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

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

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18

## 19 **Abstract**

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

37

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

40

## 41 **1. Introduction**

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

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

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

77         Native to Europe but invasive in Ireland and other islands, the freshwater amphipod  
78 *Gammarus pulex* has replaced the native Irish amphipod *Gammarus duebeni celticus* and  
79 negatively impacted native macroinvertebrate communities (Kelly et al., 2003, 2006; Dick,  
80 2008; Franceschi et al., 2008; Grabner et al., 2014). *Gammarus pulex* is an intermediate host  
81 to the fish acanthocephalan parasite *Echinorhynchus truttae* which, when developmentally  
82 ready for trophic transmission, alters host behaviour (eg drift, micro-habitat use) to facilitate  
83 consumption by its final host, brown trout (MacNeil et al., 2003). *Gammarus pulex* has also  
84 been shown to consume more prey when infected with *E. truttae*, which can reach 70%  
85 prevalence in host populations (eg in Ireland; Dick et al., 2010). Here, we therefore tested  
86 whether increased water temperatures will lead to simple additive or complex  
87 synergistic/antagonistic changes in the impact on prey populations of this invasive predator in  
88 the context of infection with the acanthocephalan. This is achieved by deriving functional  
89 responses (the relationship between prey density and prey consumption rate) under

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

96

## 97 **2. Materials and methods**

### 98 *2.1. Animal collection and husbandry*

99 *Gammarus pulex* were collected from an unpolluted 25 m stretch of the Minnowburn  
100 River, Northern Ireland (N54.548; W5.952 ) in May 2014 (Experiment (Expt.) 1) and May  
101 2016 (Expt. 2) and transported in source water to the Queen's University Belfast (Northern  
102 Ireland) laboratories. In each year, over 4 weeks, we collected four such samples of *G. pulex*,  
103 of several hundred animals each. Those infected with *E. truttae* were identified by visual  
104 inspection of the haemocoel, with parasite status checked by dissection following the  
105 experiments. Infected and uninfected *G. pulex* (size and age matched adult males, body  
106 length 1.5-1.8 cm) from each collection were kept in multiple batches of approximately 20  
107 animals in 2 L of continuously aerated source water and fed decaying leaves ad libitum at  
108 11°C with a 12:12 h light:dark cycle, for 1 week before use in experiments. We chose to use  
109 naturally infected animals because infection in the wild is essentially random, and host  
110 behavioural manipulations due to the parasite only manifest when the parasite is mature  
111 (Franceschi et al., 2008). That is, the parasite drives host behavioural modifications, rather  
112 than differences between potential hosts driving parasite acquisition. Experimental prey were  
113 chironomid larvae (0.4-0.8 cm body length) obtained online from FishAround Ltd. (UK;

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

117

## 118 2.2. *Experimental methods*

119 We used filtered Minnowburn River water (Grade 1, 11 µm Qualitative filter paper to  
120 remove suspended material) in replicates undertaken with a 12:12 h light:dark cycle over 24  
121 h, in: (Expt.1) experimental arenas 7 cm in diameter with 100 ml of water; and (Expt. 2) three  
122 separate cylindrical experimental arenas 10 cm in diameter with 500 ml of water. Water  
123 temperatures were 11°C, 16°C and 20°C, representing reasonable current autumn/winter,  
124 spring/summer and future summer temperatures (in line with the UK Climate Impacts  
125 Program 2002 (UKCIP02)  
126 [http://danida.vnu.edu.vn/cpis/files/Papers\\_on\\_CC/CC/Climate%20Change%20Scenarios%20for%20the%20United%20Kingdom.pdf](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  
127 swings throughout the daily cycle of UK freshwaters, and increased future mean temperatures  
128 (Hammond and Pryce, 2007). The maximum 20°C water temperature in this experiment is  
129 also currently experienced on hot summer days, but is below temperatures where *G. pulex*  
130 shows significant mortality (e.g. 40% mortality at 25°C; Grabner et al., 2014). All replicates  
131 were carried out in Clifton NE1B-14 water baths at 11°C, 16°C or 20°C ( $\pm 0.1^\circ\text{C}$ , unstirred).  
132 In both experiments, predators and prey were acclimated to each temperature over 2 h prior to  
133 experiments; this was achieved for the two higher temperatures by gradually increasing the  
134 water bath temperature every 30 min by either 1.25 °C or 2.25°C (i.e. to 16°C or 20°C). In  
135 Expt. 1, we then introduced single predators (i.e. *G.pulex* either uninfected or infected) to  
136 each experimental arena with prey densities of 2, 4, 6, 8, 10, 20 and 40 ( $n=3$  per experimental  
137

