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**Temperature-related intraspecific variability in the behavioral
manipulation of acanthocephalan parasites on their gammarid hosts**

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acanthocephalan

12 **Abstract.** Understanding the effect of temperature on ecologically important species has
13 become a major challenge in the context of global warming. However, the consequences of
14 climate change cannot be accurately predicted without taking into consideration biotic
15 interactions. In particular, parasitic infection constitutes a widespread biotic interaction, and
16 parasites impact their hosts in multiple ways, eventually leading to consequences on
17 communities and ecosystems. Here, we explored the effect of temperature on the anti-predator
18 behavior of a keystone freshwater invertebrate, the amphipod *Gammarus fossarum*.
19 Gammarids regularly harbor manipulative acanthocephalan parasites, which modify their anti-
20 predator behavior in ways that potentially increase the probability of trophic transmission to
21 their definitive hosts. We investigated the impact of temperature on gammarids infected by
22 two acanthocephalan parasites, *Pomphorhynchus tereticollis* and *Polymorphus minutus*.
23 Uninfected and naturally infected gammarids were acclimatized to different temperatures, and
24 their behavior was measured. Our results show that the effect of infection on the phototaxis of
25 gammarids increased with increasing temperature, with a stronger effect induced by *P.*
26 *tereticollis*. In contrast, temperature had no effect on the alteration of refuge use or geotaxis
27 observed in infected gammarids. Our results provide the first direct evidence that temperature
28 can affect the extent of behavioral alteration brought about by certain parasite species.
29 However, the consequences in terms of increased trophic transmission remain elusive, as the
30 supposedly key anti-predatory behavior was not significantly affected by exposure of
31 gammarids to different temperatures.

Introduction

32

33 Although parasites have been ignored for decades in the field of ecology, they are now
34 widely recognized as important actors within ecosystems (Hudson *et al.*, 2006; Lefèvre *et al.*,
35 2009; Hatcher *et al.*, 2012). Parasitic organisms might represent close to half of all
36 biodiversity according to certain estimations (Poulin and Morand, 2000; Dobson *et al.*, 2008),
37 making parasitic infection one of the most common biotic interactions. Parasites have
38 multiple impacts on their hosts that can have consequences on larger scales (Lefèvre *et al.*,
39 2009; Hatcher *et al.*, 2012). Differential pathogenic effects on several competing host species
40 might for instance reverse the outcome of competition, or lead to the coexistence of species
41 that would exclude each other in the absence of parasites (Hatcher *et al.*, 2012). Parasites with
42 complex life-cycles that rely on trophic transmission are particularly likely to affect many
43 components of the ecosystems, as they are embedded in large food webs and have the
44 potential to affect several host species in succession. In particular, some of these parasites are
45 able to induce phenotypic changes in their intermediate hosts, supposed to increase the
46 probability of predation by their definitive hosts, thus increasing their own probability of
47 transmission (Poulin and Thomas, 1999; Moore, 2002). Many of these effects lead to deep
48 changes in communities and ecosystems, such that these parasites are sometimes referred to
49 as ecosystem engineers (Thomas *et al.*, 1998, 1999; Sato *et al.*, 2012).

50 In the current context of global change, understanding how environmental conditions
51 might alter ecologically important species has become a major challenge, notably due to the
52 necessity to make accurate predictions about the consequences of such changes. Taking into
53 consideration biotic interactions, and in particular parasites, is therefore particularly
54 important, especially considering that climate change might induce unpredictable
55 consequences on both inter- and intra-specific interactions (Tylianakis *et al.*, 2008; Rosenblatt
56 and Schmitz, 2014). Temperature stands as a major parameter affecting many parasite-host

57 systems (Marcogliese, 2001; Harvell *et al.*, 2002; Barber *et al.*, 2016), and it is likely that the
58 impact of global change on ecologically important species might depend on the parasites that
59 they harbor. In particular, the nature of the cumulative effect of parasitism and temperature on
60 hosts, whether additive or interactive, is hardly predictable (Labaude *et al.*, 2017).

61 Gammarids are widespread and abundant crustacean amphipods that are often seen as
62 key species in freshwater ecosystems, where they constitute both important prey and predators
63 for many species, modulating the composition of freshwater macroinvertebrates (Degani *et*
64 *al.*, 1987; Friberg *et al.*, 1994; MacNeil *et al.*, 1997; Kelly *et al.*, 2002). They also play a
65 major role in the maintenance of water quality through their roles as scavengers and shredders
66 (MacNeil *et al.*, 1997), in particular through the consumption of dead leaves (Piscart *et al.*,
67 2009; Constable and Birkby, 2016). Gammarids are thus of significant ecological and
68 economic importance as the quality of water is a key parameter in the emergence of water-
69 borne diseases, ecosystem functioning, and maintenance of biodiversity (Klaphake *et al.*,
70 2001).

