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Temperature rise and parasitic infection interact to increase the impact of an invasive species

Ciaran Laverty[a], David Brenner[b], Christopher McIlwaine[a], Jack J. Lennon[a], Jaimie T. A. Dick[a,*], Frances E. Lucy[c], Keith A. Christian[d]

[a]*Institute for Global Food Security, School of Biological Sciences, Queen's University Belfast, MBC, 97 Lisburn Road, Belfast, Northern Ireland, BT9 7BL, UK*

[b]*Department of Ecology and Parasitology, Institute of Zoology, School of Chemical and Biological Sciences, Karlsruhe Institute of Technology, Germany*

[c]*Centre for Environmental Research Innovation and Sustainability, Department of Environmental Science, Institute of Technology, Sligo, Ireland*

[d]*Research Institute for Environment and Livelihoods, Charles Darwin University, Darwin, NT 0909, Australia*

*Corresponding author.

E-mail address: j.dick@qub.ac.uk (J Dick)

Abstract

Invasive species often detrimentally impact native biota, eg through predation, but predicting such impacts is difficult due to multiple and perhaps interacting abiotic and biotic context dependencies. Higher mean and peak temperatures, together with parasites, might influence the impact of predatory invasive host species additively, synergistically or antagonistically. Here, we apply the comparative functional response methodology (relationship between resource consumption rate and resource supply) in one experiment and conduct a second scaled-up mesocosm experiment to assess any differential predatory impacts of the freshwater invasive amphipod *Gammarus pulex,* when uninfected and infected with the acanthocephalan *Echinorhynchus truttae*, at three temperatures representative of current and future climate. Individual *G. pulex* showed Type II predatory functional responses. In both experiments, infection was associated with higher maximum feeding rates, which also increased with increasing temperatures. Additionally, infection interacted with higher temperatures to synergistically elevate functional responses and feeding rates. Parasitic infection also generally increased Q_{10}values. We thus suggest that the differential metabolic responses of the host and parasite to increasing temperatures drives the synergy between infection and temperature, elevating feeding rates and thus enhancing the ecological impact of the invader.

Keywords: Invasive species; Parasitic infection; Temperature; Climate change; Ecological impact

1. Introduction

Invasive species are driving changes in community structure and function throughout the world at an increasing rate (Simberloff et al., 2013; Dick et al., 2014). This includes reductions in native species richness, diversity and abundance (Dick et al., 2017), and even species extinctions (Clavero and Garcia-Berthou, 2005), with consequent disruption of ecosystem functions and services (Strayer, 2012). Further, climate change due to human activity is a global phenomenon and is predicted to influence invasive species spread and ecological impacts (Walther et al., 2009; Sorte et al., 2013; Morley and Lewis, 2014). For example, increasing temperatures may favour invasive species by providing their thermal optima, such as with the bloody–red shrimp, *Hemimysis anomala*, the predatory impacts of which increase with temperature to the point of excluding native species (Dick et al., 2013; Iacarella et al., 2015). In aquatic systems, climate change will manifest in changes in temperature regimes that may interact with other factors to influence invasion outcomes and impact (Ansa-Asare et al., 2000; Portner and Knust, 2007). Exploring such interactions among invasions and abiotic and biotic factors, or ”context dependencies” in the invasion literature (see Dick et al., 2017), may help us understand and predict the impacts of ongoing and new species invasions in a changing world (Dick et al., 2014). As an example, the environmental context of decreasing dissolved oxygen in rivers will likely increase the ecological impacts of invasive crustaceans (Laverty et al., 2015).

Furthermore, parasitic infection is a pervasive feature of biological communities that is increasingly recognised as playing a pivotal role in determining the outcomes of species interactions and shaping community structure (Wood et al., 2007; Hatcher and Dunn, 2011; Hatcher et al., 2014). Whilst both temperature and parasitic infection separately can affect the impact of invasive species (Dick et al., 2010; Sorte et al., 2013; Iacarella et al., 2015), the

interaction of temperature with infection in determining invasive species impacts has not been explored. A powerful method in predicting the ecological impacts of invading consumers (e.g. predators) on native resources (e.g. prey) is the use of comparative functional responses (Dick et al., 2014, 2017). This method uses the relationship between resource consumption rate and resource density to derive differences in the estimated maximum feeding rates of invader and native species; these patterns corroborate with known ecological impacts of invaders in the field (Dick et al., 2013, 2014, 2017; Alexander et al., 2014; Laverty et al., 2015). In essence, functional responses describe the effects on prey populations of a predator, and higher functional responses translate into higher ecological impact (e.g. Dick et al., 2013, 2017). Here, we use comparative functional responses to investigate the relationship between native prey consumption by an invasive predator, as influenced by the interaction between parasitic infection and increasing temperature.

