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Hadrien Fanton, Evelyne Franquet, Maxime Logez, Nicolas Kaldonski. Effects of temperature and a manipulative parasite on the swimming behaviour of *Gammarus pulex* in flowing water. *Hydrobiologia*, 2021, pp.1-10. 10.1007/s10750-021-04655-1 . hal-03392198

HAL Id: hal-03392198

<https://amu.hal.science/hal-03392198>

Submitted on 22 Feb 2022

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Effects of temperature and a manipulative parasite on the swimming behaviour of *Gammarus pulex* in flowing water

Hadrien Fanton  · E. Franquet · M. Logez  · N. Kaldonski

Abstract Numerous freshwater acanthocephalans are able to alter the behaviour of their intermediate hosts to increase their predation risk by final hosts, thereby enhancing trophic transmission between their two hosts. Because temperature is widely expected to impact freshwater host-parasite interactions, we investigated how it can affect movements of both uninfected and *Pomphorhynchus laevis*-infected *Gammarus pulex* in an artificial stream in 5 cm/s water flow. We found that *P. laevis* infection of *G. pulex* induced both higher frequency and higher amplitude of movements along the artificial stream. Moreover, at warmer temperature (21°C), uninfected and *P. laevis*-infected *G. pulex* moved more in the artificial stream than at 15°C. In this regard, warmer temperature could then impact gammarids distribution and increase *P. laevis* transmission rate toward their definitive host in freshwater ecosystems. Firstly, this study provides new insights into how the key temperature factor influences gammarids species movements in the stream. Secondly, elevated temperature did not

influence the intensity of *P. laevis* manipulation in *G. pulex* intermediate host. This work highlights that warmer temperature might affect the distribution and the behaviour of infected or uninfected freshwater gammarids with no direct effect on acanthocephalan trophic transmission through manipulation.

Keywords Host–parasite interaction · Freshwater · Complex lifecycle parasite · Acanthocephala · Amphipoda · *Pomphorhynchus laevis*

Introduction

Parasites form a vast network of dynamic, and ubiquitous species (Dobson et al., 2008). Found in every food web and at all trophic levels, they are part of the functioning, structure and richness of ecosystems (Horwitz & Wilcox, 2005; Marcogliese, 2005; Mouritsen & Poulin, 2005; Dunne et al., 2013). This hidden component of biodiversity participates in 75% of interactions among free-living species, and frequently impact the behaviour of their hosts (Horwitz & Wilcox, 2005; Dobson et al., 2008; Kuris et al., 2008; Grabner, 2017). This is particularly true for complex lifecycle acanthocephalans, which need at least two hosts to complete their lifecycle and a predation event whereby the intermediate invertebrate host is eaten by the vertebrate final hosts. By their multilevel position

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in food webs, acanthocephalans shape ecosystems through effects on both physiology and behaviour of their hosts species (Hudson et al., 2006; Vidal-Martinez et al., 2010).

Pomphorhynchus laevis (Zoega in Müller, 1776) is a widespread parasite across the Palearctic region (Hine & Kennedy, 1974; Dudiňák, 2001). It lays its eggs in the faeces of its definitive host fish in rivers, where they have to be eaten by an amphipod (Crustacea) to mature and become infective to definitive hosts (Kennedy, 2006). The freshwater amphipod involved in this cycle is very often *Gammarus pulex* (Linnaeus, 1758), an abundant shredder and scavenger species in Mediterranean streams (Elliott, 2002). It constitutes also an essential trophic resource for many aquatic predators like fishes (Anderson & Sedell, 1979; Elliott, 2005). Upstream and downstream migrations play a fundamental role in the population dynamic of gammarids (Elliott, 1973). Two types of amphipod movements are usually described, (1) drift which is the movement of gammarids carried by the current from upstream to downstream of the water-course (Bournaud & Thibault, 1973, Brittain & Eikeland, 1988), and (2) upstream movements which is the displacement of gammarids against the flow, generally occurring close to stream margins (Elliott, 2002). These two behaviours enable amphipods to escape unfavourable conditions like competition, lack of food or predation risk (Brittain & Eikeland, 1988).