71 Gammarids serve as intermediate hosts for several species of acanthocephalan
72 parasites that use either birds or fish as definitive hosts. These parasites affect their gammarid
73 hosts in multiple ways. In particular, acanthocephalan parasites can manipulate the behavior
74 of gammarids in a way that appears to increase their probability of being predated by their
75 definitive hosts (Lagrue *et al.*, 2007; Perrot-Minnot *et al.*, 2007; Dianne *et al.*, 2011; but see
76 Perrot-Minnot *et al.*, 2012). Along with other impacts, such as alteration of food consumption
77 (Fielding *et al.*, 2003; Médoc *et al.*, 2011; Labaude *et al.*, 2017) or metabolic rate (Rumpus
78 and Kennedy, 1974; Labaude *et al.*, 2015a), such modifications might affect the role of
79 gammarids within ecosystems.

80 Temperature affects several traits in the association between acanthocephalan parasites
81 and their gammarid hosts. Both the time of development of parasites (Olson and Pratt, 1971;

82 Tokeson and Holmes, 1982) and their success of establishment in their definitive fish host
83 (Sheath *et al.*, 2016) depend on temperature. On the other hand, temperature also affects the
84 metabolism (Pöckl and Humpesch, 1990), growth (Moenickes *et al.*, 2011), or consumption of
85 gammarids (Foucreau *et al.*, 2016), with potential effects on their interaction with parasites. In
86 addition, the cumulative effect of acanthocephalan parasites and temperature on gammarids
87 feeding behavior is dependent on gammarids' aggregation context, with different
88 consequences of the two parameters on the leave consumption of isolated individuals and
89 individuals in groups (Labaude *et al.*, 2017).

90 Temperature may also lead to variation in the rapidity or intensity of parasite
91 manipulation (i.e. how parasites manipulate host behaviour in link with predation probability),
92 whether directly or due to effects on other parameters, although only indirect evidence exists
93 so far (reviewed in Labaude *et al.*, 2015b). For instance, gammarids experimentally infected
94 during winter were slower to display altered behaviors than gammarids infected in spring with
95 the same parasite populations (Franceschi *et al.*, 2010). Such result might arise from a positive
96 effect of temperature on host and parasite metabolism. Following this hypothesis, higher
97 temperature experienced by infected gammarids might also lead to stronger manipulation, in
98 the case where such manipulation depends on host or parasite metabolism. Moreover,
99 gammarids survival decreases at high temperatures (Maazouzi *et al.*, 2011; Foucreau *et al.*,
100 2014), and parasites would benefit in increasing their manipulating effort to secure their
101 transmission (Thomas *et al.*, 2002, 2011). Given the predicted increase of temperature in
102 future years, improving our understanding of the consequences of temperature on host-
103 parasite relationships is particularly relevant (Labaude *et al.*, 2017).

104 Here, we tested the effect of exposure to different temperatures on the behavioral
105 changes induced by two acanthocephalan species, the fish parasite *Pomphorhynchus*
106 *tereticollis* and the bird parasite *Polymorphus minutus*, on their gammarid host *Gammarus*

107 *fossarum*. These parasites manipulate different behaviors that are believed to be specific to the
108 definitive host species (Tain *et al.*, 2006). While *P. tereticollis* induces an inversion of the
109 photophobic behavior of its intermediate host (Tain *et al.*, 2006) and a decrease in its use of
110 refuges (Perrot-Minnot *et al.*, 2007), infection by *P. minutus* leads to reversed geotaxis, with
111 gammarid individuals staying closer to the water surface than uninfected ones (Bauer *et al.*,
112 2005). We relied on naturally infected gammarids with cystacanth parasites, the last larval
113 stage that is infective for the definitive host and at which such changes occur in hosts, and
114 investigated the effect of acclimatization at different temperatures on the behavior of
115 uninfected and infected individuals.

116

117

Materials and Methods

Sampling and acclimatization

119 *Gammarus fossarum* individuals were collected in the Norges River (eastern France,
120 47°21'42.7"N 5°09'29.6"E, where gammarids are infected with *P. tereticollis*) in September
121 2015, and in the Vèze River (eastern France, 47°14'01.9"N 5°34'37.4"E, where gammarids are
122 infected with *P. minutus*) in June 2016, using a kick sampling method with a hand net. The
123 Norges River only contains *G. fossarum* species (Lagrue *et al.*, 2014; Labaude *et al.*, 2017).
124 Although Lagrue *et al.* (2014) found that more than half of gammarids from the Vèze River
125 belonged to the closely-related *G. pulex* species, more recent genetic analyses performed on
126 457 individuals sampled in the Vèze River in May 2015 showed that about 90% of them ($n =$
127 410) belonged to *G. fossarum* (S. Labaude, unpublished data). Given the small proportion of
128 *G. pulex*, and since the two cryptic species are often considered as a single taxonomic unit
129 (Karaman and Pinkster, 1977), all individuals were used in this study. The brightly colored
130 cystacanth stages of these parasites are visible through the cuticle of gammarids, allowing a

131 preliminary selection of infected individuals directly in the field. Uninfected individuals were
132 also captured.