Native to Europe but invasive in Ireland and other islands, the freshwater amphipod *Gammarus pulex* has replaced the native Irish amphipod *Gammarus duebeni celticus* and negatively impacted native macroinvertebrate communities (Kelly et al., 2003, 2006; Dick, 2008; Franceschi et al., 2008; Grabner et al., 2014). *Gammarus pulex* is an intermediate host to the fish acanthocephalan parasite *Echinorhynchus truttae* which, when developmentally ready for trophic transmission, alters host behaviour (eg drift, micro-habitat use) to facilitate consumption by its final host, brown trout (MacNeil et al., 2003). *Gammarus pulex* has also been shown to consume more prey when infected with *E. truttae*, which can reach 70% prevalence in host populations (eg in Ireland; Dick et al., 2010). Here, we therefore tested whether increased water temperatures will lead to simple additive or complex synergistic/antagonistic changes in the impact on prey populations of this invasive predator in the context of infection with the acanthocephalan. This is achieved by deriving functional responses (the relationship between prey density and prey consumption rate) under

infection/temperature combinations and exploring the interaction of these contexts on the estimated maximum feeding rate, and hence ecological impact, of this invader. Then, this individual-based approach is scaled up to a mesocosm experiment that more realistically mimics field conditions of multiple conspecific predators. Finally, we use Q_{10} values (eg see Bennett, 1990) to further explore any change in feeding rates and hence ecological impact of the invader associated with parasitic infection as temperature increases.

2. Materials and methods

2.1. Animal collection and husbandry

Gammarus pulex were collected from an unpolluted 25 m stretch of the Minnowburn River, Northern Ireland (N54.548; W5.952) in May 2014 (Experiment (Expt.) 1) and May 2016 (Expt. 2) and transported in source water to the Queen's University Belfast (Northern Ireland) laboratories. In each year, over 4 weeks, we collected four such samples of *G. pulex*, of several hundred animals each. Those infected with *E. truttae* were identified by visual inspection of the haemcoel, with parasite status checked by dissection following the experiments. Infected and uninfected *G. pulex* (size and age matched adult males, body length 1.5-1.8 cm) from each collection were kept in multiple batches of approximately 20 animals in 2 L of continuously aerated source water and fed decaying leaves ad libitum at 11°C with a 12:12 h light:dark cycle, for 1 week before use in experiments. We chose to use naturally infected animals because infection in the wild is essentially random, and host behavioural manipulations due to the parasite only manifest when the parasite is mature (Franceschi et al., 2008). That is, the parasite drives host behavioural modifications, rather than differences between potential hosts driving parasite acquisition. Experimental prey were chironomid larvae (0.4-0.8 cm body length) obtained online from FishAround Ltd. (UK;

http://fisharoundltd.com/); we used live prey in Expt. 1, but switched to thawed frozen prey for Expt. 2 due to the logistics of the large numbers of prey required. Individual predators were starved for 24 h to standardise hunger.

2.2. Experimental methods

We used filtered Minnowburn River water (Grade 1, 11 µm Qualitative filter paper to remove suspended material) in replicates undertaken with a 12:12 h light:dark cycle over 24 h, in: (Expt.1) experimental arenas 7 cm in diameter with 100 ml of water; and (Expt. 2) three separate cylindrical experimental arenas 10 cm in diameter with 500 ml of water. Water temperatures were 11°C, 16°C and 20°C, representing reasonable current autumn/winter, spring/summer and future summer temperatures (in line with the UK Climate Impacts Program 2002 (UKCIP02) http://danida.vnu.edu.vn/cpis/files/Papers_on_CC/CC/Climate%20Change%20Scenarios%20for%20the%20United%20Kingdom.pdf; Hulme et al., 2002) and reasonable temperature swings throughout the daily cycle of UK freshwaters, and increased future mean temperatures (Hammond and Pryce, 2007). The maximum 20°C water temperature in this experiment is also currently experienced on hot summer days, but is below temperatures where *G. pulex* shows significant mortality (e.g. 40% mortality at 25°C; Grabner et al., 2014). All replicates were carried out in Clifton NE1B-14 water baths at 11°C, 16°C or 20°C (±0.1°C, unstirred). In both experiments, predators and prey were acclimated to each temperature over 2 h prior to experiments; this was achieved for the two higher temperatures by gradually increasing the water bath temperature every 30 min by either 1.25 ^{o}C or 2.25^{o}C (i.e. to 16°C or 20°C). In Expt. 1, we then introduced single predators (i.e. *G.pulex* either uninfected or infected) to each experimental arena with prey densities of 2, 4, 6, 8, 10, 20 and 40 (*n*=3 per experimental