Like many other acanthocephalan parasites, *P. laevis* alters the behaviour of *G. pulex* to enhance trophic transmission to definitive host fishes (Kaldonski et al., 2007; Lagrue et al., 2007; Cézilly et al., 2013; Perrot-Minnot et al., 2016). The behavioural manipulation of hosts' movements in the stream by *P. laevis* constitutes one of the major targets for the parasite. *Pomphorhynchus laevis* induces a higher activity of *G. pulex* in streams and a greater drift rate, mainly at dawn and dusk when fish predators are more active (McCahon et al., 1991; Lagrue et al., 2007). Such phenotypic alterations clearly increase predation risk on the intermediate host, thereby enhancing the trophic transmission of *P. laevis* toward their definitive host (Baldauf et al., 2007).

Temperature is a key environmental factor affecting both the physiology and the behaviour of freshwater organisms (Sainte-Marie, 1991; Foucreau et al., 2014; Kobak et al., 2017; Rachalewski et al., 2018), including associated parasites (Marcogliese, 2001).

Increased water temperatures will, for example alter, spatial distribution, food intake, metabolic activity, survival and resistance to parasites in gammarids (Marcogliese, 2008; Moenickes et al., 2011). *Gammarus pulex* has been shown to have higher growth rates, food intake, oxygen consumption and energy storage when temperature increased from 15 to 30°C (Foucreau et al., 2013, 2014). As a result, acanthocephalans phenotype will be indirectly affected through intermediate hosts' physiological modifications (Brooks & Hoberg, 2007; Foucreau et al., 2013; Morley & Lewis, 2014; Labaude et al., 2015). According to Overstreet (1993), "the more complex the parasite life cycle, the more likely it is that the parasite will be influenced by environmental parameters", because acanthocephalans can be affected through effects on their hosts at all developmental stages. Warming water impacts acanthocephalan establishment, development, fecundity and lifespan in their hosts (Tokeson & Holmes, 1982; Marcogliese, 2008; Morley & Lewis, 2014; Barber et al., 2016). Labaude et al. (2017) found for example, that *Gammarus fossarum* Kock, 1836 attraction to light induced by *Pomphorhynchus tereticollis* (Rudolphi, 1809) increased with water temperature. These results demonstrate that acanthocephalan extended phenotype can be modulated according to their host aquatic environment. However, Labaude et al. (2020) found no effect of temperature on the manipulation behaviour of *P. laevis* in static water. Therefore, the way that acanthocephalan manipulate their hosts depending on such environmental constraints still requires further investigation to better understand how trophic transmission and ecosystem functioning could be affected by climate change (Marcogliese, 2001).

The main objective of this study was to assess the influence of water temperature on the host-parasite *G. pulex*-*P. laevis* interaction in an artificial stream. Using an artificial stream, we are able to assess uninfected and *P. laevis*-infected gammarids movements in the flow. We hypothesized that *P. laevis* would increase the dispersal movements (both upstream and downstream movements) of their intermediate host in flowing water. We also hypothesized that warmer water would increase the movements of uninfected and infected *G. pulex*. Providing new insights into acanthocephalan capacity for behavioural manipulation of hosts. This study helps to clarify how environmental conditions like warmer temperatures

could alter the behaviour and the ecology of a free-living freshwater species and its associated parasite.

Materials and methods

Sampling and acclimatisation to laboratory conditions

Gammarus pulex were collected in March and April 2015 from the Arc River (Bouches-du-Rhône, Southern France). Water temperature in the Arc ranges between 4°C in winter and 27°C during the warmer periods of summer (Maasri et al., 2008). During the sampling period water temperature of the Arc River ranged between 13 and 16.5°C and the average discharge range between 1 and 3 m³/s depending on weather events. Infected and uninfected gammarids were sampled with a hand net in gravel, roots and aquatic vegetation along riverbanks where gammarids are abundant (Piscart et al., 2007). Juvenile gammarids (< 0.5 cm) were excluded.

