

Adaptive parasitic manipulation as exemplified by acanthocephalans

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Abstract

Parasites with complex life cycles often change intermediate host traits in order to enhance their transmission to the next host. Acanthocephalans are excellent examples of such parasitic manipulation. Here, we summarise evidence for adaptive parasitic manipulation in this group, provide a comprehensive overview of intermediate host traits affected by these parasites and discuss critical items for parasitic manipulation such as avoidance of infected prey by target hosts and transmission to dead-end hosts.

KEYWORDS

costs of manipulation, dead-end host, intermediate host, net fitness benefit, parasite transmission, parasite-induced trait changes

1 | PARASITIC MANIPULATION OF HOST TRAITS

One of the most remarkable results of species interactions in the animal kingdom is the changed appearance, behaviour or reproduction of individuals infected with parasites (Heil, 2016; see supplementary Table S1 for parasite-induced trait changes by Acanthocephala). Such alterations are often induced by parasites with a complex life cycle that infect intermediate hosts (Heil, 2016; Moore, 2002; Poulin & Maure, 2015). Here, parasite transmission requires that the intermediate host is eaten by a further intermediate host or the final host, leading to the death of the intermediate host. It is tempting to ascribe the changes in host phenotype to parasitic manipulation, which has been described as “the ability of certain parasites to modify host behaviour, appearance or physiology to their own advantage” (Poulin & Maure, 2015). The most obvious cases of parasitic manipulation lead to enhanced transmission by increasing predation. Decreased predation prior to parasite transmission may be as well due to parasitic manipulation (Parker, Ball, Chubb, Hammerschmidt, & Milinski, 2009; see Table S1, e.g., concerning Acanthocephala).

One can distinguish two categories of parasitic manipulation that both make the intermediate host more prone to predation by the target host. First, parasites can alter the general phenotype of the intermediate host. Indeed, the appearance of many intermediate hosts is frequently changed by the parasite. While uninfected intermediate hosts

are usually coloured cryptically infected ones show bright coloration and abnormal behaviour like hyperactivity. Famous examples for such change in crypsis include the pulsating antennae of land snails (e.g., *Succinea putris*) infected by the parasitic trematode *Leucochloridium paradoxum* (Halík, 1931), or the bright red, berry-like gasters of the tropical arboreal ant *Cephalotes atratus*, which increase transmission of the parasitic nematode *Myrmeconema neotropicum* to birds (Yanoviak, Kaspari, Dudley, & Poinar, 2008). Second, behavioural responses to predation can be altered by the parasite. While uninfected intermediate hosts actively try to avoid areas of high predation risk and adjust their behaviour in the presence of predators (Lima & Dill, 1990), infected intermediate hosts are attracted by predatory cues and seek the vicinity of predators. A famous example is *Toxoplasma gondii* reversing the aversion of rats towards cats into a fatal attraction (e.g., Berdoy, Webster, & Macdonald, 2000).

Manipulation is expected to come along with costs not only for the host, but also for the parasite (Poulin, 2010; Poulin, Fredensborg, Hansen, & Leung, 2005). These may comprise production as well as maintenance costs. Consequently, parasitic manipulation should target host traits that are cheap to alter, that is they should modify pre-existing traits rather than inducing completely novel traits. For instance, exploitation of the natural predator avoidance of prey animals, that is predation suppression, is predicted to evolve easier than the opposite, that is predation enhancement (Parker et al., 2009). The evolution of predation enhancement of intermediate hosts by parasites is more likely when the parasite will be selectively transmitted to

its favoured final host (Parker et al., 2009), thus reducing the costs of ending in the wrong host.

2 | CRITICISM OF MANIPULATION

There exists considerable scepticism as to the evidence for parasitic manipulation (see, e.g., Heil, 2016 for discussion). Criticism includes: (i) the abnormal (altered) phenotype of the intermediate host is not the consequence of infection but the cause (abnormal phenotypes become easier infected); (ii) intermediate host phenotypic alterations are not adaptive for the parasite and should be considered as pathological effects, which are not adaptive to either host or parasite. Alternatively, the changes may be adaptive host responses to infection (Poulin & Thomas, 1999); (iii) evidence that manipulation increases trophic transmission is scarce (Cézilly, Thomas, Médoc, & Perrot-Minnot, 2010); (iv) manipulation increases predation by dead-end hosts and, thus, is not adaptive; (v) studies experimentally manipulating intermediate host traits are scarce, thus most evidence is correlative; (vi) there are no field data that show the net fitness benefit for parasitic manipulation under natural conditions.

Against this background of repeated scepticism of manipulation we evaluate in the following sections the empirical evidence for adaptive parasitic manipulation using acanthocephalan parasites as examples.

3 | ACANTHOCEPHALA

Classical examples of manipulative parasites are acanthocephalans (Moore, 2002). This obligatory parasitic taxon counts about 1,300 species of thorny-headed worms (Amin, 2013) that infest arthropods as intermediate hosts. In their body cavity, they reach the infective cystacanth stage. After being eaten by a final vertebrate host, they reproduce sexually in the intestine. Thus far about 30 Acanthocephala species have been investigated for induced changes in their intermediate hosts (Table S1). They manipulate the phenotype of their intermediate hosts in multifarious ways, ranging from effects on appearance (conspicuously visible cystacanths or less cryptic body coloration of the intermediate host) and behaviour (changed phototaxis, geotaxis, microhabitat preference, activity, anti-predator behaviour, grouping, odour preferences, mating behaviour) to life-history traits (mortality, fecundity, growth) and physiological traits (such as metabolic rate, energy reserves, immunity, antioxidant defence, proteins, neuromodulators) (Table S1; Moore, 1984; Cézilly, Favrat, & Perrot-Minnot, 2013). Some of these effects may be adaptive to the parasite or to the host, or be non-adaptive to both. Classifying the manipulation as adaptive requires knowledge of the benefits and costs to the parasite and the host. As Heil (2016) stated "Ultimately, parasite net fitness represents the relevant outcome of any manipulation effect." The crucial measure for a successful manipulation is thus the increased transmission rate of the parasite due to the manipulation. Table S1 summarises the evidence of such manipulation-based increase in transmission rate. Various examples have shown that infected intermediate hosts are more vulnerable to predation but there

is need for more experimental studies as only they conclusively proof that this is due to parasitic manipulation (Table S1).

4 | ADAPTIVE MANIPULATION BY ACANTHOCEPHALANS

There is ample convincing evidence for adaptive trait manipulation by acanthocephalan parasites (Table S1). While Bethel and Holmes (1973, 1974) showed already in the 1970s that *Polymorphus minutus* alters the geotaxis and clinging behaviour of its gammarid intermediate host, Jacquin, Mori, Pause, Steffen, and Médoc (2014) provided clear experimental evidence that this behavioural change indeed leads to an increased predation by the final host, a water bird. Furthermore, behavioural manipulation by the acanthocephalans *Pomphorhynchus laevis*, *Polymorphus paradoxus*, *Corynosoma constrictum*, and *Acanthocephalus tumescens* has been shown in intermediate hosts carrying the infectious cystacanth stage, but not or less pronounced in hosts carrying the non-infectious acanthella stage (e.g., Franceschi, Bauer, Bollache, & Rigaud, 2008; Dianne et al., 2010, 2011; Dianne, Perrot-Minnot, Bauer, Güvenatam, & Rigaud, 2014; reviewed in Table S1), indicating that the altered behaviour is actually a consequence of infection and not its cause. Additionally, critics of parasitic manipulation will have a hard time to explain the preference for fish predator's odour of *Gammarus pulex* infected with a *P. laevis* cystacanth (Baldauf et al., 2007). Experiments on conflicting parasitic manipulation in multiply infected intermediate hosts are highlights in the proof of parasitic manipulation (Haine, Boucansaud, & Rigaud, 2005): When infected by the waterbird parasite *P. minutus*, *Gammarus roeseli* shows changed geotaxis behaviour, that is, swim closer to the water surface than when uninfected or infected by vertically transmitted, and therefore less virulent, microsporidia. Interestingly, this altered geotaxis was sabotaged in *G. roeseli* that were simultaneously infected by *P. minutus* and microsporidia (Haine et al., 2005). Intraspecific variation in the extent to which traits in intermediate hosts are changed by acanthocephala may point to local adaptation of adaptive manipulation (Franceschi et al., 2010). Different reactions of infected intermediate hosts to host and non-host (dead-end) predators (Médoc & Beisel, 2008; Médoc & Beisel, 2009; Médoc, Rigaud, Bollache, & Beisel, 2009) are further indications for adaptive manipulation.

There exists variation in response among intermediate hosts to parasitic manipulation and of target hosts to manipulated intermediate hosts (Table S1). Such variation between studies may have been due to intraspecific differences (Mazzi & Bakker, 2003; Perrot-Minnot, 2004; Kennedy, 2006; Benesh, Kitchen, Pulkkinen, Hakala, & Valtonen, 2008; Cornet, Franceschi, Bollache, Rigaud, & Sorci, 2009; Franceschi et al., 2010; Thünken et al., unpublished data in Table S1; see also Thomas et al., 2011) or differences in host suitability. For example, *P. laevis* uses *Gammarus* species as intermediate hosts—in which they develop into the infectious cystacanths—and fishes as final hosts. Gammarids are common in many freshwater ecosystems and represent an important food source for many fishes (Wootton, 1990). Consequently, a broad array of fish species is exposed to *P.*

laevis-infected gammarids under natural conditions. Different fish species can serve as final hosts for *P. laevis*, which, however, differ in suitability. Barbel, *Barbus barbus*, and chub, *Leuciscus cephalus*, are preferred hosts of *P. laevis* (Kennedy, 2006). However, when these hosts are absent, other species can serve as host for the parasite. Thus, the usage of a species as final host differs between populations depending on ecological factors like the composition of fish community (Kennedy, 2006). As susceptibility to manipulation of the different species may differ due to different feeding habits or sensory capabilities, parasites may induce different manipulative traits in the intermediate hosts to gain access to the total range of potential hosts. Also, a broad range of manipulation may increase predation by non-hosts. Therefore, studies on that topic are essential to comprehensively assess the costs and benefits of parasitic manipulation.

A lack of repeatability of parasitic effects (see Table S1) might also be caused by methodological differences (Médoc, Bollache, & Beisel, 2006; although significant effects should be more trustworthy than non-significant effects, which sometimes has been doubted, e.g., Kaldonski, Perrot-Minnot, Dodet, Martinaud, & Cézilly, 2009), interspecific differences (e.g., local adaptation to *G. pulex* but not to invasive *G. roeseli* [Moret, Bollache, Wattier, & Rigaud, 2007;]) or interactive effects of different parasite species (e.g., Rauque, Patterson, Poulin, & Tompkins, 2011).

5 | EXPERIMENTAL MANIPULATION OF INTERMEDIATE HOST TRAITS

Because parasite-induced alterations usually comprise a range of phenotypical changes such as behaviour, physiology and appearance (called multidimensionality: Benesh, Valtonen, & Seppälä, 2008; Thomas, Poulin, & Brodeur, 2010; Cézilly et al., 2013), it is often difficult to disentangle the effects of the different traits on parasitic manipulation and to judge their relative importance. As manipulation is costly, one would expect that the parasite minimises manipulation to the extent that is sufficient to guarantee its successful transmission to the next host. Thus, some altered traits could be mere by-products (e.g., due to genetic correlation) but could also reflect an adaptive parasitic backup strategy provided that the single manipulative traits act in concert, that is the manipulative effects of the single traits add up. Additionally or alternatively, the establishment of different manipulative traits could allow the exploitation of a broad range of potential hosts, whose availability and suitability may vary on a temporal and local scale (e.g., Cézilly et al., 2013). Studies investigating a single manipulative trait independent from other traits and its impact on predation on different hosts (and non-hosts) are underrepresented. One possibility to address this question is an experimental approach trying to experimentally manipulate a specific trait. Those studies are scarce. Notable exceptions are studies on the orange/red coloration of infected gammarids, which is caused by conspicuously coloured *P. laevis* and *P. minutus* cystacanths that are visible through the transparent cuticle of the gammarids. The altered coloration was suggested to facilitate predation by and thus transmission to final hosts (fishes and

waterbirds, respectively). Indeed Bakker, Mazzi, and Zala (1997) and Jacquin, Mori, and Médoc (2013) showed that gammarids painted with an orange spot on the cuticle were preferentially preyed upon by three-spined sticklebacks and mallards, clearly indicating that the altered coloration affects predation of the intermediate host. Interestingly, a subsequent study found no significant impact on predation by trout (Kaldonski et al., 2009) suggesting the colour effects differ among species (see also Thünken et al., unpublished data in Table S1).

