parasites also form communities within hosts, and studies on the parasite communities within hosts have shown influences of within-host parasite community dynamics on host functioning (Dezfuli et al., 2001; Hafer, 2016; Kirk et al., 2018). Mesocosm studies on the influence of warming and parasitic infection on community level dynamics are needed to help elucidate the relative importance of both temperature and parasites beyond their effects on host populations (Woodward et al., 2010). As it is comparably easy to alter overall numbers of parasites within amphipod communities while setting up mesocosms, future work with different levels of parasite prevalence within realistic communities could yield important insight into the impacts of parasitism on the function of hosts under intraspecific and interspecific competition.

Perhaps most importantly, parasites with complex life cycles, such as the acanthocephalans studied in this thesis, are likely to have impacts beyond those on their intermediate hosts (VanCleave and Rausch, 1951; Moenickes et al., 2011). Alterations in temperature, both in terms of absolute temperature and temperature

variability, may impact transmission rates, definitive host parasite burden, and the survival of eggs within the environment (Lenihan et al., 1999; Poulin, 2006; Gehman et al., 2018). Community-level studies that include all hosts and allow for multiple transmission cycles, though logistically difficult, could shed light on the broader influence of parasites in their ecosystems beyond a direct functional approach.

6.2.2 *Ecosystem Stability*

As parasites and temperature are important drivers of overall ecosystem function, they likely play a major role in moderating the stability of ecosystems (Lafferty et al., 2008; Jephcott et al., 2016). Ecosystem stability is a complex concept, though recent work has begun to recognize its multidimensional nature and unite its varied components into a logical framework (Pimm, 1984; Donohue et al., 2013, 2016; Hillebrand et al., 2018). Even with newly developed analytical and computational models, the specific role of parasites in overall ecosystem stability is difficult to elucidate and has been explored solely in a trophic context (Dunne et al., 2013). In theoretical models, host-parasite interactions are typically added directly to food webs, ignoring the differences between host-parasite and predator-prey relationships, though recent work has aimed to more comprehensively examine the impacts of parasites in a generalized consumer-resource framework (Lafferty et al., 2015). The incorporation of parasitic links into food webs has been shown to both increase and reduce the stability of the network (Wood and Johnson, 2015), highlighting the lack of general consensus on the impacts of parasites and the potential for additional empirical research to clarify the drivers of these stabilizing or destabilizing relationships. As shown in this thesis and in the literature (Perrot-Minnot et al., 2014), the impacts of parasites on their hosts are often multidimensional themselves. Future studies on the relative impacts of parasitic links on network connectance, network stability, and the strength of inter-specific interactions should consider the non-trophic, as well as the trophic impacts of parasites in their ecosystems. By comprehensively examining the role parasites play in the multiple components of ecosystem stability and coupling these results with the known impacts of parasites on ecosystem function, we will be able to develop more accurate predictions of the potential impacts of climate change on ecosystems.

6.3 CONCLUDING REMARKS

Throughout this thesis, I demonstrate the critical importance of parasites and temperature for the function of hosts and their populations. By integrating laboratory experiments and *in situ* studies, the specific and interactive drivers of host-parasite interactions become apparent. The generality of my conclusions based on the work presented in this thesis could be further elucidated through additional experimental work within multiple host-parasite systems, particularly in systems with functionally important microparasites, such as *Daphnia* spp. (Johnson et al., 2006; Kirk et al., 2018). While theoretical investigations have provided excellent insights into the influence of temperature on the relationships between parasites and their hosts (Barber et al., 2016; Cohen et al., 2017; Gehman et al., 2018), we require robust empirical evidence about the influence of temperature and parasites on host function before practical solutions for the maintenance of ecosystem function through changes in climate may be proposed (Rohr et al., 2011; Altizer et al., 2013). A mechanistic understanding of the potential impacts of temperature, including the work presented in this thesis, can be combined with predictive modelling and strong theoretical understanding of ecosystem-level ecology to manage and protect the parasites of the future with the aim of enhancing ecosystem health and stability.

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APPENDIX A

SUPPLEMENTARY INFORMATION TO CHAPTER 2

TABLE A.1: Linear and additive models of the influence of temperature, parasitic infection and host sex on host physiology. Significant terms are listed in bold.

Response Model	AIC	Temperature		Infection		Sex		Temperature × Infection (Infected)		Temperature × Infection (Uninfected)	
		F	<i>p</i>	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>
<i>Consumption</i>											
Additive Model	31.00	3.48	0.09	1.04	0.31	0.80	0.37	1.84	0.27	0.08	0.82
Linear Model	31.94	2.27	0.026	0.28	0.78	-0.87	0.39	5.40	0.85		
<i>Respiration</i>											
Additive Model	944.07	110.56	<0.01	0.51	0.02	<0.01	0.97	8.63	0.02	12.32	<0.01
Linear Model	944.07	5.89	<0.01	0.82	0.41	-0.04	0.97	0.28	0.78		
<i>Growth</i>											
Additive Model	-1435.75	2.22	0.24	0.35	0.56	4.17	0.04	0.39	0.61	0.13	0.77
Linear Model	-1434.66	-1.27	0.21	0.12	0.90	2.01	0.05	0.19	0.85		
<i>Efficiency</i>											
Additive Model	989.32	9.52	<0.01	1.03	0.31	0.00	0.99	0.92	0.44	0.27	0.67
Linear Model	1007.60	0.95	0.34	-0.81	0.42	-0.04	0.97	0.56	0.58		
<i>Assimilation</i>											
Additive Model	991.46	1.72	0.15	1.16	0.29	0.03	0.87	0.01	0.94	3.98	0.11
Linear Model	993.24	1.44	0.16	0.53	0.59	-0.10	0.92	1.07	0.29		