After each sampling campaign, gammarids were placed in six 21 L aquaria (60 × 35 × 10 cm) equipped with oxygen bubblers, filled with 6–8 cm of water and 1 cm of substrate (fine gravel previously washed) for a period of 7 days. To limit intraspecific competition and cannibalism, gammarids were fed ad libitum with leaves and shrimp food and the number of gammarids was limited to 100 individuals per aquarium. Water used for acclimatisation and experiments was saturated with oxygen. Temperature was maintained at 15°C ± 1°C. A Trulite® neon light recreated 95% of the quality of the natural light spectrum (5200°K, 400–600 Lux) and operated under a cycle of 12 h/12 h light and dark regime.

Experimental design

Acclimatisation to temperature

After acclimatisation, *G. pulex* were placed for five days, in 96 L aquaria (80 × 30 × 40 cm) containing 30 cm of water and 1 cm of gravel. One aquarium was maintained at the controlled water temperature of 15°C and a second at 21°C with a 150 W Rena® Smart resistance heater. The temperature of 15°C was chosen in accordance with the natural temperature of the Arc River during the sampling period, and 21°C

simulated summer water temperature in a the Arc River (Maasri et al., 2008), and a potential effect of global warming on spring freshwater. A Plexiglas plate covered aquaria to prevent heat loss and to limit evaporation.

Experimental device: the artificial stream

After thermal acclimatisation, we observed the behaviour of gammarids in two artificial streams simultaneously, one at 15°C and the second at 21°C. The artificial stream (Fig. 1) consisted of a graduated PVC gutter of 100 × 17 × 10 cm with a slope of 0.9°, divided into seven sections of 10 cm each. This gutter was upholstered with a net (1 mm mesh) serving as a substrate for gammarids over the whole length of the gutter. A water pump placed in a 30 L tank created a constant flow of water (1200 L/h). Fresh water continuously flowed into the artificial stream, replicating a slow current (5 cm/s), and the gammarids could swim and cling in or against the flow.

Behavioural observations

Gammarus pulex were observed in April and May. For each observation, one *G. pulex* was randomly selected from the 96 L aquaria and acclimatised in the device for 5 min, in section “1” of the artificial stream (upstream section), using a grid (Fig. 1). Isolation in section “1” ensured minimum disturbances to individuals with only one grid to manipulate. The grid was then removed, marking t0 of the behavioural

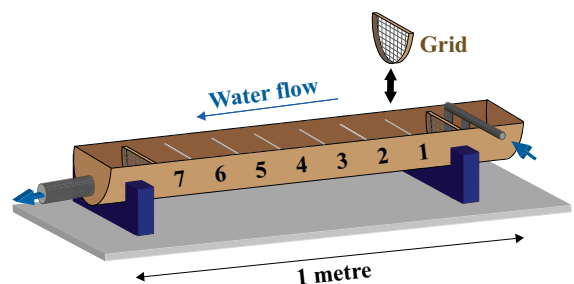


Fig. 1 Illustration of the artificial stream (100 × 17 × 10 cm) used for behavioural experiments. Gammarids were observed in a 7-section device (section length = 10 cm, numbered 1 to 7). Blue arrows indicate direction of flow. The “grid” was used to isolate individuals in section “1” of the device for 5 min. The artificial stream was supplied with fresh water via a pump placed in a 30 L tank and creating a constant flow

observation. Behavioural observations used in our study was similar to the protocol of Cézilly et al. (2000) used to assess *G. pulex* vertical distribution. *Gammarus pulex* behaviour was visually tracked for 5 min and, every thirty seconds, the observer noted the number of the section of the artificial stream where the individual was located.

Dissection and parasite identification

After behavioural observations in the artificial streams, gammarids were preserved in ethanol (90%). Individuals were measured (size of the fourth coxal plate) and sexed according to the morphology of the second pair of gnathopods (Hume et al., 2005) with a SMZ1500 Nikon binocular lens (Mitsubishi, Tokyo, Japan) attached to a R1 Nikon camera (Mitsubishi, Tokyo, Japan) connected to a computer with NIS-Br software.