6 | DEAD-END HOSTS AND SPECIFIC MANIPULATION

Parasite-induced phenotypic alteration of the intermediate host might not only increase predation by the favoured final host, but also by less suitable or even non-host species (dead-end hosts: Mouritsen & Poulin, 2003; Poulin et al., 2005; Thomas, Adamo, & Moore, 2005; Seppälä, Valtonen, & Benesh, 2008). As a consequence, the net benefit for the parasite resulting from the manipulation could be lower than expected, which might lead to a systematic overestimation of the adaptive significance of parasitic manipulation (e.g., Cézilly & Perrot-Minnot, 2005). Theory predicts that under certain conditions, manipulation should be specific (Parker et al., 2009; Seppälä & Jokela, 2008), that is it should specifically increase predation to target hosts and decrease it to non-hosts. Thus far, only few studies have addressed this question (Seppälä et al., 2008). Some studies indeed showed increased predation risk of infected individuals by non-hosts compared to uninfected individuals (Kaldonski, Perrot-Minnot, Motreuil, & Cézilly, 2008; Milinski, 1985), while others found similar non-host predation risk for infected individuals (Seppälä, Karvonen, & Valtonen, 2006). Parasitic transmission would be increased when suitable final hosts preferentially prey upon manipulated intermediate hosts (host-specific manipulation) (e.g., Levri, 1998). Fine-tuned behavioural alterations such as selective attraction to suitable host predators but not to non-host predators could result in such specific manipulation. To which extent manipulation is truly specific is difficult to estimate because most studies thus far examine the altered plastic response of infected intermediate hosts only to cues of target hosts (Table S1). The results of some studies are in accordance with the idea of specific manipulation (e.g., Bethel & Holmes, 1977; Kaldonski et al., 2009; Médoc et al., 2006). For example, *G. pulex* infected with *P. laevis* were more vulnerable to predation by the suitable final host brown trout *Salmo trutta fario*, while those infected with *P. minutus*, for which parasite the brown trout is a dead-end host, were not (Kaldonski et al., 2009). In the experimental study of Jacquin et al. (2014), however, target-host and non-host predatory cues triggered a similar alteration of the anti-predator behaviour in *P. minutus*-infected gammarids.

However, even general parasite-induced alterations in intermediate hosts may lead to host-specific transmission. For example, reversed geotaxis and clinging behaviour at material at the water surface induced by *P. minutus* may simultaneously reduce predation by dead-end fish hosts and increase predation by waterbird hosts (Jacquin et al., 2014).

7 | PARASITE AVOIDANCE BY FINAL HOSTS

Parasite-host conflict is usually most pronounced between the parasite and the intermediate hosts (because the latter die during transmission). Thus, selection primarily acts on parasites to manipulate the intermediate host to their favour, leading to the spectacular alterations in its anti-predator behaviour and appearance described above. Such increased conspicuousness may automatically facilitate transmission to the final host. However, if the definitive host faces serious costs of infection as well, prey items that signal their infection status may be actively avoided and thus parasitic manipulation might be selected against. To what extent parasite avoidance evolves in final hosts should depend on its costs, which may include physical costs of infection, but also costs of discriminating infected and uninfected prey (e.g., Mazzi & Bakker, 2003). The optimal definitive host for the parasite should suffer minimally from infection, assuming that the severity of infection predicts the strength of host response, which in turn should determine the cost of manipulation. Consequently, parasite and final-host interests may agree leading to a co-evolutionary process with benefits for both parties (parasite and final host): the final host benefits from easier access to food resources while the parasite ensures transmission (supported by a theoretical model of Lafferty, 1992). Still the selection pressure on the parasite is higher because the presence of suitable hosts is mandatory for its reproduction (life-dinner principle). Under natural conditions, the situation may be less optimal for the parasite because optimal final-host presence may differ spatially and/or temporally potentially requiring the parasite to use less optimal hosts in short term to ensure reproduction.

8 | FUTURE DIRECTIONS

Field data that show the net fitness benefit for parasitic manipulation under natural conditions are notoriously difficult to obtain. However, the ultimate proof that the parasite's net fitness benefit of manipulation is greater than that without manipulation is most likely a rather theoretical issue that is difficult to investigate experimentally (but see approach by Gréacias, Hébert, Berger, Barber, & Aubin-Horth, 2017, who manipulated host physiology in order to evoke similar altered host behaviour as in three-spined sticklebacks, *Gasterosteus aculeatus*, infected with the cestode *Schistocephalus solidus*). Indeed, various studies have demonstrated increased transmission to the final host caused by manipulation of the intermediate host under natural conditions (Table S1). In contrast, it is more difficult to assess how benefits and costs are traded off against each other. Costs entails energetic effort of the parasite, final host resistance to manipulation (Mazzi & Bakker, 2003; see previous section), intermediate host mortality (Mazzi & Bakker, 2003), conflict over manipulation when infected with different parasite stages of the same species or different parasite species

with contrasting interests (Hafer, 2016; Hafer & Milinski, 2015, 2016), or transmission to dead-end hosts (e.g., Poulin et al., 2005).

Milinski (1990) distinguishes two ways in which parasites can influence host's decision-making. First, parasites may directly manipulate host behaviour, for instance by the release of hormone or neurotransmitter analogues that influence the neuro-endocrine system of the host. Second, parasites may indirectly influence host behaviour by affecting the physiology of the host, for instance by consuming resources in nutritionally demanding parasites. Usually, only the direct effects are considered manipulation. In a recent review, Heil (2016) summarised that "Only the demonstration that a certain phenotypic alteration in the host is under the genetic control of the parasite and that it enhances the fitness of the parasite via an enhancement of its transmission rate, while decreasing the fitness of the host, would provide clear evidence in favour of adaptive host manipulation." According to this definition, indirect effects of parasites may also be called manipulation as long as they are under the genetic control of the parasite. The distinction between direct and indirect effects and who is responsible for the effects has proven to be difficult (Thomas et al., 2005). Comparative genomewide transcriptomics of parasites in the infective and the non-infective stage may elucidate the genetic contribution of the parasite to the alterations of traits in the intermediate host. This new, promising approach had recently been applied to the cestode *S. solidus* in its intermediate the three-spined stickleback, *G. aculeatus* (Hébert, Grambauer, Barber, Landry, & Aubin-Horth, 2017).

The study of the physiological mechanisms of parasitic manipulation may contribute to distinguish direct manipulation from side effects (e.g., Cézilly et al., 2013; Thomas et al., 2005). Parasites may cause various general physiological changes, for example in metabolic rate, respiration rate, osmoregulation, immune reaction, as well as in levels of lipids, glycogen, proteins and carotenoids (see Table S1 for physiological changes in intermediate hosts infected with acanthocephalans, and references therein). Interesting for the separation of direct manipulation and side effects of parasitisation are specific physiological effects, notably changes in the neuromodulator serotonin (5-hydroxytryptamine, 5-HT). Injecting serotonin in gammarids causes changes in phototaxis (Guler & Ford, 2010; Perrot-Minnot, Dion, & Cézilly, 2013; Perrot-Minnot, Maddaleno, Balourdet, & Cézilly, 2012; Perrot-Minnot, Sanchez-Thirion, & Cézilly, 2014), geotaxis (Guler & Ford, 2010; Perrot-Minnot et al., 2012; but see Tain, Perrot-Minnot, & Cézilly, 2006) and clinging behaviour (Helluy & Holmes, 1990) similar to alterations caused by infective acanthocephalans (Table S1). Indeed, brain serotonin levels have been demonstrated to differ in infected gammarids (Maynard, DeMartini, & Wright, 1996; Tain, Perrot-Minnot, & Cézilly, 2007; Tain et al., 2006), and behavioural changes can be manipulated by injection of serotonin receptor antagonists and agonists (Perrot-Minnot et al., 2013). Surprisingly, serotonin-treated gammarids had no increased predation risk (Perrot-Minnot et al., 2012). Future studies shall clarify whether this negative result is real or due to methodology (use of goldfish as atypical predator, use of airbricks as hiding place). In addition to the serotonergic system, the histaminergic

system may be involved in parasitic manipulation (Perrot-Minnot et al., 2013).

9 | CONCLUSIONS

Adaptive manipulation of intermediate hosts of parasites with a complex life cycle has been especially well documented in the Acanthocephala. But also here, only a small fraction of this large taxon has been investigated in detail, leaving much scope for future studies. In addition, it becomes increasingly evident from studies on acanthocephalans that there is much variation at all levels in the parasite's life cycle, both within and between populations and at the interspecific level. The biggest challenge for future research will be to gain knowledge of the net fitness benefits of parasitic manipulation thereby integrating the complete life cycle of the parasite in relation to ecology.

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REFERENCES

- Amin, O. M. (2013). Classification of the Acanthocephala. *Folia Parasitologica*, 60, 273–305.
- Bakker, T. C. M., Mazzi, D., & Zala, S. (1997). Parasite-induced changes in behavior and color make *Gammarus pulex* more prone to fish predation. *Ecology*, 78, 1098–1104.
- Baldauf, S. A., Thünken, T., Frommen, J. G., Bakker, T. C. M., Heupel, O., & Kullmann, H. (2007). Infection with an acanthocephalan manipulates an amphipod's reaction to a fish predator's odours. *International Journal for Parasitology*, 37, 61–65.
- Benesh, D. P., Kitchen, J., Pulkkinen, K., Hakala, I., & Valtonen, E. T. (2008). The effect of *Echinorhynchus borealis* (Acanthocephala) infection on the anti-predator behavior of a benthic amphipod. *Journal of Parasitology*, 94, 542–545.
- Benesh, D. P., Valtonen, E. T., & Seppälä, O. (2008). Multidimensionality and intra-individual variation in host manipulation by an acanthocephalan. *Parasitology*, 135, 617–626.
- Berdoy, M., Webster, J. P., & Macdonald, D. W. (2000). Fatal attraction in rats infected with *Toxoplasma gondii*. *Proceedings of the Royal Society of London Series B*, 267, 1591–1594.
- Bethel, W. M., & Holmes, J. C. (1973). Altered evasive behavior and responses to light in amphipods harboring acanthocephalan cystacanths. *Journal of Parasitology*, 59, 945–956.
- Bethel, W. M., & Holmes, J. C. (1974). Correlation of development of altered evasive behavior in *Gammarus lacustris* (Amphipoda) harboring cystacanths of *Polymorphus paradoxus* (Acanthocephala) with the infectivity to the definitive host. *Journal of Parasitology*, 60, 272–274.
- Bethel, W. M., & Holmes, J. C. (1977). Increased vulnerability of amphipods to predation owing to altered behavior induced by larval acanthocephalans. *Canadian Journal of Zoology*, 55, 110–115.
- Cézilly, F., Favrat, A., & Perrot-Minnot, M.-J. (2013). Multidimensionality in parasite-induced phenotypic alterations: ultimate versus proximate aspects. *Journal of Experimental Biology*, 216, 27–35.
- Cézilly, F., & Perrot-Minnot, M.-J. (2005). Studying adaptive changes in the behaviour of infected hosts: a long and winding road. *Behavioural Processes*, 68, 223–228.
- Cézilly, F., Thomas, F., Médoc, V., & Perrot-Minnot, M.-J. (2010). Host-manipulation by parasites with complex life cycles: adaptive or not? *Trends in Parasitology*, 26, 311–317.
- Cornet, S., Franceschi, N., Bollache, L., Rigaud, T., & Sorci, G. (2009). Variation and covariation in infectivity, virulence and immunodepression in the host-parasite association *Gammarus pulex-Pomphorhynchus laevis*. *Proceedings of the Royal Society of London Series B*, 276, 4229–4236.
- Dianne, L., Perrot-Minnot, M.-J., Bauer, A., Gailard, M., Léger, E., & Rigaud, T. (2011). Protection first then facilitation: a manipulative parasite modulates the vulnerability to predation of its intermediate host according to its own developmental stage. *Evolution*, 65, 2692–2698.
- Dianne, L., Perrot-Minnot, M.-J., Bauer, A., Güvenatam, A., & Rigaud, T. (2014). Parasite-induced alteration of plastic response to predation threat: increased refuge use but lower food intake in *Gammarus pulex* infected with the acanthocephalan *Pomphorhynchus laevis*. *International Journal for Parasitology*, 44, 211–216.
- Dianne, L., Rigaud, T., Léger, E., Motreuil, S., Bauer, A., & Perrot-Minnot, M.-J. (2010). Intraspecific conflict over host manipulation between different larval stages of an acanthocephalan parasite. *Journal of Evolutionary Biology*, 23, 2648–2655.
- Franceschi, N., Bauer, A., Bollache, L., & Rigaud, T. (2008). The effects of parasite age and intensity on variability in acanthocephalan-induced behavioural manipulation. *International Journal for Parasitology*, 38, 1161–1170.
- Franceschi, N., Cornet, S., Bollache, L., Dechaume-Moncharmont, F.-X., Bauer, A., Motreuil, S., & Rigaud, T. (2010). Variation between population and local adaptation in acanthocephalan-induced parasite manipulation. *Evolution*, 64, 2417–2430.
- Grécias, L., Hébert, F. O., Berger, C. S., Barber, I., & Aubin-Horth, N. (2017). Can the behaviour of threespine stickleback parasitized with *Schistocephalus solidus* be replicated by manipulating host physiology? *Journal of Experimental Biology*, 220, 237–246.
- Guler, Y., & Ford, A. T. (2010). Anti-depressants make amphipods see the light. *Aquatic Toxicology*, 99, 397–404.
- Hafer, N. (2016). Conflicts over host manipulation between different parasites and pathogens: investigating the ecological and medical consequences. *BioEssays*, 38, 1027–1037.
- Hafer, N., & Milinski, M. (2015). When parasites disagree: evidence for parasite-induced sabotage of host manipulation. *Evolution*, 69, 611–620.
- Hafer, N., & Milinski, M. (2016). Inter- and intraspecific conflicts between parasites over host manipulation. *Proceedings of the Royal Society B*, 283, 20152870.
- Haine, E. R., Boucansaud, K., & Rigaud, T. (2005). Conflict between parasites with different transmission strategies infecting an amphipod host. *Proceedings of the Royal Society of London Series B*, 272, 2505–2510.
- Halík, L. (1931). Über die rhythmischen Bewegungen der in Bernsteinschnecken parasitierenden Sporozystenschläuche von *Leucochloridium macrostomum* Rud. (= *paradoxum* Carus). *Zeitschrift für vergleichende Physiologie*, 14, 462–478.
- Hébert, F. O., Grambauer, S., Barber, I., Landry, C. R., & Aubin-Horth, N. (2017). Major host transitions are modulated through transcriptome-wide reprogramming events in *Schistocephalus solidus*, a threespine stickleback parasite. *Molecular Ecology*, 26, 1118–1130.
- Heil, M. (2016). Host manipulation by parasites: cases, patterns, and remaining doubts. *Frontiers in Ecology and Evolution*, 4, 80.
- Helluy, S., & Holmes, J. C. (1990). Serotonin, octopamine, and the clinging behavior induced by the parasite *Polymorphus paradoxus* (Acanthocephala) in *Gammarus lacustris* (Crustacea). *Canadian Journal of Zoology*, 68, 1214–1220.