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

148

### 149 2.3. Statistical methods

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

$$155 \quad N_e = N_0 (1 - \exp(-a(N_e h - T)))$$

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



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

167

$$168 \quad Q_{10} = \left( \frac{R_2}{R_1} \right)^{\left( \frac{10}{T_2 - T_1} \right)}$$

169 where Q<sub>10</sub> is a coefficient without units, R<sub>1</sub> is the maximum feeding rate at temperature T<sub>1</sub>  
170 and R<sub>2</sub> is the maximum feeding rate at temperature T<sub>2</sub>. Values used in the Q<sub>10</sub> analysis can be  
171 found in Table 1. The Q<sub>10</sub> coefficient measures the increase in the rate of a biological process  
172 as temperature increases by 10°C (Bennett, 1990). Q<sub>10</sub> values of 2~4 are associated with rapid  
173 increases in activity rates as temperatures increase, while values of 1~1.5 are associated with  
174 reaching a thermal plateau (Huey, 1982; Bennett, 1990).

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

181

### 182 3. Results

183 Control prey survival was >98% under all conditions after 24 h in Expt. 1, therefore  
184 deaths in experimental groups were attributed to predation by *G. pulex*. All functional  
185 response curves were Type II (Fig. 1, Table 3). Estimated maximum feeding rates were  
186 significantly higher for infected animals ( $F_{1, 174}=646.78$ ,  $P<0.001$ , Figs. 1, 2) and increased  
187 significantly with temperature ( $F_{2, 174}=667.43$ ,  $P<0.001$ , Figs. 1, 2); additionally, infection  
188 elevated maximum feeding rates to a greater degree at the higher temperatures as shown by  
189 the significant 'infection x temperature' interaction effect ( $F_{2, 174}=3.05$ ,  $P<0.05$ , Figs. 1, 2).  
190 Infected amphipod  $Q_{10}$  values indicate that, from 11-16°C ( $Q_{10}=2.57$ , Table 1), 16-20°C  
191 (2.23, Table 1) and overall from 11-20°C (2.41, Table 1), the estimated maximum feeding  
192 rates rapidly increased with the increases in temperature. Uninfected amphipods had a rapid  
193 increase in maximum feeding rate from 11-16°C (3.11, Table 1) and then it slowed  
194 considerably from 16-20°C (1.55, Table 1), and overall it is a lesser increase (2.37, Table 1)  
195 than for infected amphipods (2.41, Table 1).

196 In Expt. 2, maximum feeding rates were significantly higher for infected treatment  
197 groups ( $F_{2, 27}=84.1$ ,  $P<0.001$ ; Fig. 3) and increased significantly with temperature ( $F_{2,$   
198  $27=77.2$ ,  $P<0.001$ ; Fig. 3); additionally, as with Expt. 1, infection elevated maximum feeding  
199 rates to a greater degree at the higher temperatures as shown by the significant 'infection x  
200 temperature' interaction effect ( $F_{2, 27}=2.8$ ,  $P<0.05$ ; Fig. 3). For the 50% infection treatment,  
201  $Q_{10}$  values indicate that from 11-16°C ( $Q_{10}=2.23$ , Table 2), 16-20°C (1.38, Table 2) and  
202 overall from 11-20°C (1.81, Table 2), maximum feeding rates rapidly increased with the  
203 increases in temperature. For the 70% infection treatment,  $Q_{10}$  values indicated that from 11-  
204 16°C (1.55, Table 2), 16-20°C (1.53, Table 2) and overall from 11-20°C (1.54, Table 2)  
205 maximum feeding rates also rapidly increased with the increases in temperature. Uninfected  
206 amphipods had an increase in maximum feeding rate from 11-16°C (1.56, Table 2) and with