Gammarus pulex were dissected to check for parasite occurrence. Uninfected *G. pulex* were considered as “control” individuals. Phenotypic alterations induced by acanthocephalans in their intermediate hosts depends on both acanthocephalan species and developmental stage of the parasite. Therefore, only gammarids infected with cystacanth stages of *P. laevis* were used for the analyses, and acanthella stages were excluded. Developmental stage and species of parasites were determined based on morphological identification following Perrot-Minnot (2004).

Behavioural analysis

Two types of gammarid behaviours were determined: “movement score” and “position score”. Movement score was considered as the number of sections crossed by a gammarid. For example, an individual observed successively in sections 1–1–2–2–3–6–4–3–4–7 was considered to have crossed at least 9 sections in the flow (downstream movements) and 3 sections against the flow (upstream movements). The movement score was the total number of sections crossed, for this example above it was equal to 12. We then also broke down this movement score into downstream movements and upstream movements. Position score was obtained by adding together the ten positions (section number) recorded every 30 s over the 5 min of observation. For example, if a *G. pulex* was

observed successively in section 1–1–2–2–3–6–4–3–4–7, its score on movement amplitude was 33. This score indicated how observed individuals used the artificial stream space. For each observed gammarid, position scores ranged from 10 (always in the most upstream section of the device) to 70 (always in the most downstream section of the device).

Statistical analyses

We considered the influence of both *G. pulex* size and sex on behavioural observations using, respectively, Pearson correlation tests and Mann–Whitney tests. To analyse the potential effect of parasite load on host behaviour with Mann–Whitney tests, *G. pulex* were assigned to two different categories corresponding to gammarids harboring one or, two or more *P. laevis*. Two-way ANOVAs were performed to determine the statistical significance of the effects of *P. laevis* infection (two-modalities; no parasite, parasite occurrence), temperature (two-modalities; 15 and 21°C) and, their interaction on behavioural variables (movement score, downstream movements, upstream movements and, position score). Residual diagnostic indicated that the normality assumption for linear models were met but not the homogeneity of variances (heteroscedasticity). Therefore, we used generalized least squares (GLS) which extends the linear model by modelling the heterogeneity with covariates, here the combination of *P. laevis* infection and, temperature (Zuur et al., 2009). For each GLS, the interaction between temperature and *P. laevis* infection was not significant (*F*-tests, all *P*-values > 0.05). Therefore, we considered only the additive effects (without interaction) of temperature and *P. laevis* infection. Statistical analyses were conducted using R 3.5.0 software (R Core Team, 2018, A Language and Environment for Statistical Computing), and the additional libraries “nlme” (Pinheiro et al., 2019), “AICmodavg” (Mazerolle, 2019), “ggplot2” (Wickham, 2016) and, “car” (Fox & Weisberg, 2018).

Results

A total of 48 uninfected and 54 *P. laevis*-infected *G. pulex* were observed at 15°C, and 41 uninfected and 42 *P. laevis*-infected *G. pulex* at 21°C. Gammarid size did not affect neither the movement score (Pearson

correlation test: $r = 0.12$, $P = 0.08$), or position score of gammarids (Pearson correlation test: $r = 0.11$, $P = 0.13$). At the end of experiments, 103 males, 72 females, and 10 sexually unidentified individuals were observed. Gammarid sex did not affect the movement score (Mann–Whitney test: $W = 3,781.1$, $P = 0.12$). Male *G. pulex* had higher position score than female *G. pulex* (Mann–Whitney test: $W = 3,424.5$, $P < 0.05$).

We found 72 *G. pulex* infected with one *P. laevis* and 24 *G. pulex* infected with 2 or more than 2 *P. laevis*. Parasite load of *P. laevis* in *G. pulex* did not affect the gammarids' position score (Mann–Whitney test: $W = 1,033$, $P = 0.19$) or the movement score (Mann–Whitney test: $W = 982$, $P = 0.37$).