133 Individuals from each population were randomly allocated to several groups that were
134 acclimatized for 12 days in the laboratory at different temperatures. Individuals from the
135 Norges River were acclimatized at three temperatures (10, 14, or 18°C), whereas individuals
136 from the Vèze River were separated into only two groups (14 or 18°C), due to sampling
137 limitations resulting from the low prevalence of infection with *P. minutus*. Temperatures were
138 chosen to be in accordance with naturally fluctuating temperatures experienced by gammarids
139 in their habitat (Pöckl *et al.*, 2003), and fell within the range of temperatures measured within
140 the two rivers in 2015 (S. Labaude, personal data). To limit stress, individuals were
141 maintained together in groups at each temperature, in an oxygenated mix of water collected in
142 their river and dechlorinated, UV-treated tap water. They were fed *ad libitum* with
143 conditioned elm leaves, and maintained under a 12:12 light:dark cycle regime. Due to
144 different technical requirements associated with the behavioral tests, water temperature was
145 controlled in two different ways. Because individuals had to be visible from above during
146 behavioral tests (see below), individuals from the Norges River were maintained in water
147 baths, following Labaude *et al.* (2017). Boxes containing individuals (and further test devices)
148 were plunged into water that was constantly pumped through a temperature control device
149 (TANK TK-1000 Chiller, Teco US). Individuals from the Vèze River, which were tested in
150 vertical devices, were maintained and tested in refrigerators with transparent doors (Liebherr
151 FKv 5443). These two systems allowed acclimatization and experiments for each population
152 at all temperatures to occur concomitantly in the same room. The water temperature was
153 controlled daily using digital thermometers.

154

155 *Phototaxis and refuge use*

156 Overall, 368 individuals (167 infected by *P. tereticollis* and 201 controls) from the
157 Norges River were used for phototaxis tests and, among them, 176 individuals (76 infected
158 and 100 controls) were randomly chosen to be tested for refuge use. The two sets of
159 experiments were conducted during the same day.

160 After the acclimatization period to different temperatures, single individuals were
161 introduced into horizontal glass tubes (22 cm long, 3.2 cm diameter) containing a dark zone
162 (half of the tube being covered with black plastic to ensure complete opacity) and a light zone,
163 following the design described in Perrot-Minnot (2004). Tubes were previously filled with
164 aerated water. Water temperature was maintained during the course of the experiment with
165 the same device as described for acclimatization. After 5 min of habituation in the tube, the
166 position of every individual was recorded every 30 s during 5 min and scored as zero (dark
167 zone) or one (light zone). Summed phototaxis scores for each individual ranged from zero
168 (strongly photophobic, always in the dark zone) to 11 (strongly photophilic, always in the
169 light zone).

170 To test for the use of refuges, single individuals were placed in boxes (10.5 × 16 cm)
171 filled with 250 ml of oxygenated water with temperature controlled for each group as
172 previously described. A refuge was available in each box, consisting of a saucer terracotta pot
173 (8.5 cm of diameter) cut in half, with a 1-cm hole in the convex part (see Dianne *et al.*, 2014).
174 After 5 min of habituation in the device following the introduction of gammarids, the position
175 of each individual was recorded every 2 min during a 30-min observation period, and scored
176 as zero (outside the refuge) or one (inside the refuge). Summed refuge scores ranged from
177 zero (always outside the refuge) to 16 (always inside) for each individual.

178 For the two tests, a random number was assigned to each individual in order to ensure
179 that the experimenter was unaware of the infection status of individuals.

180

181 *Geotaxis*

182 In total, 51 individuals infected by *P. minutus* and 59 uninfected individuals from the
183 Vèze River were used for geotaxis tests.