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

209

## 210 **4. Discussion**

211 Predicting the impacts of invasive species requires the incorporation of both abiotic  
212 and biotic context dependencies (Ricciardi et al., 2013; Dick et al., 2014, 2017; Paterson et  
213 al., 2015). For example, water salinity, temperature and dissolved oxygen can all modify the  
214 strength of interactions between invasive and native species (Kestrup and Ricciardi, 2009;  
215 Iacarella et al., 2015; Laverty et al., 2015). Parasites are recognised as having community  
216 influences through both direct and indirect host interactions and these can drive biological  
217 invasions in terms of success and ecological impacts (Dick et al., 2010; Hatcher and Dunn,  
218 2011; Dunn et al., 2012). Increased temperatures can also increase the consumption of prey  
219 by predators (Maier et al., 2011). Here, we show that the biotic context dependency of  
220 infection with *E. truttae* and the abiotic context dependency of increased temperature  
221 manifest in higher functional responses of the invader *G. pulex* on chironomid prey.  
222 Importantly, however, a significant synergistic interaction occurs between the two contexts  
223 and the functional response is elevated disproportionately by infection at higher temperatures.  
224 This pattern also emerges in larger scale mesocosms that more likely reflect field conditions,  
225 indicating that functional responses of individual predators are good predictors of community  
226 dynamics with multiple conspecific predators (but see Medoc et al., 2013). This pattern was  
227 further confirmed with higher  $Q_{10}$  values for infected *G. pulex* individuals and conspecific  
228 groups in both Expt. 1 and Expt. 2, with  $Q_{10}$  values higher for infected than uninfected *G.*  
229 *pulex* in 78% of comparisons in Tables 1 and 2. Thus, overall, this indicates that infected *G.*  
230 *pulex* are increasing their maximum feeding rates synergistically with temperature to a

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

237           Maximum feeding rates, derived from functional responses, measure the predicted  
238 maximum prey consumption rate of a predator, which is a reliable indicator of impact on prey  
239 populations (Dick et al., 2013, 2014, 2017; Alexander et al., 2014; Lavery et al., 2015).  
240 Infected *G. pulex* consumed prey at a higher rate than those uninfected, indicating the  
241 increased ecological impact that infected invaders inflict on native communities. Such  
242 increased feeding rates driven by *E. truttae* in the present study likely reflect the increased  
243 metabolic demands of the host due to the reliance of the parasite on host resources (Dick et  
244 al., 2010, 2017). Higher temperatures also increased the maximum feeding rate of *G. pulex*,  
245 and this has ramifications for the future when water temperatures increase under climate  
246 change (Ozaki et al., 2003). Whilst we recognise that adaptation may occur, and short-term  
247 experiments may have limitations in this regard, increased temperatures clearly increase the  
248 metabolism of ectotherms. The interaction between parasitic infection and increasing  
249 temperature indicates that, as climate change occurs, parasites may have increasing influence  
250 over the impacts that invasive species propagate through native communities (Ozaki et al.,  
251 2003; Dick et al., 2010). We speculate that parasites may be increasing their metabolic rate at  
252 a higher rate than the host at higher temperatures, increasing the metabolic requirements of *G.*  
253 *pulex* to a greater degree than at lower temperatures, thereby increasing prey consumption  
254 rates. Also, production of heat shock proteins due to interacting factors such as parasitic  
255 infection and temperature (see Frank et al., 2013; Grabner et al., 2014) may contribute to

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

270         The use of  $Q_{10}$  analysis provided further evidence that the metabolic rates of  
271 amphipods increase as temperatures increase, as is commonly seen in other ectotherms  
272 (Litzgus and Hopkins, 2003; Deban and Lappin, 2011). Furthermore, in our experiments,  
273 infected individuals and groups clearly increased their metabolic rates to a greater degree  
274 than uninfected individuals, as has been noted in a number of previous studies (Booth et al.,  
275 1993; Giorgi et al., 2001; Nilsson, 2003; Dick et al., 2010). When the invader *G. pulex* is  
276 infected with *E. truttae*, such individuals are differentially affected by temperature compared  
277 with uninfected individuals and increased prey consumption is a symptom of the metabolic  
278 demand being placed upon the host by the parasite as temperatures increase. Given that  $Q_{10}$   
279 values of 2~4 are associated with rapid increases in activity rates as temperatures increase,  
280 while values of 1~1.5 are associated with reaching a thermal plateau (Huey, 1982; Bennett,