- Jacquin, L., Mori, Q., & Médoc, V. (2013). Does the carotenoid-based colouration of *Polymorphus minutus* facilitate its trophic transmission to definitive hosts? *Parasitology*, 140, 1310–1315.
- Jacquin, L., Mori, Q., Pause, M., Steffen, M., & Médoc, V. (2014). Non-specific manipulation of gammarid behaviour by *P. minutus* parasite enhances their predation by definitive bird hosts. *PLoS ONE*, 9, 101684.
- Kaldonski, N., Perrot-Minnot, M.-J., Dodet, R., Martinaud, G., & Cézilly, F. (2009). Carotenoid-based colour of acanthocephalan cystacanths plays no role in host manipulation. *Proceedings of the Royal Society of London Series B*, 276, 169–176.
- Kaldonski, N., Perrot-Minnot, M.-J., Motreuil, S., & Cézilly, F. (2008). Infection with acanthocephalans increases the vulnerability of *Gammarus pulex* (Crustacea, Amphipoda) to non-host invertebrate predators. *Parasitology*, 135, 627–632.
- Kennedy, C. R. (2006). *Ecology of the Acanthocephala*. Cambridge: Cambridge University Press.
- Lafferty, K. D. (1992). Foraging on prey that are modified by parasites. *The American Naturalist*, 140, 854–867.
- Levri, E. P. (1998). The influence of non-host predators on parasite-induced behavioral changes in a freshwater snail. *Oikos*, 81, 531–537.
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68, 619–640.
- Maynard, B. J., DeMartini, L., & Wright, W. G. (1996). *Gammarus lacustris* harboring *Polymorphus paradoxus* show altered patterns of serotonin-like immunoreactivity. *Journal of Parasitology*, 82, 663–666.
- Mazzi, D., & Bakker, T. C. M. (2003). A predator's dilemma: prey choice and parasite susceptibility in three-spined sticklebacks. *Parasitology*, 126, 339–347.
- Médoc, V., & Beisel, J.-N. (2008). An acanthocephalan parasite boosts the escape performance of its intermediate host facing non-host predators. *Parasitology*, 135, 977–984.
- Médoc, V., & Beisel, J.-N. (2009). Field evidence for non-host predator avoidance in a manipulated amphipod. *Naturwissenschaften*, 96, 513–523.
- Médoc, V., Bollache, L., & Beisel, J.-N. (2006). Host manipulation of a freshwater crustacean (*Gammarus roeseli*) by an acanthocephalan parasite (*Polymorphus minutus*) in a biological invasion context. *International Journal for Parasitology*, 36, 1351–1358.
- Médoc, V., Rigaud, T., Bollache, L., & Beisel, J.-N. (2009). A manipulative parasite increasing an antipredator response decreases its vulnerability to a nonhost predator. *Animal Behaviour*, 77, 1235–1241.
- Milinski, M. (1985). Risk of predation of parasitized sticklebacks (*Gasterosteus aculeatus* L.) under competition for food. *Behaviour*, 93, 203–216.
- Milinski, M. (1990). Parasites and host decision-making. In C. J. Barnard & J. M. Behnke (Eds.), *Parasitism and Host Behaviour* (pp. 95–116). London: Taylor and Francis.
- Moore, J. (1984). Altered behavioral responses in intermediate hosts – an acanthocephalan parasite strategy. *The American Naturalist*, 123, 572–577.
- Moore, J. (2002). *Parasites and the behavior of animals*. Oxford: Oxford University Press.
- Moret, Y., Bollache, L., Wattier, R., & Rigaud, T. (2007). Is the host or the parasite the most locally adapted in an amphipod-acanthocephalan relationship? a case study in a biological invasion context. *International Journal for Parasitology*, 37, 637–644.
- Mouritsen, K. N., & Poulin, R. (2003). Parasite-induced trophic facilitation exploited by a non-host predator: a manipulator's nightmare. *International Journal for Parasitology*, 33, 1043–1050.
- Parker, G. A., Ball, M. A., Chubb, J. C., Hammerschmidt, K., & Milinski, M. (2009). When should a trophically transmitted parasite manipulate its host? *Evolution*, 63, 448–458.
- Perrot-Minnot, M.-J. (2004). Larval morphology, genetic divergence, and contrasting levels of host manipulation between forms of *Pomphorhynchus laevis* (Acanthocephala). *International Journal for Parasitology*, 34, 45–54.
- Perrot-Minnot, M.-J., Dion, E., & Cézilly, F. (2013). Modulatory effects of the serotonergic and histaminergic systems on reaction to light in the crustacean *Gammarus pulex*. *Neuropharmacology*, 75, 31–37.
- Perrot-Minnot, M.-J., Maddaleno, M., Balourdet, A., & Cézilly, F. (2012). Host manipulation revisited: no evidence for a causal link between altered photophobia and increased trophic transmission of amphipods infected with acanthocephalans. *Functional Ecology*, 26, 1007–1014.
- Perrot-Minnot, M.-J., Sanchez-Thirion, K., & Cézilly, F. (2014). Multidimensionality in host manipulation mimicked by serotonin injection. *Proceedings of the Royal Society of London Series B*, 281, 20141915.
- Poulin, R. (2010). Parasite manipulation of host behavior: an update and frequently asked questions. *Advances in the Study of Behavior*, 41, 151–186.
- Poulin, R., Fredensborg, B. L., Hansen, E. K., & Leung, T. L. (2005). The true cost of host manipulation by parasites. *Behavioral Processes*, 68, 241–244.
- Poulin, R., & Maure, F. (2015). Host manipulation by parasites: a look back before moving forward. *Trends in Parasitology*, 31, 563–570.
- Poulin, R., & Thomas, F. (1999). Phenotypic variability induced by parasites: extent and evolutionary implications. *Parasitology Today*, 15, 28–32.
- Rauque, C. A., Patterson, R. A., Poulin, R., & Tompkins, D. M. (2011). Do different parasite species interact in their effects on host fitness? a case study on parasites of the amphipod *Paracalliope fluviatilis*. *Parasitology*, 138, 1176–1182.
- Seppälä, O., & Jokela, J. (2008). Host manipulation as a parasite transmission strategy when manipulation is exploited by non-host predators. *Biology Letters*, 4, 663–666.
- Seppälä, O., Karvonen, A., & Valtonen, E. T. (2006). Host manipulation by parasites and risk of non-host predation: is manipulation costly in an eye fluke–fish interaction? *Evolutionary Ecology Research*, 8, 871–879.
- Seppälä, O., Valtonen, E. T., & Benesh, D. P. (2008). Host manipulation by parasites in the world of dead-end predators: adaptation to enhance transmission? *Proceedings of the Royal Society of London Series B*, 275, 1611–1615.
- Tain, L., Perrot-Minnot, M.-J., & Cézilly, F. (2007). Differential influence of *Pomphorhynchus laevis* (Acanthocephala) on brain serotonergic activity in two congeneric host species. *Biology Letters*, 3, 68–71.
- Tain, L., Perrot-Minnot, M.-J., & Cézilly, F. (2006). Altered host behaviour and brain serotonergic activity caused by acanthocephalans: evidence for specificity. *Proceedings of the Royal Society of London Series B*, 273, 3039–3045.
- Thomas, F., Adamo, S., & Moore, J. (2005). Parasitic manipulation: where are we and where should we go? *Behavioural Processes*, 68, 185–199.
- Thomas, F., Brodeur, T., Maure, F., Franceschi, N., Blanchet, S., & Rigaud, T. (2011). Intraspecific variability in host manipulation by parasites. *Infection, Genetics and Evolution*, 11, 262–269.
- Thomas, F., Poulin, R., & Brodeur, J. (2010). Host manipulation by parasites: a multidimensional phenomenon. *Oikos*, 119, 1217–1223.
- Wootton, R. J. (1990). *Ecology of teleost fishes*. London: Chapman and Hall.
- Yanoviak, S. P., Kaspari, M., Dudley, R., & Poinar, G. Jr (2008). Parasite-induced fruit mimicry in a tropical canopy ant. *The American Naturalist*, 171, 536–544.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Supplementary material
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Supplementary Table S1: overview of traits affected by aquatic and terrestrial acanthocephalan parasites in their arthropod intermediate hosts. Traits are classified into “visual appearance” (like conspicuously visible orange cystacanth, whole body lightening or darkening), “behaviour” (like changed geotaxis, phototaxis, hydrotaxis, photophilia, activity, hiding, preferences), “life-history” (like changed fecundity, mortality, growth, body size), and “physiology” (like changed immunity, sensitivity to stress factors, energy reserves). Also listed are studies in which the investigated traits showed no change after infection, whether the study had been experimental or not, and whether infected intermediate hosts suffered greater predation by final host of non-host (NH) species.

Parasite species:	aquatic species	terrestrial species			
Changed trait:	visual appearance	behaviour	life history	physiology	no trait change

Parasite species	Intermediate host species	Final host species (NH=non-host)	Experimental infection or manipulation?	Changed trait	Increased transmission?	Refs
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	increase in fluctuating asymmetry		64
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	orange cystacanth visible through the cuticle		e.g. 2, 9, 35, 60, 158
<i>Pomphorhynchus tereticollis</i>	<i>Gammarus pulex</i>		no	orange cystacanth visible through the cuticle		158
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	orange cystacanth visible through the cuticle		e.g. 35, 127, 158
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	increase in fluctuating asymmetry		64
<i>Polymorphus minutus</i>	<i>Gammarus lacustris</i>		no	changed body coloration		26
<i>Polymorphus minutus</i>	<i>Echinogammarus tibaldii</i>		no	orange cystacanth visible through the cuticle		144
<i>Polymorphus contortus</i>	<i>Gammarus lacustris</i>		no	orange cystacanth visible through the cuticle		39
<i>Polymorphus contortus</i>	<i>Asellus aquaticus</i>		no	darker body coloration		159