group); in Expt. 2, each of the three arenas contained 10 *G. pulex* and 300 prey (i.e. in excess) with the following proportions of infected *G. pulex*; zero infected (0%) five individuals infected (50%), and seven individuals infected (70%) with n=4 per experimental group. Oxygen was monitored using a YSI model 550A (UK) dissolved oxygen meter, with oxygen levels kept between 9.50 and 10.50 mg/l by bubbling air for 1 min, when required, through both predator and control replicates. Controls were prey in the absence of predators in the prey density/temperature/parasite groups as above (n=3 per group). When experiments were finished, individual *G. pulex* were killed using hot water and confirmed for the presence/absence of a single *E. truttae* parasite. All individuals were found to have been visually ascribed correctly as uninfected or harbouring *E. truttae*.

2.3. Statistical methods

All statistical analyses were conducted in R v3.0.2. Functional responses were considered to be Type II when there was a significant negative first order linear coefficient from logistic regressions (proportion of prey killed versus prey density) and functional response curves were fitted using Rogers' random predator equation without prey replacement (Trexler et al., 1988; Juliano, 2001):

$$N_e = N_0 (1- \exp(a(N_e h\text{-T})))$$

where N_e is the number of prey eaten, N_0 is the initial density of prey, a is the attack constant, h is the handling time and T is the total experimental period, in this case 24 h. Model fitting used the Lambert W function (Bolker, 2008) in R due to the implicit nature of the random predator equation. As data were not normally distributed (Shapiro-Wilks W-test, P<0.05) and heteroscedastic (Bartlett's test, P<0.05), we used ANOVA (with Tukey's post-hoc tests) on

Log_{10} transformed bootstrapped (*n*=30) functional response data to test for differences in the estimated maximum feeding rate '1/hT' (T= experimental time, h= handling time; where handling time is the efficiency of capturing and consuming prey) between uninfected and infected *G. pulex* at the three experimental temperatures. We also calculated Q_{10} values to quantify the effect of increased temperature and to further examine the effect of infection on feeding rates as temperatures increased:

$$Q_{10}=\left(\frac{R_2}{R_1}\right)^{\left(\frac{10}{T2-T1}\right)}$$

where Q_{10} is a coefficient without units, R_1 is the maximum feeding rate at temperature T_1 and R_2 is the maximum feeding rate at temperature T_2. Values used in the Q_{10} analysis can be found in Table 1. The Q_{10} coefficient measures the increase in the rate of a biological process as temperature increases by 10ºC (Bennett, 1990). Q_{10} values of 2~4 are associated with rapid increases in activity rates as temperatures increase, while values of 1~1.5 are associated with reaching a thermal plateau (Huey, 1982; Bennett, 1990).

As data from Expt. 2 were not normally distributed (Shapiro-Wilks *W*-test, $P<0.05$) and heteroscedastic (Bartlett's test, $P<0.05$), we used ANOVA (with Tukey's post-hoc tests) on Log_{10} transformed feeding data to test for differences in the mean numbers of prey eaten with respect to infection and temperature treatments. Q_{10} values were then calculated for each infection treatment as temperatures increased in a similar manner to Expt. 1. Values used in this Q_{10} analysis can be found in Table 2.