Pomphorhynchus laevis infection increased the movement score ($P < 0.001$, Table 1; Fig. 2), downstream movements ($P < 0.001$, Table 1; Fig. 3), upstream movements ($P < 0.001$, Table 1; Fig. 4) of gammarids. *Pomphorhynchus laevis* infection also increased the position score of gammarids ($P < 0.001$, Table 1; Fig. 4).

Temperature significantly increased movement score of gammarids ($P < 0.05$, Table 1; Fig. 2) and upstream movements by uninfected and *P. laevis*-infected *G. pulex* ($P < 0.01$, Table 1; Fig. 4) but did not affect the downstream movements of *P. laevis*-infected *G. pulex* (Table 1; Fig. 3). Temperature did not affect the position score of uninfected or infected *G. pulex* with *P. laevis* (Table 1; Fig. 5). Gammarid position score in our experimental device was not affected by temperature, regardless of whether or not they were infected by *P. laevis*. There was no interaction between infection and temperature were found for any of the four behaviour observed.

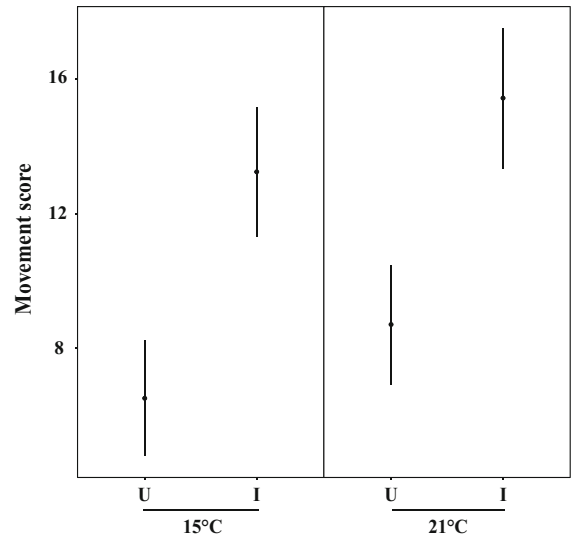


Fig. 2 Marginal effects of temperature and parasitism on the movement score represented by the expected values of each group (dots) and their confidence interval (95%, lines). (U) represent uninfected *G. pulex* and (I) *P. laevis*-infected *G. pulex* at the temperature tested (15°C and 21°C)

Discussion

Effects of *P. laevis* infection

The aim of this study was to explore how *P. laevis* manipulate the behaviour of their intermediate host *G. pulex* in flowing water and to determine whether water temperature impacts this behavioural manipulation and the behaviour of uninfected *G. pulex*. First, our results clearly indicate that *P. laevis* infection increased not only the movements of their hosts but also the position in the artificial stream. Compared to uninfected gammarids, *P. laevis*-infected gammarids were found more often in the downstream sections of

Table 1 Effects of the *P. laevis* infection (uninfected or *P. laevis*-infected *G. pulex*), and temperature (15°C or 21°C)

		MS	DM	UM	PS
<i>P. laevis</i> infection	<i>F</i> value	35.505	40.598	27.023	41.390
	<i>P</i> value	***	***	***	***
Temperature	<i>F</i> value	4.708	1.719	7.717	3.269
	<i>P</i> value	*	0.152	**	0.072

No effect of interaction between *P. laevis* infection and temperature were found for any of the four behaviour observed. Each column represents one GLS model for the movement score (MS), downstream movements (DM), upstream movements (UM) and position score (PS) covered by hosts. The observed *F*-statistic values and their associated significance levels represented by stars (***) $P < 0.001$, (**) $P < 0.01$, (*) $P < 0.05$, nothing if $P > 0.05$)