<i>Polymorphus marilis</i>	<i>Gammarus lacustris</i>		no	orange cystacanth visible through the cuticle		6, 39
<i>Polymorphus paradoxus</i>	<i>Gammarus lacustris</i>		no	orange cystacanth visible through the cuticle		6, 39
<i>Echinorhynchus truttae</i>	<i>Gammarus</i> sp.		no	orange cystacanth visible through the cuticle		35
<i>Corynosoma constrictum</i>	<i>Hyalella azteca</i>		no	orange cystacanth visible through the cuticle		6, 122
<i>Acanthocephalus dirus</i>	<i>Asellus intermedius</i>		no	lighter body coloration		11, 24, 30
<i>Acanthocephalus dirus</i>	<i>Caecidotea intermedius</i>		no	lighter body coloration		31
<i>Acanthocephalus dirus</i>	<i>Lirceus garmani</i>		no	lighter body coloration		30
<i>Acanthocephalus dirus</i>	<i>Asellus intermedius</i>		no	lighter body coloration		140
<i>Acanthocephalus anguillae</i>	<i>Asellus aquaticus</i>		yes (experimental infection 160) and no	darker body coloration		40, 160
not specified	<i>Asellus aquaticus</i>		no	darker body coloration		37
<i>Acanthocephalus parksidei</i>	<i>Caecidotea militaris</i>		no	lighter body coloration		88
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>		yes (experimental infection 87, 160) and no	darker coloration (respiratory opercula ¹⁹ : 38; abdomen: 77, 84, 87; body: 160)		38, 77, 84, 87, 160
<i>Acanthocephalus jacksoni</i>	<i>Lirceus lineatus</i>		no	lighter body coloration		25, 30
<i>Acanthocephalus jacksoni</i>	<i>Asellus intermedius</i>		yes (experimental infection)	lighter body coloration		137
<i>Acanthocephalus rhinensis</i>	<i>Echinogammarus tibaldii</i>		no	orange cystacanth visible through the cuticle		145
<i>Sclerocollum saudii</i>	<i>Megaluropus agilis</i>		yes (experimental infection)	orange cystacanth visible through the cuticle		142
<i>Profilicollis antarcticus</i>	<i>Hemigrapsus crenulatus</i>		yes (experimental infection)	increased colour intensity in the lab		17
not specified (family Oligacanthorhynchidae)	<i>Nasutitermes acajutlae</i>		no	lighter head and body colour of parasitized workers		147
<i>Profilicollis antarcticus</i>	<i>Hemigrapsus crenulatus</i>		no	no effect on visual appearance in the field		17
<i>Profilicollis</i> spp.	<i>Macrophthalmus hirtipes</i>		no	no effect on visual appearance		27
<i>Echinorhynchus truttae</i>	<i>Echinogammarus tibaldii</i>		no	no effect on visual appearance		144
<i>Dentitruncus truttae</i>	<i>Echinogammarus tibaldii</i>		no	no effect on visual appearance		144
<i>Acanthocephalus ranae</i>	<i>Asellus aquaticus</i>		yes (experimental infection)	no effect on visual appearance		160
<i>Pomphorhynchus tereticollis</i>	<i>Gammarus pulex</i>		no	reduced hiding behaviour when fish (<i>Cottus gobio</i>) present		104
<i>Pomphorhynchus tereticollis</i> ⁸	<i>Gammarus pulex</i>		no	predator-odour preference (<i>Cottus gobio</i>)		104
<i>Pomphorhynchus tereticollis</i>	<i>Gammarus fossarum</i>		no	reduced food consumption at various temperatures		131
<i>Pomphorhynchus tereticollis</i>	<i>Gammarus fossarum</i>		no	changed phototaxis (from 0 to +) ²²		165
<i>Pomphorhynchus tereticollis</i>	<i>Gammarus fossarum</i>		no	decreased hiding ²²		165
<i>Pomphorhynchus tereticollis</i>	<i>Gammarus pulex</i>		no	change in phototaxis (from – to 0)		67, 157
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	changed phototaxis (from – to 0 or +, dependent on population)		105, 123
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	predator-odour preference (<i>Perca fluviatilis</i>)		3
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (experimental infection)	changed phototaxis (from – to 0 or +) ^{2, 3, 10, 11}		106, 117,

						123, 124, 125, 126
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (experimental infection)	increased photophilic with fish (<i>Salmo trutta fario</i>) odour		117
<i>Pomphorhynchus laevis</i>	<i>Gammarus fossarum</i>		no	changed phototaxis (from – to +)		106
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (experimental infection)	changed geotaxis (from + to 0)		106
<i>Pomphorhynchus laevis</i>	<i>Gammarus fossarum</i>		no	changed geotaxis (from + to 0)		106
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (experimental infection)	decreased hiding ¹²		106, 130
<i>Pomphorhynchus laevis</i>	<i>Gammarus fossarum</i>		no	decreased hiding		106
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (experimental infection)	decreased aggregation behaviour relative to uninfected gammarids with fish (<i>Salmo trutta fario</i>) odour		117
<i>Pomphorhynchus laevis</i>	<i>Gammarus fossarum</i>		no	decreased aggregation behaviour		106
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (experimental infection)	reduced activity		106
<i>Pomphorhynchus laevis</i>	<i>Gammarus fossarum</i>		no	reduced activity		106
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (injection of serotonin)	changed phototaxis (from – to +)		106
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (injection of serotonin)	changed geotaxis (from + to 0)		106
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (injection of serotonin)	reduced activity		106
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	decreased hiding behaviour with fish (<i>Cottus gobio</i>) odour and sound		129
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	predator-odour preference (<i>Cottus gobio</i>)		129
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	reduced feeding rate		44, 45, 46, 47, 70
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (experimental infection)	reduced hiding behaviour independent of fish (<i>Salmo trutta fario</i>) odour ⁵		83
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (experimental infection)	reduced activity in acanthella stage without fish host odour		98
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (experimental infection)	increased hiding in acanthella stage when food was outside refuge		98
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (experimental infection)	reduced food intake in acanthella stage particularly with fish host odour		98
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	reduced pairing success		62
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	positive phototaxis		9, 33, 51, 67, 68
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	increased time in surface vegetation		9
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (injection of serotonin)	positive phototaxis		67, 68
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (injection of serotonin receptor antagonist and agonists)	changed phototaxis		107
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (injection of histamine receptor antagonist)	changed phototaxis		107
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	vertical distribution		51
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no (8, 157) and yes (experimental infection; 157)	change in phototaxis (from – to 0)		8, 157
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	changed habitat preference (open water and attached to surface vegetation instead of on		8

				or under stones)		
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	vertical distribution		51
<i>Pomphorhynchus laevis</i>	<i>Gammarus roeseli</i> (invasive)		yes (injection of serotonin)	change in phototaxis (from – to +)		68
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	increased presence in the drift		13, 61
<i>Pomphorhynchus laevis</i>	<i>Echinogammarus stammerii</i>		no	increased presence in the drift		14, 72
<i>Pomphorhynchus laevis</i>	<i>Gammarus roeseli</i>		no	increased presence in the drift		61
<i>Pomphorhynchus laevis</i>	<i>Echinogammarus stammerii</i>		no	increased activity (independent of fish <i>Leuciscus cephalus</i> odour: 15, 72)		14, 15, 72
<i>Pomphorhynchus laevis</i>	<i>Echinogammarus stammerii</i>		no	photophilic		14
<i>Polymorphus minutus</i>	<i>Echinogammarus berilloni</i>		no	decreased activity, avoidance of fish (NH) and mallard (host) odour		94
<i>Polymorphus minutus</i>	<i>Echinogammarus berilloni</i>		no	decreased geotaxis independent of fish (NH) and mallard (host) odour ¹⁵		94
<i>Polymorphus minutus</i>	<i>Echinogammarus berilloni</i>		no	increased proportion at surface independent of fish (NH) presence		94
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	decreased activity independent of NH fish (<i>Gasterosteus aculeatus</i>) odour		43
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i>		no	decreased geotaxis		82
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i> (invasive)		no	changed geotaxis (from – to 0)		100
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i> (invasive)		no	increased clinging		100
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	changed geotaxis (100: from – to + or 157: from – to 0)		100, 157
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	increased clinging		100
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	reduced pairing success		55, 62, 139
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	change in phototaxis		51
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	vertical distribution		51
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	increased time swimming in surface water		139
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	decreased swimming time and distance travelled and changed path (to surface) after disturbance		139
<i>Polymorphus minutus</i>	<i>Gammarus lacustris</i>		no	photophilic		26
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i>		no	increased swimming speed		92
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i>		no	increased escape speed after <i>Dikerogammarus villosus</i> (NH) encounter		92
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i> (invasive)		no	changed microdistribution in the field, more at surface closer to bank		135
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i> (invasive)		no	changed vertical distribution with the presence of <i>Dikerogammarus villosus</i> (NH)		135
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i>		no	changed microdistribution in the field, mainly in floating material, resulting in decreased		133

				overlap with potential invertebrate NH predators	
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i>		no	changed habitat preference (near-surface vs. bottom)	134
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i>		no	increased time on refuges and near surface both even increased with odour of <i>Gasterosteus aculeatus</i> (NH), and increased clinging near surface independent of fish odour	134
<i>Polymorphus minutus</i>	<i>Gammarus fossarum</i>		no	changed geotaxis (from + to -) ²³	165
<i>Polymorphus paradoxus</i>	<i>Gammarus lacustris</i>		no	reduced pairing success	57
<i>Polymorphus paradoxus</i>	<i>Gammarus lacustris</i>		yes (experimental infection, 5) and no (5, 10)	photophilic and positive phototaxis, and when disturbed, skimming, clinging ^{1,3}	5, 10
<i>Polymorphus paradoxus</i>	<i>Gammarus lacustris</i>		no and yes (injection of serotonin)	increased clinging	156
<i>Polymorphus paradoxus</i>	<i>Gammarus lacustris</i>		yes (injection of octopamine)	decreased clinging of infected gammarids	156
<i>Polymorphus marilis</i>	<i>Gammarus lacustris</i>		no	reduced pairing success	57
<i>Polymorphus marilis</i>	<i>Gammarus lacustris</i>		no	photophilic	10
<i>Corynosoma constrictum</i>	<i>Hyalella azteca</i>		no	photophilic and positive phototaxis ³	10
<i>Corynosoma constrictum</i>	<i>Hyalella azteca</i>		yes (experimental infection)	decreased activity	122
<i>Corynosoma constrictum</i>	<i>Hyalella azteca</i>		yes (experimental infection)	increased propensity for green and red light (phototaxis, intensity preference)	122
<i>Corynosoma</i> sp.	<i>Gammarus pseudolimnaeus</i>		no	decreased aggregation behaviour independent of fish odour (<i>Culaea inconstans</i>)	114
<i>Corynosoma</i> sp.	<i>Hyalella patagonica</i>		no	reduced pairing success of both sexes	153
not specified	<i>Echinogammarus marinus</i>		yes (injection of serotonin or fluoxetine) and no	positive phototaxis	80
not specified	<i>Echinogammarus marinus</i>		yes (injection of serotonin or fluoxetine) and no	negative geotaxis	80
<i>Acanthocephalus dirus</i>	<i>Asellus intermedius</i>		no	activity (anecdotal obs.)	11
<i>Acanthocephalus dirus</i>	<i>Caecidotea intermedius</i>		no	decreased pairing success (91, 161), and decreased willingness of males to mate (41, 161, 163) ²¹	41, 91, 161, 163
<i>Acanthocephalus dirus</i>	<i>Caecidotea intermedius</i>		no	more likely to be near predator (<i>Semotilus atromaculatus</i>)	48
<i>Acanthocephalus dirus</i>	<i>Caecidotea intermedius</i>		no	decreased hiding behaviour independent of number of fish (<i>Semotilus atromaculatus</i>)	48
<i>Acanthocephalus dirus</i>	<i>Caecidotea intermedius</i>		no	decreased reproductive behaviour	42
<i>Acanthocephalus tehlequahensis</i>	<i>Caecidotea communis</i>		no	reduced feeding rate	73
<i>Acanthocephalus tehlequahensis</i>	<i>Caecidotea communis</i>		no	increased feeding rate	154
<i>Acanthocephalus tumescens</i>	<i>Hyalella patagonica</i>		no	reduced pairing success of both sexes ³	153
<i>Acanthocephalus jacksoni</i>	<i>Lirceus lineatus</i>		no	decreased hiding behaviour, increased activity	109