3. Results

Control prey survival was >98% under all conditions after 24 h in Expt. 1, therefore deaths in experimental groups were attributed to predation by *G. pulex*. All functional response curves were Type II (Fig. 1, Table 3). Estimated maximum feeding rates were significantly higher for infected animals ($F_{1, 174}$=646.78, P<0.001, Figs. 1, 2) and increased significantly with temperature ($F_{2, 174}$=667.43, P<0.001, Figs. 1, 2); additionally, infection elevated maximum feeding rates to a greater degree at the higher temperatures as shown by the significant 'infection x temperature' interaction effect ($F_{2, 174}$=3.05, P<0.05, Figs. 1, 2). Infected amphipod Q_{10} values indicate that, from 11-16ºC (Q_{10}=2.57, Table 1), 16-20ºC (2.23, Table 1) and overall from 11-20ºC (2.41, Table 1), the estimated maximum feeding rates rapidly increased with the increases in temperature. Uninfected amphipods had a rapid increase in maximum feeding rate from 11-16ºC (3.11, Table 1) and then it slowed considerably from 16-20ºC (1.55, Table 1), and overall it is a lesser increase (2.37, Table 1) than for infected amphipods (2.41, Table 1).

In Expt. 2, maximum feeding rates were significantly higher for infected treatment groups ($F_{2, 27}$=84.1, P<0.001; Fig. 3) and increased significantly with temperature ($F_{2, 27}$=77.2, P<0.001; Fig. 3); additionally, as with Expt. 1, infection elevated maximum feeding rates to a greater degree at the higher temperatures as shown by the significant 'infection x temperature' interaction effect ($F_{2, 27}$=2.8, P<0.05: Fig. 3). For the 50% infection treatment, Q_{10} values indicate that from 11-16ºC (Q_{10} =2.23, Table 2), 16-20ºC (1.38, Table 2) and overall from 11-20ºC (1.81, Table 2), maximum feeding rates rapidly increased with the increases in temperature. For the 70% infection treatment, Q_{10} values indicated that from 11-16ºC (1.55, Table 2), 16-20ºC (1.53, Table 2) and overall from 11-20ºC (1.54, Table 2) maximum feeding rates also rapidly increased with the increases in temperature. Uninfected amphipods had an increase in maximum feeding rate from 11-16ºC (1.56, Table 2) and with

it plateauing from 16-20°C (1.19 Table 2), and overall it was a lower increase (1.39, Table 2) than infected groups of amphipods (50%: 1.81; 70%: 1.54, Table 2).

4. Discussion

Predicting the impacts of invasive species requires the incorporation of both abiotic and biotic context dependencies (Ricciardi et al., 2013; Dick et al., 2014, 2017; Paterson et al., 2015). For example, water salinity, temperature and dissolved oxygen can all modify the strength of interactions between invasive and native species (Kestrup and Ricciardi, 2009; Iacarella et al., 2015; Laverty et al., 2015). Parasites are recognised as having community influences through both direct and indirect host interactions and these can drive biological invasions in terms of success and ecological impacts (Dick et al., 2010; Hatcher and Dunn, 2011; Dunn et al., 2012). Increased temperatures can also increase the consumption of prey by predators (Maier et al., 2011). Here, we show that the biotic context dependency of infection with *E. truttae* and the abiotic context dependency of increased temperature manifest in higher functional responses of the invader *G. pulex* on chironomid prey. Importantly, however, a significant synergistic interaction occurs between the two contexts and the functional response is elevated disproportionately by infection at higher temperatures. This pattern also emerges in larger scale mesocoms that more likely reflect field conditions, indicating that functional responses of individual predators are good predictors of community dynamics with multiple conspecific predators (but see Medoc et al., 2013). This pattern was further confirmed with higher Q_{10} values for infected *G. pulex* individuals and conspecific groups in both Expt. 1 and Expt. 2, with Q_{10} values higher for infected than uninfected *G. pulex* in 78% of comparisons in Tables 1 and 2. Thus, overall, this indicates that infected *G. pulex* are increasing their maximum feeding rates synergistically with temperature to a

greater degree than uninfected *G. pulex.* Thus, under climate change, parasitic infection is likely to exacerbate the known ecological impacts of *G. pulex* invasions, which result in native gammarid species displacements and reductions in broader macroinvertebrate species richness, diversity, abundance and range (Kelly et al., 2003, 2006). These impacts may also manifest in the native range of *G. pulex* throughout Europe, and thus monitoring plus experimental testing are required to elucidate this point.