281 1990), it is clear that parasitic infection is driving rapid increases in host feeding rates at our  
282 study temperatures with little sign of plateau. However, plateau is more evident with  
283 uninfected compared with infected animals (Tables 1, 2). This suggests that further rises in  
284 temperature, especially under host adaptation to increased temperature, may further elevate  
285 predation rates and impacts of this and other invasive species when hosting parasites.

286 Overall, infected *G. pulex* had a greater impact than did uninfected individuals and  
287 at higher temperatures such impacts increased disproportionately. This is the first known study  
288 to examine the synergy between temperature increase and parasitic infection concerning the  
289 ecological impact of an invasive predator on recipient prey populations. Our study shows  
290 biotic and abiotic conditions interact to synergistically influence predatory impacts of  
291 invasive species and these influences should be taken into consideration when legislating  
292 against and managing invasive species (Dick et al., 2013; Sorte et al., 2013). For example,  
293 many invasive species are placed on “black lists” as they are perceived to be unwanted  
294 potential invaders (eg European Union legislation; see Caffrey et al., 2014). However, their  
295 parasites go largely ignored, and the present study indicates that parasites may enhance the  
296 ecological impacts of their hosts and this should be incorporated into any black listing in  
297 future. Further, the comparative functional response methodology, and scaled-up mesocosms,  
298 are clearly valuable tools in facilitating predictions of ecological impacts of invaders under  
299 context dependencies such as parasitic infection and temperature (see also Dick et al., 2013,  
300 2017; Alexander et al., 2014).

301

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306

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- 461

462 **Figure legends**

463

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

467

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

472

473 **Fig. 3.** Experiment 2 of this study. Mean  $\pm$  S.D. maximum feeding rates of uninfected (dark  
 474 grey), 50% infected (middle grey) and 70% infected (light grey) *Gammarus pulex* at low  
 475 (11°C), medium (16°C) and high (20°C) temperatures. Tukey's post-hoc tests and trend lines  
 476 help illustrate the significant interaction effect. NS, not significant.

477

478

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

| Infection status | $\Delta$ Temp (°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           |

481

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

| Infected proportion (%) | $\Delta$ Temp ( $^{\circ}\text{C}$ ) | 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           |

484

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

488

489

| Parasite status   | Temperature ( $^{\circ}\text{C}$ ) | Linear coefficient<br>(1 <sup>st</sup> order) | <i>P</i> value |
|-------------------|------------------------------------|---|----------------|
| <b>Infected</b>   | 11                                 | -0.051  | <0.001         |
|                   | 16                                 | -0.073  | <0.001         |
|                   | 20                                 | -0.079  | <0.001         |
| <b>Uninfected</b> | 11                                 | -0.079  | <0.001         |
|                   | 16                                 | -0.084  | <0.001         |
|                   | 20                                 | -0.092  | <0.001         |