<i>Acanthocephalus galaxii</i>	<i>Paracalliope fluviatilis</i>		no	reduced pairing success (especially for males)	103
<i>Acanthocephalus galaxii</i>	<i>Paracalliope fluviatilis</i>		no	increase in positive phototaxis, but unchanged phototaxis when co-infected with <i>Microcephallus</i> sp.	103
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>		no	decreased hiding behaviour ⁷	76, 77, 84
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>		yes (experimental infection)	increased activity, increased presence in surface zone	160
<i>Acanthocephalus anguillae</i>	<i>Asellus aquaticus</i>		yes (experimental infection)	increased activity, increased presence in surface zone	160
<i>Acanthocephalus ranae</i>	<i>Asellus aquaticus</i>		yes (experimental infection)	increased activity, increased presence in surface zone	160
<i>Profilicollis altmani</i>	<i>Emerita analoga</i>		no	increased burrowing time	96
<i>Profilicollis</i> spp.	<i>Macrophthalmus hirtipes</i>		no	Increased hiding behaviour	27, 93
<i>Profilicollis antarcticus</i>	<i>Hemigrapsus crenulatus</i>		no	increased activity	81
<i>Neoechinorhynchus cylindricus</i>	<i>Phytocypria pustulosa</i>		yes (experimental infection)	skimming at surface	29
<i>Octospiniferoides chandleri</i>	<i>Cypridopsis vidua</i>		yes (experimental infection)	skimming at surface and photophilic	29
<i>Octospiniferoides chandleri</i>	<i>Physocypria pustulosa</i>		yes (experimental infection)	skimming at surface and photophilic	29
<i>Echinorhynchus truttae</i>	<i>Gammarus pulex</i> (invasive)		no	habitat choice (current, water depth)	74
<i>Echinorhynchus truttae</i>	<i>Gammarus pulex</i> (invasive)		no	activity	74
<i>Echinorhynchus truttae</i>	<i>Gammarus pulex</i> (invasive)		no	changed phototaxis (from – to +)	74
<i>Echinorhynchus truttae</i>	<i>Gammarus pulex</i> (invasive)		no	reduced tendency to kill live prey	78
<i>Echinorhynchus truttae</i>	<i>Gammarus pulex</i> (invasive)		no	increased prey consumption ²⁰	118, 162
<i>Echinorhynchus borealis</i>	<i>Pallasea quadrispinosa</i>		no	decreased hiding behaviour with fish odour (<i>Lota lota</i>) compared to uninfected amphipods	76
<i>Leptorhynchoides thecatus</i>	<i>Hyalella azteca</i>		yes (experimental infection)	decreased response to fish kairomones (refuge use and activity) and gammarid alarm cues (activity)	75
<i>Plagiorhynchus cylindraceus</i>	<i>Armadillidium vulgare</i>		yes (experimental infection)	behaviour (increased activity of females, decreased shelter, decreased preference for humid places)	20
<i>Plagiorhynchus cylindraceus</i>	<i>Armadillidium vulgare</i>		yes (experimental infection)	substrate preference (more preference for white in females and for black in males)	20
<i>Moniliformes moniliformes</i>	<i>Periplaneta americana</i>		yes (experimental infection)	substrate preference behaviour	112
<i>Moniliformes moniliformes</i>	<i>Periplaneta americana</i>		yes (experimental infection)	less photophobic, decreased reactivity to sudden light	21
<i>Moniliformes moniliformes</i>	<i>Periplaneta americana</i>		yes (experimental infection)	increased activity	21

<i>Moniliformes moniliformes</i>	<i>Periplaneta americana</i>		yes (experimental infection)	odour preference		34
<i>Moniliformes moniliformes</i>	<i>Periplaneta americana</i>		yes (experimental infection)	reduced distance travelled		112
<i>Moniliformes moniliformes</i>	<i>Periplaneta americana</i>		yes (experimental infection)	decreased escape response		113
<i>Moniliformes moniliformes</i>	<i>Periplaneta australasiae</i>		yes (experimental infection)	substrate preference behaviour ⁹		111
<i>Moniliformes moniliformes</i>	<i>Periplaneta australasiae</i>		yes (experimental infection)	tendency to reduced activity		111
<i>Moniliformes moniliformes</i>	<i>Periplaneta brunnea</i>		yes (experimental infection)	changed substrate preference		22
<i>Moniliformes moniliformes</i>	<i>Periplaneta brunnea</i>		yes (experimental infection)	changed response to sudden light (more individuals freezing but shorter)		22
<i>Moniliformes moniliformes</i>	<i>Blatta orientalis</i>		yes (experimental infection)	decreased activity		111
<i>Moniliformes moniliformes</i>	<i>Blatella germanica</i>		yes (experimental infection)	substrate preference behaviour		112
<i>Moniliformes moniliformes</i>	<i>Blatella germanica</i>		yes (experimental infection)	reduced distance travelled		112
<i>Moniliformes moniliformes</i>	<i>Supella longipalpa</i>		yes (experimental infection)	substrate preference		36
<i>Moniliformes moniliformes</i>	<i>Supella longipalpa</i>		yes (experimental infection)	less movement in response to light, tendency to avoid light		36
not specified (family Oligacanthorhynchidae)	<i>Nasutitermes acajutlae</i>		no	increased exposure during trail breaks		147
<i>Pomphorhynchus tereticollis</i>	<i>Gammarus pulex</i>		no	unchanged photophobic behaviour		105
<i>Pomphorhynchus tereticollis</i>	<i>Gammarus pulex</i>		no	no change in predator-odour preference (<i>Carassius auratus</i>)		56
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (experimental infection)	no effect on aggregation behaviour		106, 117
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (injection of serotonin)	no changed hiding behaviour		106
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (injection of serotonin)	no changed aggregation behaviour		106
<i>Pomphorhynchus laevis</i>	<i>Gammarus roeseli</i>		no	no effect on phototaxis		82, 110
<i>Pomphorhynchus laevis</i>	<i>Gammarus roeseli</i>		no	no effect on geotaxis		82, 110
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (injection of serotonin)	no change in geotaxis		67
<i>Pomphorhynchus laevis</i>	<i>Gammarus roeseli</i> (invasive)		no	no change in phototaxis		33, 68
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	unchanged aggregation behaviour relative to uninfected gammarids with NH fish (<i>Gasterosteus aculeatus</i>) odour		43
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	unchanged hiding behaviour relative to uninfected gammarids with NH fish (<i>Cottus gobio</i>) odour and sound		129
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	no change in predator-odour preference (NH <i>Cottus gobio</i>)		129
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i>		no	no effect on phototaxis		82
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i>		no	no effect on geotaxis when also infected by a microsporidian		82
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	no changed phototaxis		67
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	no change in phototaxis		139
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	unchanged microdistribution in the field with respect to presence of <i>Cottus gobio</i> or NH <i>Astacus astacus</i>		132
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i>		no	no change in activity		79, 92

<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i> (invasive)		no	unchanged vertical distribution with the presence of <i>Atyaephyra desmarestii</i> (non-predatory NH)		135
<i>Corynosoma constrictum</i>	<i>Hyalella azteca</i>		yes (experimental infection)	unchanged reactions to blue light		122
not specified	<i>Echinogammarus marinus</i>		yes (injection of carbamazepine or diclofenac)	no change in phototaxis		80
not specified	<i>Echinogammarus marinus</i>		yes (injection of carbamazepine or diclofenac)	no change in geotaxis		80
<i>Acanthocephalus galaxii</i>	<i>Paracalliope fluviatilis</i>		no	unchanged activity		103
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>		no	no changed activity		77
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>		no	no changed substrate choice		77
<i>Profilicollis antarcticus</i>	<i>Hemigrapsus crenulatus</i>		yes (experimental infection) and no (field)	no behavioral effects (fleeting in lab and field; hydrotaxis and phototaxis in lab)		17
<i>Profilicollis</i> spp.	<i>Hemigrapsus crenulatus</i>		no	no effect on hiding behaviour		93
<i>Echinorhynchus truttae</i>	<i>Gammarus pulex</i>		no	unchanged microdistribution in the field with respect to presence of <i>Cottus gobio</i> or NH <i>Astacus astacus</i>		132
<i>Echinorhynchus borealis</i>	<i>Pallasea quadrispinosa</i>		no	unchanged hiding behaviour without fish odour		76
<i>Echinorhynchus borealis</i>	<i>Pallasea quadrispinosa</i>		no	no changed hiding behaviour of amphipods (population without fish predators) with fish odour compared to uninfected controls		76
<i>Pseudocorynosoma</i> sp.	<i>Hyalella patagonica</i>		no	unchanged activity		143
<i>Pseudocorynosoma</i> sp.	<i>Hyalella patagonica</i>		no	unchanged phototaxis		143
<i>Plagiorhynchus cylindraceus</i>	<i>Armadillidium vulgare</i>		yes (experimental infection)	unchanged phototaxis		20
<i>Moniliformes moniliformes</i>	<i>Periplaneta americana</i>		yes (experimental infection)	unchanged activity		34, 112
<i>Moniliformes moniliformes</i>	<i>Periplaneta americana</i>		yes (experimental infection)	unchanged phototaxis		112
<i>Moniliformes moniliformes</i>	<i>Periplaneta australasiae</i>		yes (experimental infection)	unchanged phototaxis		111
<i>Moniliformes moniliformes</i>	<i>Periplaneta brunnea</i>		yes (experimental infection)	unchanged activity		22
<i>Moniliformes moniliformes</i>	<i>Periplaneta brunnea</i>		yes (experimental infection)	unchanged phototaxis		22
<i>Moniliformes moniliformes</i>	<i>Blatta orientalis</i>		yes (experimental infection)	unchanged substrate preference		111
<i>Moniliformes moniliformes</i>	<i>Blatta orientalis</i>		yes (experimental infection)	unchanged phototaxis		111
<i>Moniliformes moniliformes</i>	<i>Blatella germanica</i>		yes (experimental infection)	unchanged activity		112
<i>Moniliformes moniliformes</i>	<i>Blatella germanica</i>		yes (experimental infection)	unchanged phototaxis		112
<i>Moniliformes moniliformes</i>	<i>Supella longipalpa</i>		yes (experimental infection)	unchanged activity		36
<i>Moniliformes moniliformes</i>	<i>Diptoptera punctata</i>		yes (experimental infection)	unchanged substrate preference		32
<i>Moniliformes moniliformes</i>	<i>Diptoptera punctata</i>		yes (experimental infection)	unchanged activity		32
<i>Moniliformes moniliformes</i>	<i>Diptoptera punctata</i>		yes (experimental infection)	unchanged phototaxis and reaction to light		32
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	increased mortality rate		4, 45, 46, 47, 66
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (experimental infection)	increased mortality rate dependent on parasite and host population		125, 130

<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	reduced female fecundity		7, 54, 63
<i>Pomphorhynchus laevis</i>	<i>Gammarus roeseli</i>		no	fecundity reduction in larger females		82
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	increased mortality rate		61
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	increased (predation?) mortality		107
<i>Pomphorhynchus laevis</i>	<i>Echinogammarus stammeri</i>		no	reduced female fecundity (fewer and smaller eggs)		23
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	sterilisation of females		63
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	reduced female fecundity		16
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i>		no	sterilisation of part of females		82
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	increased (predation?) mortality		107
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i> (invasive)		no	increased (predation?) mortality		135
<i>Polymorphus minutus</i>	<i>Gammarus fossarum</i>		no	decreased body mass		120
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	decreased body size		139
<i>Polymorphus minutus</i>	<i>Gammarus lacustris</i>		no	decreased body size		19
<i>Polymorphus minutus</i>	<i>Gammarus lacustris</i>		no	reduced female fecundity		19
<i>Polymorphus minutus</i>	<i>Echinogammarus tibaldii</i>		no	reduced female fecundity (no eggs and young)		144
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i>		no	reduced mortality		52
<i>Acanthocephalus dirus</i>	<i>Asellus intermedius</i>		no	increased mortality rate		24
<i>Acanthocephalus dirus</i>	<i>Caecidotea intermedius</i>		no	body size (increase in females, decrease in males)		42
<i>Acanthocephalus dirus</i>	<i>Caecidotea intermedius</i>		no	increased body size in males		41
<i>Acanthocephalus anguillae</i>	<i>Asellus aquaticus</i>		no	reproduction		40
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>		no	sterilisation of females		38
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>		no	reduced female fecundity		28
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>		yes (experimental infection)	increased growth		89
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>		yes (experimental infection)	increased survival of females (decreased in resistant and increased in susceptible females)		86
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>		yes (experimental infection)	changed survival (increased in exposed juveniles and maturing adults but decreased in exposed adults) ¹³		89, 138
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>		yes (experimental infection)	increased mortality of exposed hosts during the early (102) or later (28) part of the infection		28, 102
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>		yes (experimental infection)	accelerated moulting of exposed hosts		102
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>		yes (experimental infection)	reduced offspring size at birth		86
<i>Acanthocephalus rhinensis</i>	<i>Echinogammarus tibaldii</i>		no	reduced female fecundity		145
<i>Acanthocephalus</i> sp.	<i>Asellus hilgendorfi</i>		no	increased intersexuality		149
<i>Acanthocephalus</i> sp.	<i>Asellus hilgendorfi</i>		no	reduced female fecundity		149
<i>Acanthocephalus</i> sp.	<i>Asellus hilgendorfi</i>		no	increased body size		149
<i>Acanthocephalus tumescens</i>	<i>Hyalella patagonica</i>		no	reduced female fecundity ¹⁸		153