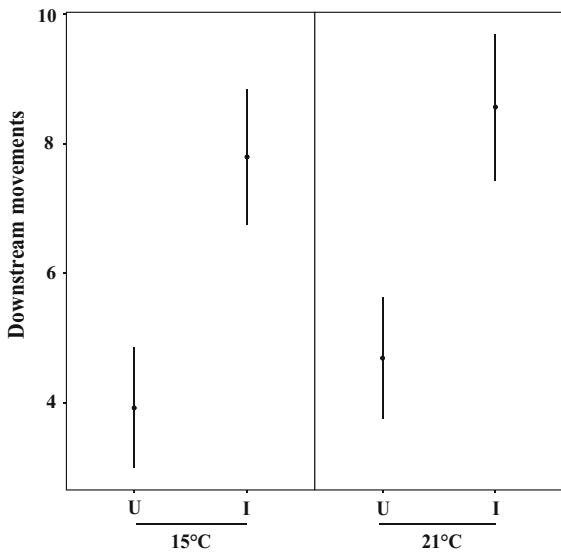


Fig. 3 Marginal effects of temperature and parasitism on downstream movements represented by the expected values of each group (dots) and their confidence interval (95%, lines). (U) represent uninfected *G. pulex* and (I) *P. laevis*-infected *G. pulex* at the temperature tested (15°C and 21°C)

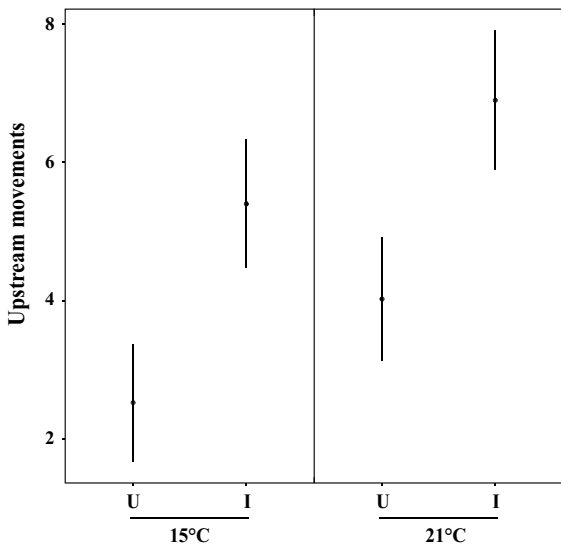


Fig. 4 Marginal effects of temperature and parasitism on upstream movements represented by the expected values of each group (dots) and their confidence interval (95%, lines). (U) represent uninfected *G. pulex* and (I) *P. laevis*-infected *G. pulex* at the temperature tested (15°C and 21°C)

the artificial stream. Moreover, our results show that *P. laevis* increase both downstream and the upstream movements of *G. pulex*. Consistent with the experimental studies of Maynard et al. (1998) and Wellnitz

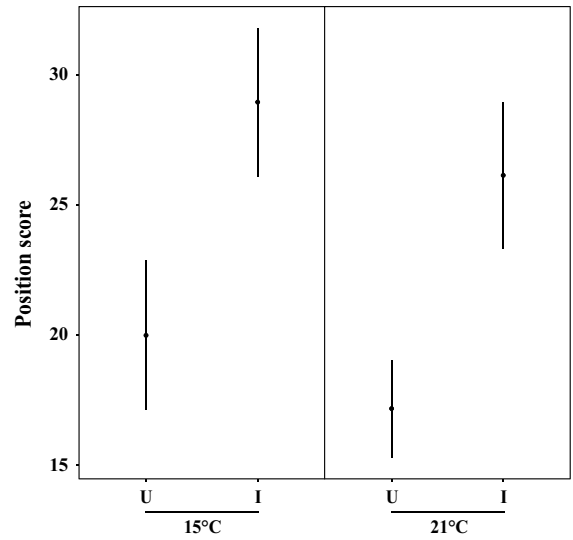


Fig. 5 Marginal effects of temperature and parasitism on the position score represented by the expected values of each group (dots) and their confidence interval (95%, lines). (U) represent uninfected *G. pulex* and (I) *P. laevis*-infected *G. pulex* at the temperature tested (15°C and 21°C)