Maximum feeding rates, derived from functional responses, measure the predicted maximum prey consumption rate of a predator, which is a reliable indicator of impact on prey populations (Dick et al., 2013, 2014, 2017; Alexander et al., 2014; Laverty et al., 2015). Infected *G. pulex* consumed prey at a higher rate than those uninfected, indicating the increased ecological impact that infected invaders inflict on native communities. Such increased feeding rates driven by *E. truttae* in the present study likely reflect the increased metabolic demands of the host due to the reliance of the parasite on host resources (Dick et al., 2010, 2017). Higher temperatures also increased the maximum feeding rate of *G. pulex*, and this has ramifications for the future when water temperatures increase under climate change (Ozaki et al., 2003). Whilst we recognise that adaptation may occur, and short-term experiments may have limitations in this regard, increased temperatures clearly increase the metabolism of ectotherms. The interaction between parasitic infection and increasing temperature indicates that, as climate change occurs, parasites may have increasing influence over the impacts that invasive species propagate through native communities (Ozaki et al., 2003; Dick et al., 2010). We speculate that parasites may be increasing their metabolic rate at a higher rate than the host at higher temperatures, increasing the metabolic requirements of *G. pulex* to a greater degree than at lower temperatures, thereby increasing prey consumption rates. Also, production of heat shock proteins due to interacting factors such as parasitic infection and temperature (see Frank et al., 2013; Grabner et al., 2014) may contribute to

higher metabolic demands and hence feeding rates of hosts. Indeed, since parasites also produce heat shock proteins (e.g. see Perez-Morales and Espinoza, 2015), any differential production by hosts and parasites may go some way towards explaining our parasite/temperature interaction. Whatever the mechanism, our results indicate that retaining natural enemies under climate change may increase rather than decrease the ecological impact of invasive species. This is counter to the 'enemy release' hypothesis (see Torchin et al., 2003; Dick et al., 2010), which posits that release from parasites may be causal in the invasion process, including increasing the ecological impact of invaders. However, our present study shows the opposite, with parasites likely increasing ecological impact, illustrating the utility of functional response analyses and mesocosms in testing popular hypotheses in invasion ecology. Finally, parasites can both increase and decrease host feeding rates (Wood et al., 2007; Larsen and Mouritsen, 2009; Dick et al., 2010; O'Shaughnessy et al., 2014; Toscano et al., 2014) and thus we require more individual studies and meta-analyses to determine why different parasites have different effects in this regard.

The use of Q_{10} analysis provided further evidence that the metabolic rates of amphipods increase as temperatures increase, as is commonly seen in other ectotherms (Litzgus and Hopkins, 2003; Deban and Lappin, 2011). Furthermore, in our experiments, infected individuals and groups clearly increased their metabolic rates to a greater degree than uninfected individuals, as has been noted in a number of previous studies (Booth et al., 1993; Giorgi et al., 2001; Nilsson, 2003; Dick et al., 2010). When the invader *G. pulex* is infected with *E. truttae*, such individuals are differentially affected by temperature compared with uninfected individuals and increased prey consumption is a symptom of the metabolic demand being placed upon the host by the parasite as temperatures increase. Given that Q_{10} values of 2~4 are associated with rapid increases in activity rates as temperatures increase, while values of 1~1.5 are associated with reaching a thermal plateau (Huey, 1982; Bennett,

1990), it is clear that parasitic infection is driving rapid increases in host feeding rates at our study temperatures with little sign of plateau. However, plateau is more evident with uninfected compared with infected animals (Tables 1, 2). This suggests that further rises in temperature, especially under host adaptation to increased temperature, may further elevate predation rates and impacts of this and other invasive species when hosting parasites.

Overall, infected *G. pulex* had a greater impact than did uninfected individuals and at higher temperatures such impacts increased disproportionally. This is the first known study to examine the synergy between temperature increase and parasitic infection concerning the ecological impact of an invasive predator on recipient prey populations. Our study shows biotic and abiotic conditions interact to synergistically influence predatory impacts of invasive species and these influences should be taken into consideration when legislating against and managing invasive species (Dick et al., 2013; Sorte et al., 2013). For example, many invasive species are placed on “black lists” as they are perceived to be unwanted potential invaders (eg European Union legislation; see Caffrey et al., 2014). However, their parasites go largely ignored, and the present study indicates that parasites may enhance the ecological impacts of their hosts and this should be incorporated into any black listing in future. Further, the comparative functional response methodology, and scaled-up mesocosms, are clearly valuable tools in facilitating predictions of ecological impacts of invaders under context dependencies such as parasitic infection and temperature (see also Dick et al., 2013, 2017; Alexander et al., 2014).