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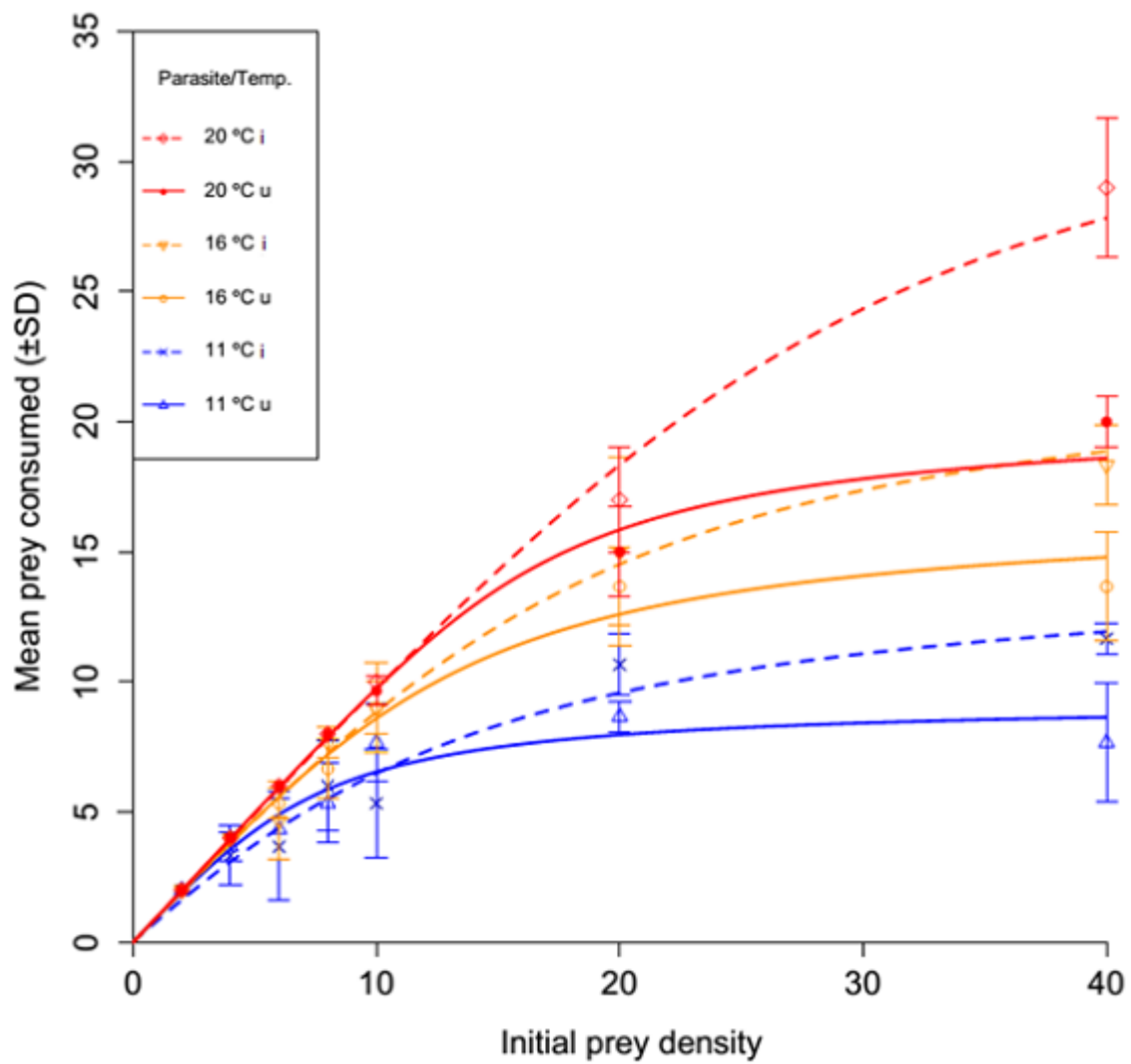
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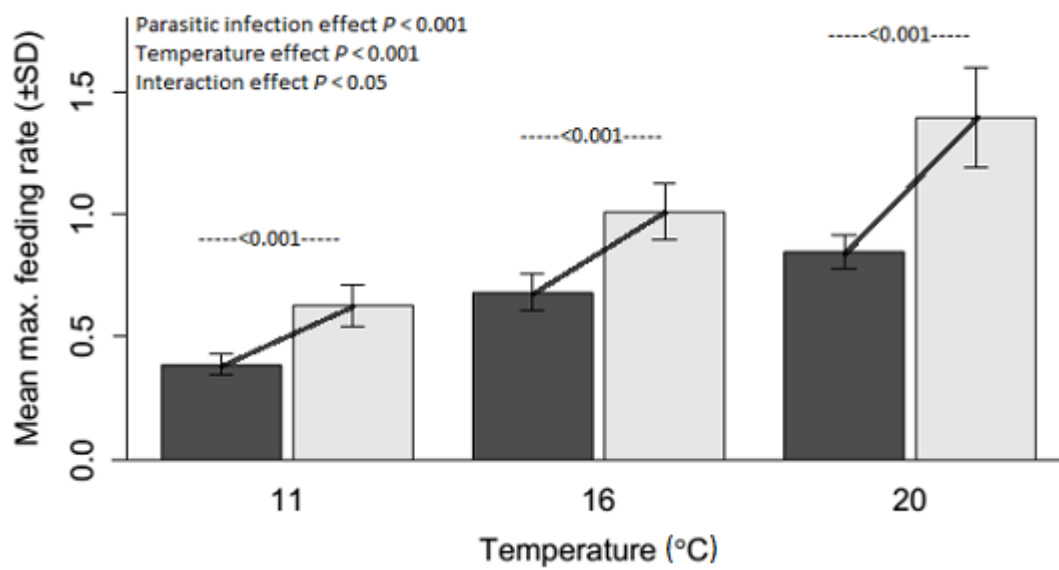
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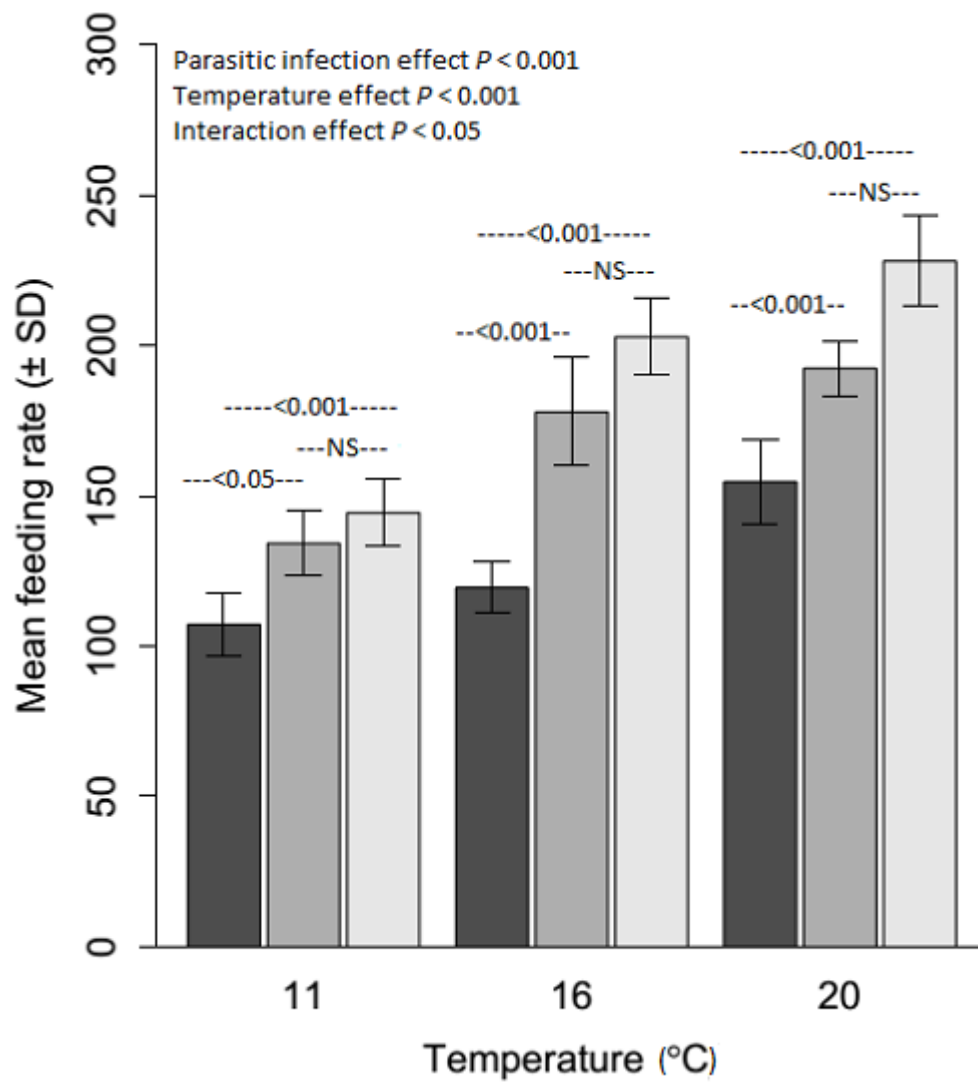
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497 **Figure 1**

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499 **Figure 2**

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501 **Figure 3**

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