184 Geotaxis, the response of individuals to gravity, was estimated as the average vertical
185 position of individuals in the water column. After the acclimatization period, single
186 individuals were introduced in 500 ml-graduated measuring cylinders (35 cm high, 6 cm
187 diameter) filled with aerated water. Cylinders were vertically divided into five zones of equal
188 height. A plastic net was placed along the inside wall of each cylinder, providing gammarids a
189 substrate on which they could cling, as available on river banks. This was important since
190 both the swimming and clinging behaviors can be altered by the parasite (Bauer *et al.*, 2005).
191 Each cylinder was placed in a refrigerator at the relevant temperature. The light was presented
192 only horizontally, through the glass door, thus preventing any confounding vertical
193 phototactic reaction. After 2 min of habituation in the cylinder, the position of each gammarid
194 was recorded every 30 s for 5 min, and a score was given according to the zone within the
195 water column (from one for the bottom to five for the top). Summed geotaxis scores ranged
196 from 11 (always at the bottom) to 55 (always at the top) for each individual.

197

198 *Measurements and dissections*

199 At the end of the experiment, the sex of each individual was determined using the size
200 and shape of its first and second pairs of gnathopods, which are sexually dimorphic in
201 amphipods (Hume *et al.*, 2005). All individuals were measured (height of the fourth coxal
202 plate) using a Nikon ZMZ1500 dissecting microscope and Lucia G 4.81 software, and
203 dissected. The developmental stage (acanthella or cystacanth) and the species of parasites

204 found within gammarids were determined based on morphological identification. As
205 manipulation of the parasite depends on both acanthocephalan species and developmental
206 stage, only individuals harboring *P. tereticollis* (for phototaxis and refuge use tests) and *P.*
207 *minutus* (for geotaxis tests) parasites at the cystacanth stage were kept (hereafter referred as
208 “parasitized” individuals). Individuals harboring other acanthocephalan species (a few
209 *Pomphorhynchus laevis* and *Echinorhynchus truttae* were found), or acanthella stages were
210 discarded. Gammarids in which no parasite could be found were considered as “control”
211 individuals.

212

213 *Data analyses*

214 None of the three scores (phototaxis scores, refuge scores, and geotaxis scores) met
215 normality and homoscedasticity conditions, even after data transformation. We therefore used
216 non-parametric statistics. In both populations, the size of gammarids did not differ between
217 parasitized and control individuals (data not shown), and was thus not considered in
218 subsequent analyses. Comparisons between males and females for each infection status and at
219 each temperature showed that there was no difference in the scores of individuals, for the
220 three behaviors tested (data not shown). Therefore, sex was not considered in subsequent
221 analyses.

222 First, the effect of temperature on each score was assessed using Kruskal-Wallis tests.
223 The effect size of the differences between each temperature was then calculated for each score
224 and for each infection status (control or parasitized) using Cliff’s delta (Cliff, 1996). Cliff’s
225 delta was also used to compare the scores between control and parasitized individuals, at each
226 temperature. Cliff’s delta is a scale-less parameter, ranging from -1 to 1, that is robust to non-
227 normally distributed data. It is used to represent the size of the effect, in this case the

228 difference between two groups, as well as the direction of this difference. Moreover, its
229 confidence intervals can be used to assess the significance between these differences,
230 replacing classical statistic tests or post hoc tests. Medians and 95% confidence intervals of
231 the Cliff's delta were calculated using the R-package 'orddom' (version 3.1). Other statistical
232 analyses were performed using R version 3.1.1 software (R Foundation for Statistical
233 Computing).

234

235 **Results**

236 Temperature significantly affected the amount of time spent in light ("phototaxis
237 score") of *G. fossarum* individuals infected by *P. tereticollis* (Kruskal-Wallis, $\chi_2 = 22.86$, d.f.
238 = 2, $P < 0.0001$, Fig. 1A), and control individuals (Kruskal-Wallis, $\chi_2 = 23.30$, d.f. = 2, $P <$
239 0.0001 , Fig. 1A). The phototaxis score was significantly higher at 14°C and 18°C compared
240 to 10°C, in both parasitized and control individuals (Fig. 2A). However, while there was a
241 clear trend for phototaxis score to increase with temperature between 14°C and 18°C for
242 parasitized individuals, that of control individuals did not differ significantly between these
243 two temperatures (Fig. 2A), with even a trend to decrease. As a result, the difference of
244 behavior between control and parasitized individuals was significant at 14°C and 18°C, with a
245 stronger effect at 18°C (Fig. 2B).

246 Temperature had no effect on the amount of time spent inside refuges ("refuge score")
247 for both control individuals (Kruskal-Wallis, $\chi_2 = 0.57$, d.f. = 2, $P = 0.75$, Fig. 1B) and
248 infected ones (Kruskal-Wallis, $\chi_2 = 1.83$, d.f. = 2, $P = 0.40$, Fig. 1B). The refuge score of
249 individuals infected by *P. tereticollis* was lower than that of controls (Fig. 1B), illustrating a
250 lower trend to use refuges, although this difference was significant only at 18°C (Fig. 2B).

251 The non-significant differences were probably due to high inter-individual variation relative
252 to the small sample size.