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Figure legends

Fig. 1. Experiment 1 of this study. Functional responses of infected (i, dashed lines) and uninfected (u, solid lines) *Gammarus pulex* at low (11°C, blue), medium (16°C, orange) and high (20°C, red) temperatures. Means are ± S.D.

Fig. 2. Experiment 1 of this study. Mean ± S.D. bootstrapped (*n*=30) estimated maximum (max.) feeding rates of uninfected (dark grey) and infected (light grey) *Gammarus pulex* at low, medium and high temperatures. Tukey's post-hoc tests and trend lines help illustrate the significant interaction effect.

Fig. 3. Experiment 2 of this study. Mean ± S.D. maximum feeding rates of uninfected (dark grey), 50% infected (middle grey) and 70% infected (light grey) *Gammarus pulex* at low (11°C), medium (16°C) and high (20°C) temperatures. Tukey's post-hoc tests and trend lines help illustrate the significant interaction effect. NS, not significant.

Table 1. Experiment 1. Q_{10} values associated with mean maximum feeding rates (prey killed per h) at each temperature difference for infected and uninfected *Gammarus pulex*.

Infection status	Δ Temp (^{o}C)	Mean maximum feeding rates	Q_{10} Value
Infected	Overall	0.63-1.39	2.41
	11-16	0.63-1.00	2.57
	16-20	1.00-1.39	2.23
Uninfected	Overall	0.39-0.85	2.37
	11-16	0.39-0.68	3.11
	16-20	0.68-0.85	1.55

Table 2. Experiment 2. Q_{10} values associated with mean prey eaten at each temperature difference and infected proportion of *Gammarus pulex*.

Infected proportion (%)	Δ Temp (ºC)	Mean prey eaten	Q_{10} Value
0	Overall	107-144	1.39
	11-16	107-134	1.56
	16-20	134-144	1.19
50	Overall	119-203	1.81
	11-16	119-178	2.23
	16-20	178-203	1.38
70	Overall	154-228	1.54
	11-16	154-192	1.55
	16-20	192-228	1.53

Table 3. First order linear coefficients (lc) from logistic regressions for *Gammarus pulex* infection status with *Echinorhynchus truttae* and experimental temperature combinations. All indicate Type II functional responses (see Section 3).

Parasite status	**Temperature (ºC)**	**Linear coefficient (1st order)**	***P* value**
Infected	11	-0.051	<0.001
	16	-0.073	<0.001
	20	-0.079	<0.001
Uninfected	11	-0.079	<0.001
	16	-0.084	<0.001
	20	-0.092	<0.001