<i>Acanthocephalus tehlequahensis</i>	<i>Caecidotea communis</i>		no	increased mortality rate		154
<i>Acanthocephalus tehlequahensis</i>	<i>Caecidotea communis</i>		no	increased body size		154
<i>Echinorhynchus truttae</i>	<i>Gammarus pulex</i> (invasive)		no	increased body size		118
<i>Echinorhynchus truttae</i>	<i>Gammarus pulex</i> (invasive)		no	reduced female fecundity		118
not specified	<i>Asellus aquaticus</i>		no	increased intersexuality		37
<i>Echinorhynchus truttae</i>	<i>Echinogammarus tibaldii</i>		no	reduced female fecundity		144
<i>Dentitruncus truttae</i>	<i>Echinogammarus tibaldii</i>		no	reduced female fecundity		144
<i>Corynosoma</i> sp.	<i>Hyalella patagonica</i>		no	reduced female fecundity		153
<i>Profilicollis novaezelandensis</i> (and <i>P. antarcticus</i>)	<i>Macrophthalmus hirtipes</i>		no	increased (predation?) mortality		90
<i>Profilicollis novaezelandensis</i> (and <i>P. antarcticus</i>)	<i>Hemigrapsus edwardsi</i>		no	increased (predation?) mortality		90
<i>Profilicollis novaezelandensis</i> (and <i>P. antarcticus</i>)	<i>Hemigrapsus crenulatus</i>		no	increased (predation?) mortality		90
<i>Profilicollis chasmagnathi</i>	<i>Cyrtograpsus angulatus</i>		no	increased (predation?) mortality		151
<i>Plagiorhynchus cylindraceus</i>	<i>Armadillidium vulgare</i>		yes (experimental infection)	reduced growth in females		20
<i>Plagiorhynchus cylindraceus</i>	<i>Armadillidium vulgare</i>		yes (experimental infection)	sterilisation of females		20
<i>Plagiorhynchus cylindraceus</i>	<i>Trachelipus squamuliger</i>		no	reduced female fecundity		146
<i>Moniliformes moniliformes</i>	<i>Supella longipalpa</i>		yes (experimental infection)	reduced female fecundity ¹⁷		148
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	no effect on mortality rate (some sibships)		66
<i>Pomphorhynchus laevis</i>	<i>Gammarus roeseli</i> (invasive)		no	no effect on mortality rate		61
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	unchanged body mass		49, 69
<i>Polymorphus paradoxus</i>	<i>Gammarus lacustris</i>		no	no parasitic castration of males		57
<i>Polymorphus marilis</i>	<i>Gammarus lacustris</i>		no	no parasitic castration of males		57
<i>Polymorphus minutus</i>	<i>Gammarus fossarum</i>		no	no effect on mortality without and with cadmium exposure		120
<i>Leptorhynchiodes thecatus</i>	<i>Hyalella azteca</i>		yes (experimental infection)	no effect on mortality of exposed and unexposed hosts		101
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>		no	no effect on mortality rate		84
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>		no	no sterilisation of males		38
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>		yes (experimental infection)	no effect on growth		86, 102
<i>Profilicollis novaezelandensis</i> (and <i>P. antarcticus</i>)	<i>Macrophthalmus hirtipes</i>		no	no effect on fecundity		90

<i>Profilicollis novaezelandensis</i> (and <i>P. antarcticus</i>)	<i>Hemigrapsus edwardsi</i>		no	no effect on fecundity		90
<i>Echinorhynchus truttae</i>	<i>Gammarus pulex</i> (invasive)		no	unchanged body condition		118
<i>Moniliformes moniliformes</i>	<i>Supella longipalpa</i>		yes (experimental infection)	no effect on mortality rate		148
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (injection of serotonin)	higher metabolic rate		106
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	carbohydrate mobilisation		50
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	increased sensitivity to cadmium at low exposure concentration		47
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	reduction of respiration rate ⁴		53
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	increased glycogen content		58
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	lower lipid contents in gravid females		58
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (experimental infection)	increased oxygen consumption		130
<i>Pomphorhynchus laevis</i>	<i>Echinogammarus stammeri</i>		no	displacement of the alimentary tract		12, 59
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (experimental infection; 119, 157) and no (65, 157)	immunosuppression		65, 119, 157
<i>Pomphorhynchus laevis</i>	<i>Gammarus roeseli</i> (invasive)		no	enhanced immune response (various French and Hungarian populations)		65, 110
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	increased brain serotonin		67, 68
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	disturbed osmoregulation (sodium)		121
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	decreased protein and copper content of midgut glands		69
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	increased haemolymph proteins		49
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	reduced immunocompetence, reduced bacterial clearance efficiency		99
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	reduced sugar content		99
<i>Pomphorhynchus teriticollis</i>	<i>Gammarus pulex</i>		no	increased brain serotonin		67
<i>Pomphorhynchus teriticollis</i>	<i>Gammarus pulex</i>		no	immunosuppression		157
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	immunosuppression		65, 66, 157
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i>		no	decreased antioxidant defence capacity (GSH, GCL)		18, 155
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i>		no	decreased MDA (malondialdehyde) levels		18
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i>		no	increased glycogen content		155
<i>Polymorphus minutus</i>	<i>Gammarus lacustris</i>		no	decreased carotenoid content		26
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i>		no	increased salinity tolerance		79
<i>Polymorphus minutus</i>	<i>Gammarus fossarum</i>		no	increased level of heat shock proteins		71
<i>Polymorphus minutus</i>	<i>Gammarus fossarum</i>		no	decreased glycogen level in males when exposed to cadmium otherwise no effect		120
<i>Polymorphus minutus</i>	<i>Gammarus fossarum</i>		no	decreased lipid levels except for males exposed to cadmium		120

<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i>		no	suppression of heat shock protein induction	52
<i>Polymorphus paradoxus</i>	<i>Gammarus lacustris</i>		no	increased serotonin in ventral nerve cord	164
<i>Profilicollis antarcticus</i>	<i>Hemigrapsus crenulatus</i>		no	increased oxygen consumption	81
<i>Profilicollis antarcticus</i>	<i>Hemigrapsus crenulatus</i>		yes (experimental infection)	increase in haemolymph dopamine	97
<i>Echinorhynchus truttae</i>	<i>Gammarus pulex</i> (invasive)		no	decreased ammonia tolerance	85
<i>Corynosoma</i> sp.	<i>Gammarus pseudolimnaeus</i>		no	increased estrogen concentration in paired females and decreased testosterone concentration in males independent of pairing status	115
<i>Corynosoma</i> sp.	<i>Hyalella patagonica</i>		no	decreased carotenoid content	153
<i>Acanthocephalus anguillae</i>	<i>Asellus aquaticus</i>		no	displacement of the alimentary tract	40
<i>Acanthocephalus dirus</i>	<i>Caecidotea intermedius</i>		no	increased lipid (150) and glycogen content	41, 150
<i>Acanthocephalus tehlequahensis</i>	<i>Caecidotea communis</i>		no	increased respiration rate	154
<i>Plagiorhynchus cylindraceus</i>	<i>Armadillidium vulgare</i>		yes (experimental infection)	increased water loss in females	20
<i>Moniliformis moniliformis</i>	<i>Periplaneta americana</i>		yes (experimental infection)	immunosuppression	152
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		yes (experimental infection)	no effect on metabolic rate	106
<i>Pomphorhynchus laevis</i>	<i>Gammarus fossarum</i>		no	no effect on metabolic rate	106
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	unchanged sensitivity to cadmium at high exposure concentration	47
<i>Pomphorhynchus laevis</i>	<i>Gammarus roeseli</i> (invasive)		no	no effect on immunocompetence (various French populations)	110
<i>Pomphorhynchus laevis</i>	<i>Gammarus roeseli</i> (invasive)		no	no change in brain serotonin	68
<i>Pomphorhynchus laevis</i>	<i>Gammarus roeseli</i> (invasive)		no	no effect on immunocompetence, sugar content, lipid content, and bacterial clearance efficiency	99
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	no mortality effect when exposed to different concentrations of cadmium	44
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>		no	no effect on lipid content	99
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	no change in brain serotonin	67
<i>Polymorphus minutus</i>	<i>Gammarus fossarum</i>		no	no effect on heat-shock protein	120
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>		no	unchanged level and composition of carotenoids	116
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i>		no	unchanged level and composition of carotenoids	116
<i>Polymorphus marilis</i>	<i>Gammarus lacustris</i>		no	no change in serotonin in ventral nerve cord	164
<i>Profilicollis antarcticus</i>	<i>Hemigrapsus crenulatus</i>		yes (experimental infection)	no change in hemolymph serotonin	97

<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Gasterosteus aculeatus</i>	yes (infection masked by brown spot)	behaviour	yes	1
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Salmo trutta</i>	yes (infection masked by brown spot)	behaviour	yes	60
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Gasterosteus aculeatus</i>	yes (infection mimicked by orange spot)	visual appearance	yes	1, 2
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Gasterosteus aculeatus</i>	yes (infection mimicked by orange spot)	visual appearance	no, decreased	2
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Salmo trutta</i>	no		yes	60
<i>Pomphorhynchus laevis</i>	<i>Gammarus fossarum</i>	<i>Thymallus thymallus</i>	no		yes ¹⁶	141
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Barbus barbuis</i>	yes (infection mimicked by orange spot)	visual appearance	yes	2
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Orconectes limosus</i> (NH)	no		yes independent of refuge availability	128
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Nepa cinerea</i> (NH)	no		yes independent of refuge availability	128
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Cottus gobio</i>	no		yes with refuge, no without refuge	129
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Salmo trutta fario</i>	yes (experimental infection)		yes ⁵	83
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Gasterosteus aculeatus</i>	no		yes	4
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Leuciscus leuciscus</i>	no		yes	9
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Thymallus thymallus</i>	no		yes	9
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Gobio Gobio</i>	no		yes	8
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Rutilus rutilus</i>	no		yes	8
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Alburnus alburnus</i>	no		yes	8
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Leuciscus cephalus</i>	no		yes	8
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Cottus gobio</i>	no		yes	61
<i>Pomphorhynchus tereticollis</i>	<i>Gammarus pulex</i>	<i>Cottus gobio</i>	no		yes	104
<i>Pomphorhynchus tereticollis</i> ⁸	<i>Gammarus pulex</i>	<i>Nepa cinerea</i> (NH) (water scorpion)	no		yes independent of refuge availability	128
<i>Pomphorhynchus tereticollis</i>	<i>Gammarus pulex</i>	<i>Carassius auratus</i>	no	change in phototaxis (from - to 0) ⁵	yes	56
<i>Polymorphus minutus</i>	<i>Echinogammarus berilloni</i>	<i>Anas platyrhynchos</i> (mallard)	no		yes	94
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>	<i>Nepa cinerea</i> (NH)	no		yes without refuge but no (decreased predation) with refuge availability	128
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>	<i>Anas platyrhynchos</i>	yes (infection mimicked by orange spot)	visual appearance	yes independent of aggregation of gammarids	127
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>	<i>Carassius auratus</i>	no		yes	139
<i>Polymorphus minutus</i>	<i>Gammarus lacustris</i>	<i>Anas platyrhynchos</i>	no		yes	26

<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i> (invasive)	<i>domesticus</i> <i>Dikergammarus villosus</i> (NH)	no		no, decreased when water level was 12cm	135
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i> (invasive)	<i>Dikergammarus villosus</i> (NH)	no		yes, when water level was 4cm	135
<i>Polymorphus minutus</i>	<i>Gammarus roeseli</i>	<i>Gasterosteus aculeatus</i> (NH)	no		no, even decreased when plants reached the surface	134
<i>Polymorphus paradoxus</i>	<i>Gammarus lacustris</i>	<i>Anas platyrhynchos</i>	no		yes	6
<i>Polymorphus paradoxus</i>	<i>Gammarus lacustris</i>	<i>Ondatra zibethica</i> (muskrat)	no		yes	6
<i>Corynosoma constrictum</i>	<i>Hyalella azteca</i>	<i>Anas platyrhynchos</i>	no		yes	6
<i>Acanthocephalus dirus</i>	<i>Asellus intermedius</i>	<i>Semotilus atromaculatus</i>	no		yes ¹⁴	11
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>	<i>Perca fluviatilis</i>	no		yes	38, 136
<i>Acanthocephalus lucii</i>	<i>Asellus aquaticus</i>	dragonfly (NH, unspecified)	no		yes, but less pronounced as to fish host	136
<i>Echinorhynchus truttae</i>	<i>Gammarus pulex</i>	<i>Cottus gobio</i>	no		yes	132
<i>Profilicollis chasmagnathi</i>	<i>Neohelice granulata</i>	<i>Larus atlanticus</i>	no		yes	151
<i>Profilicollis chasmagnathi</i>	<i>Cyrtograpsus angulatus</i>	sharks? fish?	no		yes (indirect evidence)	151
<i>Plagiorhynchus cylindraceus</i>	<i>Armadillidium vulgare</i>	<i>Sturnus vulgaris</i>	no		yes	20
not specified (family Oligacanthorhynchidae)	<i>Nasutitermes acajutlae</i>	<i>Anolis cristatellus</i> and <i>A. stratulus</i>	no		yes (parasitized workers were eaten before unparasitized workers)	147
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>	<i>Salmo trutta</i> (NH)	yes (infection masked by brown spot)	behaviour	no	60
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>	<i>Salmo trutta</i> (NH)	no		no	60
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>	<i>Salmo trutta</i> (NH)	yes (infection mimicked by orange spot)	visual appearance	no	60
<i>Polymorphus minutus</i>	<i>Echinogammarus berilloni</i>	<i>Anas platyrhynchos</i>	no		no (when preventing vertical distribution)	94
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>	<i>Orconectes limosus</i> (NH)	no		no independent of refuge availability	128
<i>Polymorphus minutus</i>	<i>Gammarus. pulex</i>	<i>Cottus gobio</i> (NH)	no		no independent of refuge availability	129
<i>Polymorphus minutus</i>	<i>Gammarus pulex</i>	<i>Cottus gobio</i> (NH)	no		no	132
<i>Polymorphus paradoxus</i>	<i>Gammarus lacustris</i>	<i>Anas platyrhynchos</i>	yes (infection mimicked by orange spot)	visual appearance	no	6
<i>Polymorphus marilis</i>	<i>Gammarus lacustris</i>	<i>Ondatra zibethica</i> (muskrat) (NH)	no		no	6
<i>Polymorphus marilis</i>	<i>Gammarus lacustris</i>	<i>Anas platyrhynchos</i>	no		no	6