et al. (2003) showing that *P. laevis*-infected *Echinogammarus stammerii* (S. Karaman, 1931) drift more and had higher activity, our results confirm the same behavioural alterations in the *G. pulex*-*P. laevis* host-parasite complex. Furthermore, these results are consistent with *in natura* experiments that have shown that infection by *P. laevis* modify the intentional drift and the upstream movements of gammarids (McCahon et al., 1991; Maynard et al., 1998; Lagrue et al., 2007). The prevalence of *P. laevis* can reach 25% in gammarids (Dezfuli et al., 1999), enough to potentially impact gammarid distribution and dispersion in the stream. Shaping *G. pulex* individuals and therefore the population, *P. laevis* could modify food webs through their capacity to increase host dispersal in the stream. For example, the study of Wellnitz et al. (2003) showed that *P. laevis*-infected *E. stammerii* increased their drifting behaviour and compensated less with upstream movements than uninfected gammarids, and this may disrupt gammarids distribution in the stream or moreover increase downstream overcrowding. Moreover, gammarids use these downstream or upstream displacements to find food or sexual partners and to avoid intraspecific competition or predation. This is why any behavioural shift

induced by acanthocephalan parasites may have wide-ranging consequences.

Fishes are known to feed extensively on drifting invertebrates, and this is considered as an adaptative behaviour to avoid predators, which hunt mainly by sight during the day (Macneil et al., 1999). Changes in the movements of their intermediate hosts induced by acanthocephalans increase the probability of predation by definitive hosts and enhance transmission rate (Maynard et al., 1998; Cézilly & Perrot-Minnot, 2005; Lagrue et al., 2007). Increasing movements with or against the flow by a gammarid host undoubtedly increases the risk of predation by a definitive host, because the intermediate host spends more time outside shelter and exposed to the definitive host predator (Waters, 1984). Energy costs could be higher if a gammarid swims or clings against the flow, however, *P. laevis*-infected gammarids moved more, both with and against the flow, despite potential higher metabolic cost against the flow. All the *G. pulex* movements were affected by *P. laevis* cystacanths to potentially increased definitive host predation rate and its own transmission.

Effects of temperature

Our results indicate that temperature is an important environmental factor influencing both: host and acanthocephalan parasites. At a temperature of 21°C, *P. laevis*-infected and uninfected *G. pulex* had higher movement score and higher upstream movements in the artificial stream than at 15°C. Nevertheless, no interaction effect between temperature and *P. laevis* infection was found. These results highlight that temperature is a factor influencing the movements of gammarids but that it does not influence the manipulation effects of *P. laevis* on *G. pulex*. In accordance with the study of Labaude et al. (2020) in static water, we did not find an amplification of *P. laevis* manipulation under warmer conditions in flowing water. According to Marcogliese (2008), acanthocephalan parasites could be affected by variations in water temperature: if water temperature increases, metabolic changes induce a shorter lifespan and faster growth, with a modification in their transmission capacities. Findings of Labaude et al. (2017), provide the first evidence that temperature affects the behavioural alteration of *P. terreticollis* in its *G. fossarum* intermediate host. These results show that temperature

is a key environmental factor which could activate host manipulation (Labaude et al., 2017). Another study by Benesh et al. (2009) showed seasonal changes in the behavioural manipulation of *Acanthocephalus lucii* (Müller, 1776) according to temperature. Our results provide evidence that behavioural manipulation of *P. laevis* was not affected by water temperature. At the highest temperature of 21°C, *P. laevis* did not modify or adjust their manipulation capacities compare to 15°C. In the Arc River, freshwater temperature easily reaches 21°C and *G. pulex* density is at its highest during summer (Maasri et al., 2008; Zganec et al., 2013). *Pomphorhynchus laevis* still induce the same intensity of manipulation when the water temperature is warmer in order to potentially increase the predation rate by definitive host on its intermediate host and therefore its transmission rate. However, elevated temperature could affect the behavioural manipulation indirectly through effects on many parameters of the metabolism of acanthocephalans (Labaude et al., 2020). For example, a faster development of acanthocephalans induced by warmer temperature reduced the time to reach the infective cystacanth stage in their intermediate host. It could be interesting to compare the capacity of transmission with more extreme hotter and colder water temperature than tested in this study and in Labaude et al. (2020), to see if parasite metabolic changes induced by warmer temperature could have an effect on their manipulation ability.