Figure 1

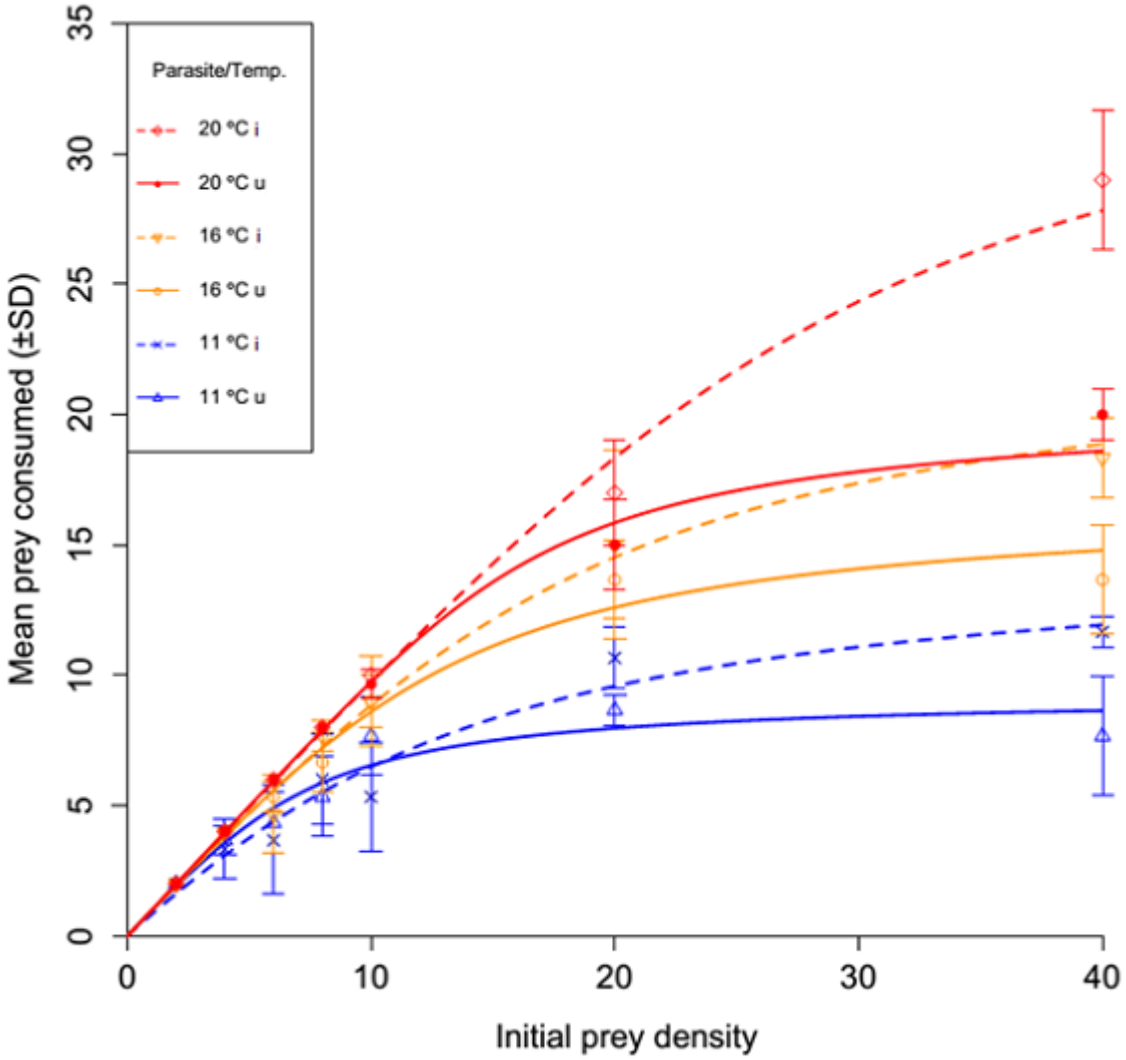


Figure 2

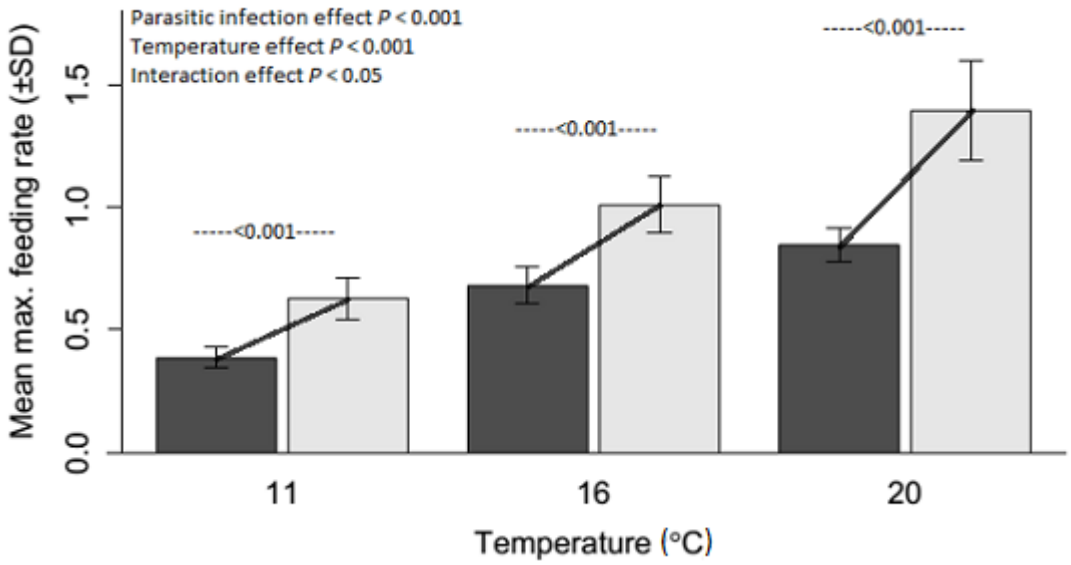
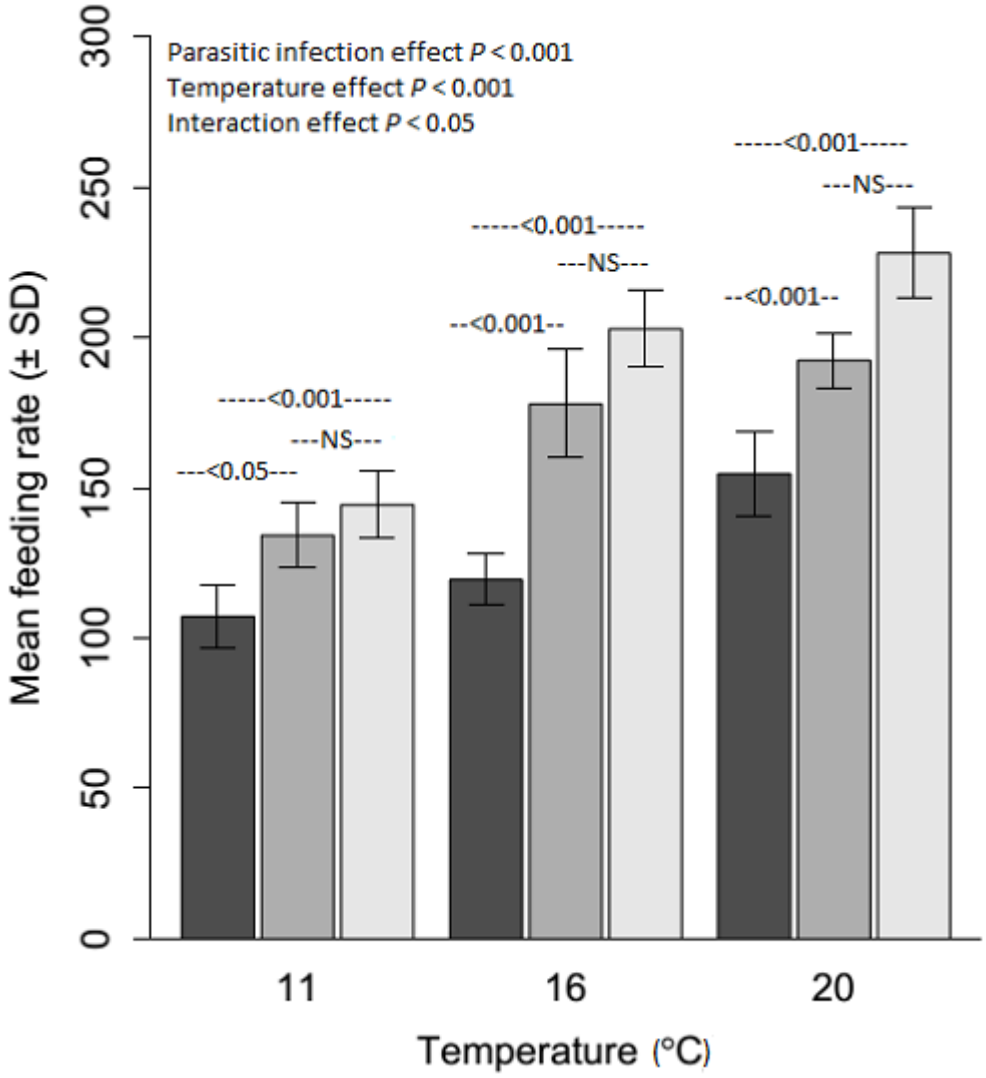


Figure 3


Parasitic infection effect P < 0.001
Temperature effect P < 0.001
Interaction effect P < 0.05
---<0.05---
-----<0.001-----
---NS---
--<0.001--
-----<0.001-----
---NS---
--<0.001--
-----<0.001-----
---NS---
Mean feeding rate (± SD)
0
50
100
150
200
250
300
11
16
20
Temperature (°C)