<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	(NH) <i>Gymnocephalus cernuus</i>	yes (infection mimicked by orange spot)	visual appearance	no	2
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Perca fluviatilis</i>	yes (infection mimicked by orange spot)	visual appearance	no	2
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Salmo trutta</i>	yes (infection mimicked by orange spot)	visual appearance	no	2, 60
<i>Pomphorhynchus laevis</i>	<i>G. roeseli</i> (invasive)	<i>Cottus gobio</i>	no		no	61
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Rana esculenta</i> (NH)	no		no	61
<i>Pomphorhynchus laevis</i>	<i>Gammarus pulex</i>	<i>Gobio Gobio</i>	yes (infection mimicked by orange spot)		no	8
<i>Pomphorhynchus tereticollis</i>	<i>Gammarus pulex</i>	<i>Carassius auratus</i>	yes (injection of serotonin and fluoxetine)	change in phototaxis (from – to 0)	no	56
<i>Pomphorhynchus tereticollis</i> ⁸	<i>Gammarus pulex</i>	<i>Orconectes limosus</i> (NH) (crayfish)	no		no independent of refuge availability	128

¹not observed when infected with young cystacanths (5)

²effect less in acanthella stage (31, 123) while dependent on parasite population and intensity of infection (124)

³no effect in acanthella stage (10, 124, 153)

⁴not significant at lower temperatures and in the acanthella stage (53)

⁵no effect of light intensity (56)

⁶opposite effect in acanthella stage (83)

⁷effect of age (84)

⁸called *P. laevis* W type, likely *P. tereticollis* based on morphology and molecular genetics (105)

⁹effect of light colour (111)

¹⁰effect less in young cystacanths while dependent on intensity of infection (124), sibship (126) and time of year (126)

¹¹effect dependent on parasite population, host population and naivety of host population (125)

¹²effect only after repeated testing while depending on parasite population (130)

¹³mortality of resistant adults dependent on host population (138)

¹⁴more pronounced on dark than on white substrate as infected isopods are light (11)

¹⁵geotaxis confounded with phototaxis (94)

¹⁶indirect evidence: more cystacanth than acanthella stage in fish stomach (141)

¹⁷only at higher temperatures and later in infection (148)

¹⁸but females with eggs were more frequently infected by acanthella (153)

¹⁹but lighter opercula in some years (160)

²⁰increase with temperature (162)

²¹willingness to mate less suppressed in males with multiple infections (163)

²²only at higher temperatures (165)

²³independent of temperature (165)

Reference numbers:

1. Bakker et al. 1997; 2. Thünken et al. 2017; 3. Baldauf et al. 2007; 4. Mazzi & Bakker 2003; 5. Bethel & Holmes 1974; 6. Bethel & Holmes 1977; 7. Poulton & Pascoe 1990; 8. Brown & Thompson 1986; 9. Kennedy et al. 1978; 10. Bethel & Holmes 1973; 11. Camp & Huizinga 1979; 12. Dezfuli et al. 2008a; 13. McCahon et al. 1991; 14. Maynard et al. 1998; 15. Dezfuli et al. 2003; 16. Hynes & Nicholas 1963; 17. Pulgar et al. 1995; 18. Gismondi et al. 2012a; 19. Hynes 1955; 20. Moore 1983a; 21. Moore 1983b; 22. Carmichael & Moore 1991; 23. Dezfuli et al. 1999; 24. Seidenberg 1973; 25. Muzzall & Rabalais 1975a; 26. Hindsbo 1972; 27. Latham & Poulin 2001; 28. Bratley 1986; 29. DeMont & Corkum 1982; 30. Oetinger & Nickol 1981; 31. Sparkes et al. 2004; 32. Allely et al. 1992; 33. Bauer et al. 2000; 34. Wilson & Edwards 1986; 35. Barrett & Butterworth 1968; 36. Moore & Gotelli 1992; 37. Munro 1953; 38. Bratley 1983; 39. Denny 1969; 40. Dezfuli et al. 1994; 41. Caddigan et al.

2014; 42. Oetinger 1987; 43. Thünken et al. 2010; 44. McCahon et al. 1988; 45. McCahon et al. 1989; 46. McCahon & Poulton 1991; 47. Brown & Pascoe 1989; 48. Hechtel et al. 1993; 49. Bentley & Hurd 1993; 50. Bentley & Hurd 1996; 51. Cézilly et al. 2000; 52. Sures & Radszuweit 2007; 53. Rumpus & Kennedy 1974; 54. Poulton & Thompson 1987; 55. Ward 1986; 56. Perrot-Minnot et al. 2012; 57. Zohar & Holmes 1998; 58. Plaistow et al. 2001; 59. Dezfuli et al. 1991; 60. Kaldonski et al. 2009; 61. Lagrue et al. 2007; 62. Bollache et al. 2001; 63. Bollache et al. 2002; 64. Alibert et al. 2002; 65. Rigaud & Moret 2003; 66. Cornet et al. 2009a; 67. Tain et al. 2006; 68. Tain et al. 2007; 69. Bentley & Hurd 1995; 70. Pascoe et al. 1995; 71. Frank et al. 2013; 72. Wellnitz et al. 2003; 73. Hernandez & Sukhdeo 2008; 74. MacNeil et al. 2003; 75. Stone & Moore 2014; 76. Benesh et al. 2008a; 77. Benesh et al. 2008b; 78. Fielding et al. 2003; 79. Piscart et al. 2007; 80. Guler & Ford 2010; 81. Haye & Ojeda 1998; 82. Haine et al. 2005; 83. Dianne et al. 2011; 84. Benesh et al. 2009a; 85. Prenter et al. 2004; 86. Hasu et al. 2006; 87. Benesh et al. 2009b; 88. Amin et al. 1980; 89. Hasu et al. 2007; 90. Latham & Poulin 2002a; 91. Sparkes et al. 2006; 92. Medoc & Beisel 2008; 93. Latham & Poulin 2002b; 94. Jacquin et al. 2014; 95. Gismondi et al. 2012b; 96. Kolluru et al. 2011; 97. Rojas & Ojeda 2005; 98. Dianne et al. 2014; 99. Cornet et al. 2010; 100. Bauer et al. 2005; 101. Uznanski & Nickol 1980; 102. Benesh & Valtonen 2007; 103. Rauque et al. 2011; 104. Perrot-Minnot et al. 2007; 105. Perrot-Minnot 2004; 106. Perrot-Minnot et al. 2014; 107. Perrot-Minnot et al. 2013; 108. Outreman et al. 2007; 109. Muzzall & Rabalais 1975b; 110. Moret et al. 2007; 111. Moore et al. 1994; 112. Gotelli & Moore 1992; 113. Libersat & Moore 2000; 114. Lewis et al. 2012; 115. Lewis et al. 2016; 116. Gaillard et al. 2004; 117. Durieux et al. 2012; 118. Dick et al. 2010; 119. Cornet 2011; 120. Chen et al. 2015; 121. Brooks & Lloyd Mills 2011; 122. Benesh et al. 2005; 123. Dianne et al. 2010; 124. Franceschi et al. 2008; 125. Franceschi et al. 2010a; 126. Franceschi et al. 2010b; 127. Jacquin et al. 2013; 128. Kaldonski et al. 2008; 129. Kaldonski et al. 2007; 130. Labaude et al. 2015; 131. Labaude et al. 2017a; 132. Lagrue et al. 2013; 133. Medoc & Beisel 2009; 134. Medoc et al. 2009; 135. Medoc et al. 2006; 136. Seppälä et al. 2008; 137. Oetinger & Nickol 1982a; 138. Hasu et al. 2009; 139. Marriott et al. 1989; 140. Oetinger & Nickol 1982b; 141. van Maren 1979; 142. Al-Jahdali et al. 2015; 143. Casalins et al. 2015; 144. Dezfuli et al. 2008b; 145. Dezfuli et al. 2012; 146. Dimitrova 2009; 147. Fuller et al. 2003; 148. Guinnee & Moore 2004; 149. Kakizaki et al. 2003; 150. Korkofigas et al. 2016; 151. La Sala et al. 2012; 152. Lackie & Holt 1989; 153. Rauque & Semenas 2009; 154. Lettini & Sukhdeo 2010; 155. Gismondi et al. 2012c; 156. Helluy & Holmes 1990; 157. Cornet et al. 2009b; 158. Perrot-Minnot et al. 2011; 159. Pilecka-Rapacz 1984; 160. Pilecka-Rapacz 1986; 161. Bierbower & Sparkes 2007; 162. Laverty et al. 2017; 163. Caddigan et al. 2017; 164. Maynard et al. 1996; 165. Labaude et al. 2017b

Literature Cited:

- Alibert, P., Bollache, L., Corberant, D., Guesdon, V. & Cézilly, F. 2002: Parasitic infection and developmental stability: fluctuating asymmetry in *Gammarus pulex* infected with two acanthocephalan species. *J. Parasitol.* **88**, 47-54.
- Al-Jahdali, M. O., Hassanine, R. M. E.-S. & Touliabah, H. E.-S. 2015: The life cycle of *Sclerocollum saudii* Al-Jahdali, 2010 (Acanthocephala: Palaeacanthocephala: Rhadinorhynchidae) in amphipod and fish hosts from the Red Sea. *J. Helminthol.* **89**, 277-287.
- Allely, Z., Moore, J. & Gotelli, N. J. 1992: *Moniliformis moniliformis* infection has no effect on some behaviors of the cockroach *Diploptera punctata*. *J. Parasitol.* **78**, 524-526.
- Amin, O. M., Burns, L. A. & Redlin, M. J. 1980: The ecology of *Acanthocephalus parksidei* (Acanthocephala: Echinorhynchidae) in its isopod intermediate host. *P. Helm. Soc. Wash.* **47**, 37-46.
- Bakker, T. C. M., Mazzi, D. & Zala, S. 1997: Parasite-induced changes in behavior and color make *Gammarus pulex* more prone to fish predation. *Ecology* **78**, 1098-1104.
- Baldauf, S. A., Thunken, T., Frommen, J. G., Bakker, T. C. M., Heupel, O. & Kullmann, H. 2007: Infection with an acanthocephalan manipulates an amphipod's reaction to a fish predator's odours. *Int. J. Parasitol.* **37**, 61-65.
- Barrett, J. & Butterworth, P. E. 1968: The carotenoids of *Polymorphus minutus* (acanthocephala) and its intermediate host, *Gammarus pulex*. *Comp. Biochem. Physiol.* **27**, 575-581.
- Bauer, A., Haine, E. R., Perrot-Minnot M. J. & Rigaud, T. 2005: The acanthocephalan parasite *Polymorphus minutus* alters the geotactic and clinging behaviours of two sympatric amphipod hosts: the native *Gammarus pulex* and the invasive *Gammarus roeseli*. *J. Zool.* **279**, 39-43.
- Bauer, A., Trouve, S., Gregoire, A., Bollache, L. & Cézilly, F. 2000: Differential influence of *Pomphorhynchus laevis* (Acanthocephala) on the behaviour of native and invader gammarid species. *Int. J. Parasitol.* **30**, 1453-1457.
- Benesh, D. P., Duclos, L. M. & Nickol, B. B. 2005: The behavioral response of amphipods harboring *Corynosoma constrictum* (Acanthocephala) to various components of light. *J. Parasitol.* **91**, 731e736.
- Benesh, D. P., Hasu, T., Seppälä, O. & Valtonen, E. T. 2009a: Seasonal changes in host phenotype manipulation by an acanthocephalan: time to be transmitted? *Parasitology* **136**, 219e230.
- Benesh, D. P., Kitchen, J., Pulkkinen, K., Hakala, I. & Valtonen, E. T. 2008a: The effect of *Echinorhynchus borealis* (Acanthocephala) infection on the anti-predator behavior of a benthic amphipod. *J. Parasitol.* **94**, 542-545.
- Benesh D. P., Seppälä O. & Valtonen E. T. 2009b: Acanthocephalan size and sex affect the modification of intermediate host colouration. *Parasitology* **136**, 847-854.
- Benesh D. P. & Valtonen E. T. 2007: Effects of *Acanthocephalus lucii* (Acanthocephala) on intermediate host survival and growth: implications for exploitation strategies. *J. Parasitol.* **93**, 735-741.
- Benesh, D. P., Valtonen, E. T. & Seppälä, O. 2008b: Multidimensionality and intra-individual variation in host manipulation by an acanthocephalan. *Parasitology* **135**, 617-626.
- Bentley, C. R. & Hurd, H. 1993: *Pomphorhynchus laevis* (Acanthocephala) – elevation of hemolymph protein concentrations in the intermediate host, *Gammarus pulex* (Crustacea, Amphipoda). *Parasitology* **107**, 193-198.
- Bentley, C. R. & Hurd, H. 1995: Depressed protein and copper content of the midgut gland in an intermediate host, *Gammarus pulex* (Crustacea), infected with cystacanths of *Pomphorhynchus laevis* (Acanthocephala). *J. Inv. Pathol.* **66**, 1-5.
- Bentley, C. R. & Hurd, H. 1996: Carbohydrate titres in the haemolymph and midgut of *Gammarus pulex* infected with the acanthocephalan *Pomphorhynchus laevis*. *J. Helminthol.* **70**, 103-107.
- Bethel, W. M. & Holmes, J. C. 1973: Altered evasive behavior and responses to light in amphipods harboring acanthocephalan cystacanths. *J. Parasitol.* **59**, 945-956.