253 Correlations between phototaxis scores and refuge scores were all non-significant. The
254 only trend observed was a negative correlation in parasitized individuals at 18°C (Table 1),
255 with the more photophilic animals spending also more time out of refuges.

256 The geotaxis score of *G. fossarum* individuals infected by *P. minutus* was significantly
257 higher than the score of control individuals (Fig. 3 and Fig 2B). Geotaxis scores were not
258 influenced by temperature, with no difference between the two temperatures tested for both
259 parasitized and control individuals (Fig. 3 and Fig 2).

260

261

Discussion

262 The temperature at which *Gammarus fossarum* were exposed for two weeks affected
263 the intensity of phototaxis of *G. fossarum*, particularly in those infected with
264 *Pomphorhynchus tereticollis* parasites. However, it had no impact on the time spent by
265 gammarids inside refuges, independently of infection. No effect of temperature was found on
266 gammarids geotaxis, whether infected or not by *Polymorphus minutus* parasites.

267 The differences in phototaxis observed between infected and control individuals across
268 the three temperature tested here suggest that parasite manipulation was less efficient at low
269 temperatures. Although both infected and uninfected animals were photophobic at low
270 temperature, a gradual reversal of photophobia was observed in infected individuals at higher
271 temperature, while this phenomenon stabilized in control individuals at the highest
272 temperature. The increase in the manipulation of gammarids by *P. tereticollis* might be due to
273 a physiological effect of temperature. Indeed, the metabolism of ectotherm species increases

274 with temperature (Gillooly *et al.*, 2001), including in acanthocephalan parasites which
275 develop faster at high temperature (Olson and Pratt, 1971; Tokeson and Holmes, 1982). Thus,
276 if the manipulation of host behavior is influenced by the physiology of parasites, it is possible
277 that increased temperatures led to more pronounced manipulation. However, such a
278 phenomenon hardly does not explain the increased phototaxis also observed in uninfected
279 individuals between 10°C and 14°C. The differences in phototactic behavior observed at
280 different temperatures might instead stem from the mechanisms underlying this behavior.
281 Serotonin plays a major role in the expression of phototactic behavior in gammarids:
282 *Pomphorhynchus* parasites increase the brain serotonergic activity of gammarids (Tain *et*
283 *al.*, 2006, 2007), and experimental injection of serotonin in uninfected individuals mimics the
284 behavioral changes induced by parasites (Perrot-Minnot *et al.*, 2014). The mechanisms by
285 which acanthocephalans induce modifications in gammarids serotonergic activity are
286 unknown (Lafferty and Shaw, 2013). However, serotonin production increases with increased
287 temperatures in invertebrates (Stefano and Catapane, 1977; Stefano *et al.*, 1977), as well as
288 many visual neural processes in invertebrates (Lim-Kessler *et al.*, 2008). These changes are
289 associated with modifications of other neuromodulators (Stefano and Catapane, 1977; Stefano
290 *et al.*, 1977), such that the consequences of these modifications can hardly be predictable.
291 However, an increase in serotonin levels could explain the increase of phototaxis between the
292 lowest temperature and the highest temperatures in our study, including in uninfected
293 gammarids. It is possible that in infected individuals, the level of serotonin due to increased
294 temperature and parasitic infection combine in the gammarid's brain to produce a higher
295 photophilic response. Serotonin levels were not measured here. Therefore, since the
296 invertebrate nervous system has a number of mechanisms designed to maintain homeostatic
297 function despite the temperature-driven changes (Lim-Kessler *et al.*, 2008) further studies are

298 needed to explore the mechanisms of the link between temperature, acanthocephalan parasites
299 and photophily in gammarids, in order to verify this hypothesis.

300 Although variations in serotonin levels explain variations in the phototaxis behavior of
301 gammarids, they have no significant effect on the gammarids' ability to use refuges (Perrot-
302 Minnot *et al.*, 2014). This may explain the absence of significant effect of temperature on this
303 trait in our study, and the lack of correlation between these two behaviors. Similarly, the
304 manipulation of *G. fossarum* by *P. minutus*, in terms of geotaxis, was not affected by
305 temperature, although the lowest temperature was not tested. However, the alteration of
306 geotaxis may not rely on the same mechanisms as the ones involved in the alteration of
307 phototaxis. Indeed, Tain *et al.* (2006) showed that the geotaxis of gammarids was not affected
308 by experimental injections of serotonin, and that infection by *P. minutus* did not induce
309 modifications in the serotonergic activity of gammarids. A recent study suggested a role of
310 anaerobic metabolism and hypoxia in the manipulation induced by *P. minutus*: uninfected
311 *Gammarus roeseli* displayed a negative geotaxis under hypoxia, while an injection of lactate
312 and succinate in uninfected gammarids also mimicked the parasite-induced reversion of
313 geotaxis (Perrot-Minnot *et al.*, 2015). It would be interesting to test the effect of temperature
314 variations large enough to induce higher changes in the amount of oxygen dissolved in the
315 water. If this were the mechanism, we would expect the geotaxis of both infected and
316 uninfected individuals to increase at high temperatures.