For uninfected gammarids, we found evidence of a temperature effect on movement score and upstream movements in our artificial stream. Temperature is known to be a key factor for the dispersal of gammarids, since seasonal changes in drift are usually positively correlated with water temperature (Goedmakers & Pinkster, 1981) and density (Elliott, 2002). Our results corroborate with those of Zganec et al. (2013) that found that temperature was the most significant driver of upstream displacements for *G. fossarum*. This study highlights a temperature effect on *G. pulex* behaviour, but gammarids physiology can also be affected by temperature changes. According to Foucreau et al. (2014), *G. pulex* have a reduced lifespan above 21°C. We also know that thermal optimum differs among gammarids species and sex (Rachalewski et al., 2018), and there is local adaptation by different populations of *G. pulex* living in contrasting thermal conditions (Foucreau et al., 2016).

Mediterranean *G. pulex* populations exhibit a higher survival rate and better thermal window than northern populations (Foucreau et al., 2013), and *G. pulex* are accustomed to high variability of temperatures (Cid et al., 2017). During summer, the Mediterranean rivers water temperature easily reaches 21°C or more, and *G. pulex* could show behavioural adaptations to the high temperature variability between seasons (5–27°C). In Mediterranean populations of *G. pulex*, the highest peak of density occurs from the beginning of summer until autumn (Zganec et al., 2013). In this regard, increased displacements in the stream by *G. pulex* should be common during summer, and principally driven by intraspecific competition for resources or reproduction due to high population density. At warmer temperature gammarid's upstream foraging movements could increase to avoid downstream overcrowding and competition and to reach colder upstream water (Zganec et al., 2013).

Conclusion

This study highlights (1) the higher movement in or against the flow by *G. pulex* infected with the parasite *P. laevis* compared to uninfected *G. pulex*, (2) higher temperature led to greater movements of uninfected and *P. laevis*-infected *G. pulex* in flowing water, and (3) that higher temperature did not influence the manipulation of *P. laevis* on its *G. pulex* intermediate host. In the current context of global warming, Mediterranean freshwaters constitute one of the most vulnerable ecosystems, and future shifts in water temperature may modify the ecology of aquatic acanthocephalan parasites and their host populations (Daufresne et al., 2004; Diffenbaugh et al., 2007; Marcogliese, 2008). Elevated temperature might affect the behaviour of host–parasite complex but have low effect on parasite trophic transmission. Further investigations of the effect of temperature will be required, to shed light on how these new environmental conditions will alter the ecology and the behaviour of free-living freshwater species and their associated parasites (Cizauskas et al., 2017; Buchholz et al., 2019).

Acknowledgements We thank Benjamin Oursel and Anthony Penalva for their help with gammarid sampling. We thank Eric Meineri for his help with statistics. We are grateful to Coralie

Jacquemin and Maxine Thorel for their comments and suggestions, which helped improve an earlier version of the manuscript. Finally, we thank Marjorie Sweetko for improving the English wording of this manuscript.

Funding This work was funded by the Labex DRIIHM, French Program “Investissements d’Avenir” (ANR-11-LABX-0010) managed by the ANR within the Observatoire Hommes-Milieux Bassin Minier de Provence (OHM BMP) and the ECCOREV Research Federation (FR 3098). Hadrien Fanton received a PhD Fellowship from the Ministère de la Recherche et de l’Enseignement Supérieur, the Aix-Marseille Université, École Doctorale Sciences de l’environnement (ED 251), and this paper is part of his Ph.D. thesis.

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