TABLE A.2: Coefficients for linear models

Response	Intercept	Infection Status(U)	Temperature	Sex(M)	Infection(U) × Temperature
Consumption	0.43	0.032	0.016	-0.048	-0.009
Respiration	-0.0009	-0.004	-0.002	-0.002	-0.00005
Growth	0.00014	0.000012	-0.000008	0.000097	0.0000017
Efficiency	87.76	-1.72	0.20	-1.18	-0.01
Assimilation	0.39	0.003	0.012	-0.027	-0.009

SUPPLEMENTARY INFORMATION TO CHAPTER 3

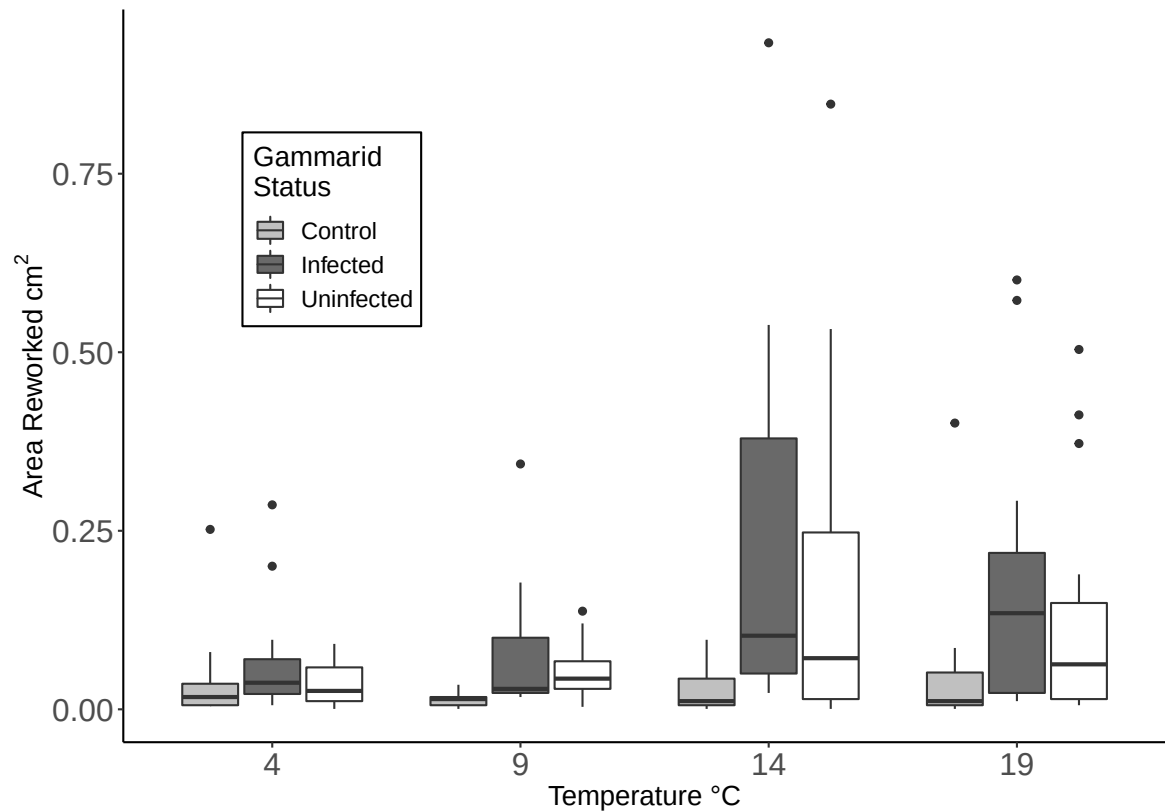


FIGURE B.1: Boxplot of the area of sediment turned over by the gammarids at each temperature. Control treatments, without amphipods, had little to no sediment turnover and rates of turnover in control treatments did not vary with temperature.

APPENDIX C

SUPPLEMENTARY INFORMATION TO CHAPTER 5

TABLE C.1: [Coefficients for linear models of winter experiments.

Parameter	Shredding <i>per capita</i>	Shredding total	Survival
Intercept	2235.65	0.99	0.79
Infection (U)	-66.48	0.03	-0.10
Density (M)	-1301.40	-0.37	
Density (S)	-1929.80	-0.44	-0.17
Warming (H)	-99.05	0.11	0.10
Infection (U): Density (M)	-351.62	0.34	
Infection (U): Density (S)			-0.04
Infection (U): Warming (H)	64.20	-0.09	-0.072
Density (M): Warming (H)	-8.18	0.01	
Density (S): Warming (H)	20.54	0.17	0.16
Infection (U): Density (M): Warming (H)	215.74	-0.23	
Infection (U): Density (S): Warming (H)			0.12

TABLE C.2: Coefficients for linear models of seasonal experiments.

Parameter	Shredding <i>per capita</i>	Shredding total	Survival
Intercept	8.80	1.68	0.88
Infection (U)	-0.13	-0.53	0.09
Density (M)	-7.06	0.16	
Density (S)	-8.58	0.0009	-0.24
Season	-3.60	-0.62	-0.09
Infection (U): Density (M)	-1.35	-1.12	
Infection (U): Density (S)			-0.30
Infection (U): Season	0.09	0.44	-0.19
Density (M): Season	2.93	0.38	
Density (S): Season	3.54	0.72	0.07
Infection (U): Density (M): Warming (H)	0.71	0.62	
Infection (U): Density (S): Season			0.26