317 Overall, our study suggests that temperature might be responsible for variations in the
318 efficiency of the manipulation of certain behaviors of gammarids by acanthocephalans. In
319 particular, the global increase of temperature might induce a higher efficiency of manipulation
320 by some parasites, while other aspects of manipulation, or behavioral changes in other
321 species, might not be affected. Some of our results are in line with those obtained by Benesh
322 *et al.* (2009) in isopods. They found that, whereas the intensity of phenotypic changes induced

323 by the acanthocephalan *Acanthocephalus lucii* varied between seasons, experimental exposure
324 to different temperatures did not change the intensity of manipulation of host behavior. Our
325 study shows that some components of parasite-induced behavioral changes may be affected
326 by temperature variation. Although the metabolism of acanthocephalan parasites is highly
327 dependent on temperature, thus resulting in longer developmental time during cold periods
328 (Olson and Pratt, 1971; Tokeson and Holmes, 1982), variations in the rapidity of their
329 transmission to the next host might also arise from differences in their manipulation and
330 partly explain the seasonal distribution documented in some acanthocephalan parasites (Van
331 Cleave, 1916; Muzzall and Rabalais, 1975; Brown, 1989).

332 Parasites have numerous effects on communities and ecosystems, especially through
333 the manipulation of the behaviour of their hosts (see Lefèvre *et al.*, 2009; Labaude *et al.*,
334 2015b for reviews). Consequently, modifications in manipulation following changes in
335 temperature are also likely to have consequences at larger scales. In particular,
336 acanthocephalan parasites are responsible for many modifications in the ecology of
337 gammarids, including their feeding behaviour or microhabitat choice (Labaude *et al.*, 2017;
338 MacNeil *et al.*, 2003). More to the point, an increase in the predation facilitation induced by
339 parasites in response to increasing temperature might affect food webs, through alteration in
340 the interaction between gammarids and their predators, as well as the dynamics of the
341 populations of parasites, hosts and their predators. However, further studies are needed to
342 determine the effect of temperature on the ecological outcome of manipulation, *i.e.* its effects
343 in terms of predation facilitation induced by parasites. Indeed, although infected gammarids
344 are more predated by the definitive hosts of parasites than uninfected ones (Bethel and
345 Holmes, 1977; Perrot-Minnot *et al.*, 2007; Jacquin *et al.*, 2014), only certain behavioral
346 changes have been demonstrated to be linked to this predation enhancement. More precisely,
347 in gammarids, the presence of refuges and the intensity of their use was directly linked to

348 differences in predation rate of gammarids infected by *Pomphorhynchus* parasites vs.
349 uninfected ones (Kaldonski *et al.*, 2007; Dianne *et al.*, 2011, respectively), while the intensity
350 of change in phototaxis was not (Perrot-Minnot *et al.*, 2012). Similarly, the reversed geotaxis
351 behavior was responsible for an increased predation in gammarids infected by *Polymorphus*
352 parasites (Jacquin *et al.*, 2014). Here, it is worth noting that the only behavior affected by
353 temperature is the one for which no causal link with predation enhancement could be
354 established. However, many other parameters might interact in the success of predation. In
355 particular, the behavior of gammarids depends on predation risk (Médoc *et al.*, 2009; Durieux
356 *et al.*, 2012; Lewis *et al.*, 2012), while temperature might also alter the behavior of predators
357 themselves (Brett, 1971; Elliott, 1976). In addition, temperature is likely to affect other
358 parameters, such as the reproduction of parasites (Barber *et al.*, 2016), leading to
359 modifications in the population dynamics of both hosts and parasites that are hardly
360 predictable. Finally, we did not control the environmental conditions during the development
361 of parasites, and this can lead to other sources of variability. For instance, acanthocephalans
362 develop faster at high temperatures (Olson and Pratt, 1971; Tokeson and Holmes, 1982), and
363 the efficiency of their manipulation increases with time after they reached the cystacanth stage
364 (Franceschi *et al.*, 2008; Labaude *et al.*, 2015a). Thus, it cannot be discounted that, in our
365 experiments involving naturally-infected gammarids, those maintained at 18°C harbored
366 parasites that already reached their highest manipulative intensity, while the manipulative
367 intensity of gammarids kept at lower temperatures was still increasing. In addition, gammarid
368 metabolism increases with temperature to a certain extent (Roux and Roux, 1967; Pöckl and
369 Humpesch, 1990; Issartel *et al.*, 2005), along with their mortality (Maazouzi *et al.*, 2011;
370 Foucreau *et al.*, 2014). As parasites completely depend on the survival of their hosts before
371 transmission, they would benefit in increasing their manipulating effort when the life
372 expectancy of their hosts decreases to secure their transmission (Thomas *et al.*, 2002, 2011).

373 Consistent with this hypothesis, Poulin (1993) found that the intensity of behavioral changes
374 induced by trematode parasites was greater when their intermediate fish hosts were older.
375 However, contradicting with this hypothesis, no significant changes in refuge use were
376 observed in *G. pulex* infected with *P. laevis* under different survival conditions (Labaude *et*
377 *al.*, 2015a). Future studies might therefore benefit from investigating the effect of temperature
378 using experimental infestations, to control for environmental conditions during the
379 development of the parasites.

380

381

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607

608 **Tables**

609 **Table 1.** Correlations (Spearman’s rho) between phototaxis and refuge use scores in control
 610 and parasitized *G. fossarum*, at each temperature (10, 14, and 18°C).

Infection status	Temperature	Spearman’s rho	<i>P</i>
Control	10°C	-0.167	0.344
	14°C	-0.310	0.124
	18°C	-0.053	0.743
Parasitized	10°C	-0.017	0.936
	14°C	-0.186	0.432
	18°C	-0.416	0.020 ¹

611 ¹ non-significant after Bonferroni correction

612

613

614 **Figure Legends**

615 **Figure 1.** Individual *Gammarus fossarum* behavior scores for (A) phototaxis tests and (B)
616 refuge use tests, according to their infection status (P or C, respectively parasitized by *P.*
617 *tereticollis* or control) and temperature (10, 14, or 18°C). Thick lines represent medians,
618 boxes represent upper and lower quartiles, and dotted lines represent upper and lower deciles.
619 Sample sizes are indicated at the bottom of the graph.

620

621 **Figure 2.** Effect sizes (Cliff's delta, d) of the behavioral differences (A) between
622 temperatures, for each test and each infection status (parasitized and control), and (B) between
623 parasitized and control *G. fossarum* individuals, for each test (phototaxis, refuge use, and
624 geotaxis) at each temperature (10, 14, and 18°C). Cliff's delta effect sizes are represented
625 with their 95% confidence intervals, and their values are given. Values below zero (dotted
626 line) indicate that the behavioral score was higher for the group specified on the left, while
627 values above zero indicate higher scores for the group mentioned on the right. The difference
628 is significant when the bar does not overlap zero. For instance, the first row indicates that
629 phototaxis scores of control individuals were significantly higher at 14°C compared to 10°C.

630

631 **Figure 3.** Individual *Gammarus fossarum* geotaxis scores according to their infection status
632 (P or C, respectively parasitized by *P. minutus* at the cystacanth stage, or control) and
633 temperature (14 or 18°C). Thick lines represent medians, boxes represent upper and lower
634 quartiles, and dotted lines represent upper and lower deciles. Sample sizes are indicated at the
635 bottom of the graph.

636

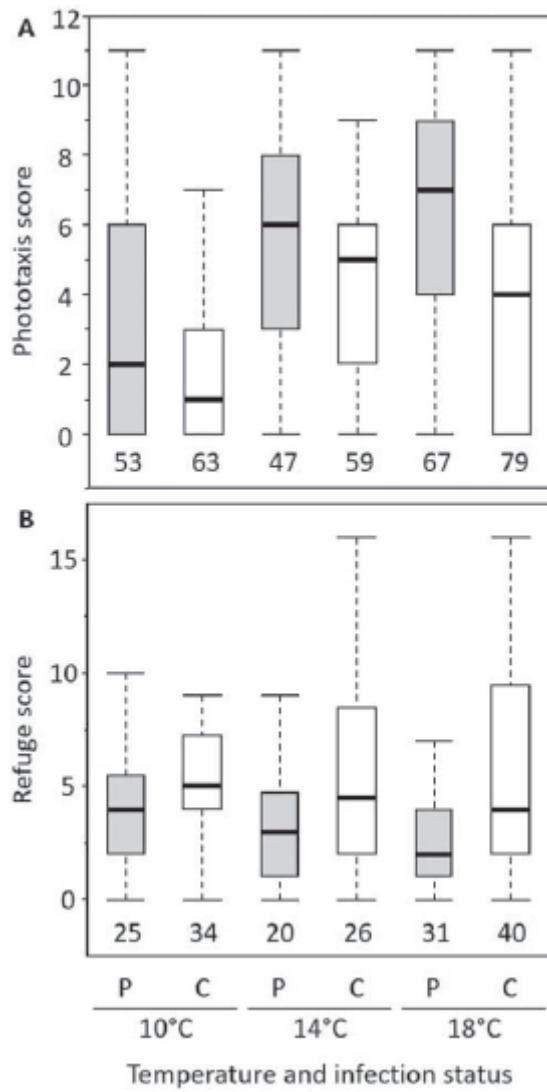
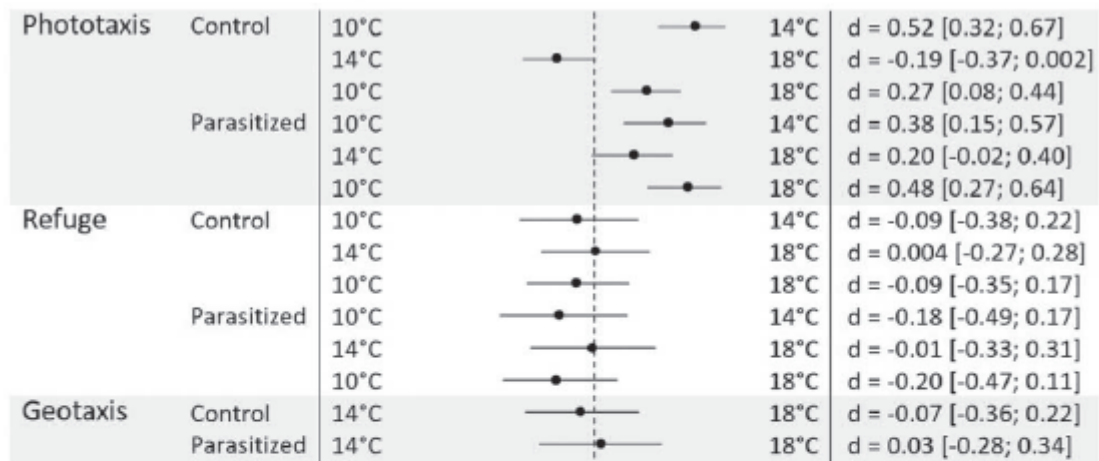


Figure 1

A. Comparisons between temperatures



B. Comparisons between control and parasitized individuals

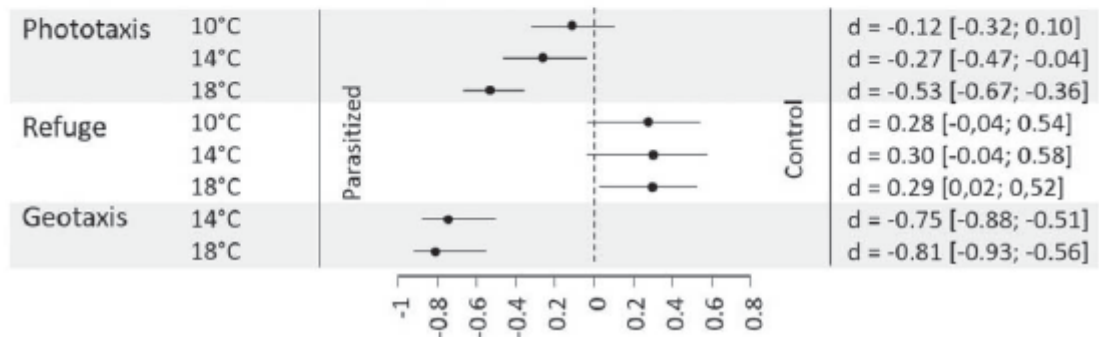


Figure 2

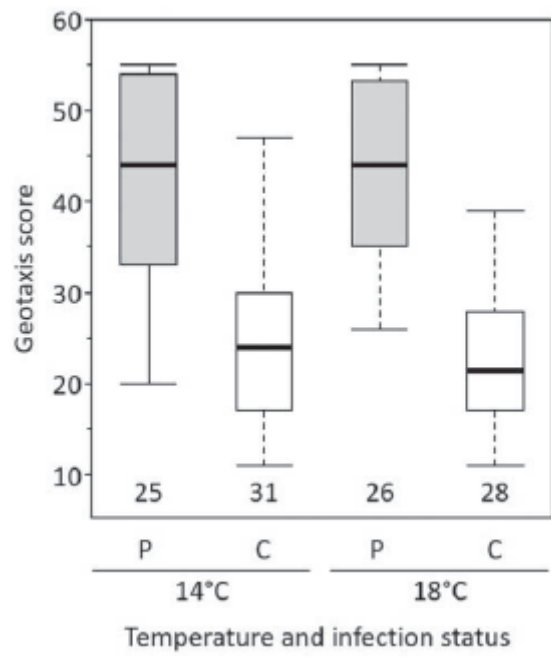


Figure 3