- Bethel, W. M. & Holmes, J. C. 1974: Correlation of development of altered evasive behavior in *Gammarus lacustris* (Amphipoda) harboring cystacanths of *Polymorphus paradoxus* (Acanthocephala) with the infectivity to the definitive host. *J. Parasitol.* **60**, 272-274.
- Bethel, W. M. & Holmes, J. C. 1977: Increased vulnerability of amphipods to predation owing to altered behavior induced by larval acanthocephalans. *Can. J. Zool.* **55**, 110–115.
- Bierbower, S. M. & Sparkes, T. C. 2007: Parasite-induced pairing success in an intermediate host, *Caecidotea intermedius* (Isopoda): effects of male behavior and reproductive physiology. *J. Parasitol.* **93**, 445-449.
- Bollache, L., Gambade, G. & Cézilly, F. 2001: The effects of two acanthocephalan parasites, *Pomphorhynchus laevis* and *Polymorphus minutus*, on pairing success in male *Gammarus pulex* (Crustacea: Amphipoda). *Behav. Ecol. Sociobiol.* **49**, 296-303.
- Bollache, L., Rigaud, T. & Cézilly, F. 2002: Effects of two acanthocephalan parasites on the fecundity and pairing status of female *Gammarus pulex* (Crustacea: Amphipoda). *J. Invertebr. Pathol.* **79**, 102–110.
- Bratley, J. 1983: The effects of larval *Acanthocephalus lucii* on the pigmentation, reproduction, and susceptibility to predation of the isopod *Asellus aquaticus*. *J. Parasitol.* **69**, 1172–1173.
- Bratley, J. 1986: Life history and population biology of larval *Acanthocephalus lucii* (Acanthocephala: Echinorhynchidae) in the isopod *Asellus aquaticus*. *J. Parasitol.* **72**, 633–645.
- Brooks, S. J. & Lloyd Mills, C. 2011: Parasitic infection manipulates sodium regulation in the freshwater amphipod *Gammarus pulex* (L.). *Comp. Biochem. Physiol. A* **159**, 247-252.
- Brown, A. F. & Pascoe, D. 1989: Parasitism and host sensitivity to cadmium: an acanthocephalan infection of the freshwater amphipod *Gammarus pulex*. *J. Appl. Ecol.* **26**, 473e487.
- Brown, A. F. & Thompson, D. B. A. 1986: Parasite manipulation of host behaviour: acanthocephalans and shrimps in the laboratory. *J. Biol. Educ.* **20**, 121-127.
- Caddigan, S. C., Barkauskas, R. T. & Sparkes, T. C. 2014: Intra-population variation in behavior modification by the acanthocephalan *Acanthocephalus dirus*: are differences mediated by host condition? *Parasitol. Res.* **113**, 4307-4311.
- Caddigan, S. C., Pfennig, A. C. & Sparkes, T. C. 2017: Competitive growth, energy allocation, and host modification in the acanthocephalan *Acanthocephalus dirus*: field data. *Parasitol. Res.* **116**, 199-206.
- Camp, J. W. & Huizinga, H. W. 1979: Altered color, behavior and predation susceptibility of the isopod *Asellus intermedius* infected with *Acanthocephalus dirus*. *J. Parasitol.* **65**, 667-669.
- Carmichael, L. M. & Moore, J. 1991: A comparison of behavioral alterations in the brown cockroach, *Periplaneta brunnea*, and the American cockroach, *Periplaneta americana*, infected with the acanthocephalan, *Moniliformis moniliformis*. *J. Parasitol.* **77**, 931-936.
- Casalins, L. M., Brugni, N. L. & Rauque, C. A. 2015: The behavior response of amphipods infected by *Hedruris suttonae* (Nematoda) and *Pseudocorynosoma* sp. (Acanthocephala). *J. Parasitol.* **101**, 647-650.
- Cézilly, F., Gregoire, A. & Bertin, A. 2000: Conflict between co-occurring manipulative parasites? An experimental study of the joint influence of two acanthocephalan parasites on the behaviour of *Gammarus pulex*. *Parasitology* **120**, 625-630.
- Chen, H.-Y., Grabner, D. S., Nachev, M., Shih, H.-H. & Sures, B. 2015: Effects of the acanthocephalan *Polymorphus minutus* and the microsporidian *Dictyocoela duebenum* on energy reserves and stress response of cadmium exposed *Gammarus fossarum*. *PeerJ* **3**, e1353.
- Cornet, S. 2011: Density-dependent effects on parasite growth and parasite-induced host immunodepression in the larval helminth *Pomphorhynchus laevis*. *Parasitology* **138**, 257-265.
- Cornet, S., Franceschi, N., Bauer, A., Rigaud, T. & Moret, Y. 2009b: Immune depression induced by acanthocephalan parasites in their intermediate crustacean host: consequences for the risk of superinfection and links with host behavioural manipulation. *Int. J. Parasitol.* **39**, 221-229.
- Cornet, S., Franceschi, N., Bollache, L., Rigaud, T. & Sorci, G. 2009a: Variation and covariation in infectivity, virulence and immunodepression in the host-parasite association *Gammarus pulex*-*Pomphorhynchus laevis*. *Proc. R. Soc. Lond. B* **276**, 4229–4236.
- Cornet, S., Sorci, G. & Moret, Y. 2010. Biological invasion and parasitism: invaders do not suffer from physiological alterations of the acanthocephalan *Pomphorhynchus laevis*. *Parasitology* **137**, 137-147.
- DeMont, D. J. & Corkum, K. C. 1982: The life cycle of *Octospiniferoides chandleri* Bullock, 1957 (Acanthocephala: Neoechinorhynchidae) with some observations on parasite-induced, photophilic behavior in ostracods. *J. Parasitol.* **68**, 125-130.
- Denny, M. 1969: Life-cycles of helminth parasites using *Gammarus lacustris* as an intermediate host in an Alberta lake. *Parasitology* **59**, 795–827.
- Dezfuli, B. S., Lui, A., Giovinazzo, G. & Giari, L. 2008b: Effect of Acanthocephala infection on the reproductive potential of crustacean intermediate hosts. *J. Invertebr. Pathol.* **98**, 116–119.
- Dezfuli, B. S., Lui, A., Squerzanti, S., Lorenzoni, M. & Shinn, A. P. 2012: Confirmation of the hosts involved in the life cycle of an acanthocephalan parasite of *Anguilla anguilla* (L.) from Lake Piediluco and its effect on the reproductive potential of its amphipod intermediate host. *Parasitol. Res.* **110**, 2137-2143.
- Dezfuli, B. S., Maynard, B. J. & Wellnitz, T. A. 2003: Activity levels and predator detection by amphipods infected with an acanthocephalan parasite, *Pomphorhynchus laevis*. *Folia Parasit.* **50**, 129-134.
- Dezfuli, B. S., Rossetti, E., Bellettato, C. M. & Maynard, B. J. 1999: *Pomphorhynchus laevis* in its intermediate host *Echinogammarus stammeri* in the River Brenta, Italy. *J. Helminthol.* **73**, 95-102.
- Dezfuli, B. S., Rossetti, E., Fano, E. A. & Rossi, R. 1994: Occurrence of larval *Acanthocephalus anguillae* (Acanthocephala) in the *Asellus aquaticus* (Crustacea, Isopoda) from the River Brenta. *Boll. Zool.* **61**, 77–81.
- Dezfuli, B. S., Simoni, E., Duclos, L. & Rossetti, E. 2008a: Crustacean-acanthocephalan interaction and host cell-mediated immunity: parasite encapsulation and melanization. *Folia Parasit.* **55**, 53–59.
- Dezfuli, B. S., Zanini, N., Reggiani, G. & Rossi, R. 1991: *Echinogammarus stammeri* (Amphipoda) as an intermediate host for *Pomphorhynchus laevis* (Acanthocephala) parasite of fishes from the River Brenta. *Boll. Zool.* **58**, 267–271.

- Dianne, L., Perrot-Minnot, M.-J., Bauer, A., Gailard, M., Léger, E. & Rigaud, T. 2011: Protection first then facilitation: a manipulative parasite modulates the vulnerability to predation of its intermediate host according to its own developmental stage. *Evolution* **65**, 2692-2698.
- Dianne, L., Perrot-Minnot, M.-J., Bauer, A., Güvenatam, A. & Rigaud, T. 2014: Parasite-induced alteration of plastic response to predation threat: increased refuge use but lower food intake in *Gammarus pulex* infected with the acanthocephalan *Pomphorhynchus laevis*. *Int. J. Parasitol.* **44**, 211-216.
- Dianne, L., Rigaud, T., Léger, E., Motreuil, S., Bauer, A. & Perrot-Minnot, M.-J. 2010: Intraspecific conflict over host manipulation between different larval stages of an acanthocephalan parasite. *J. Evol. Biol.* **23**, 2648-2655.
- Dick, J. T. A., Armstrong, M., Clarke, H. C., Farnsworth, K. D., Hatcher, M. J., Ennis, M., Kelly, A. & Dunn, A. M. 2010: Parasitism may enhance rather than reduce the predatory impact of an invader. *Biol. Lett.* **6**, 636-638.
- Dimitrova, Z. M. 2009: Occurrence of cystacanths of *Plagiorhynchus cylindraceus* (Acanthocephala) in the terrestrial isopods *Trachelipus squamuliger* and *Armadillidium vulgare* (Oniscidea) in Bulgaria. *Acta Parasitol.* **54**, 53-56.
- Durieux, R., Rigaud, T. & Médoc, V. 2012: Parasite-induced suppression of aggregation under predation risk in a freshwater amphipod: sociality of infected amphipods. *Behav. Process.* **91**, 207-213.
- Fielding, N. J., MacNeil, C., Dick, J. T. A., Elwood, R. W., Riddell, G. E. & Dunn, A. M. 2003: Effects of the acanthocephalan parasite *Echinorhynchus truttae* on the feeding ecology of *Gammarus pulex* (Crustacea: Amphipoda). *J. Zool.* **261**, 321-325.
- Franceschi, N., Bauer, A., Bollache, L. & Rigaud, T. 2008: The effects of parasite age and intensity on variability in acanthocephalan-induced behavioural manipulation. *Int. J. Parasitol.* **38**, 1161-1170.
- Franceschi, N., Bollache, L., Cornet, S., Bauer, A., Motreuil, S. & Rigaud, T. 2010b: Covariation between the intensity of behavioural manipulation and parasite development time in an acanthocephalan-amphipod system. *J. Evol. Biol.* **23**, 2143-2150.
- Franceschi, N., Cornet, S., Bollache, L., Dechaume-Moncharmont, F.-X., Bauer, A., Motreuil, S. & Rigaud, T. 2010a: Variation between population and local adaptation in acanthocephalan-induced parasite manipulation. *Evolution* **64**, 2417-2430.
- Frank, S. N., Godehardt, S., Nachev, M., Trubiroha, A., Kloas, W. & Sures, B. 2013: Influence of the cestode *Ligula intestinalis* and the acanthocephalan *Polymorphus minutus* on levels of heat shock proteins (HSP70) and metallothioneins in their fish and crustacean intermediate hosts. *Environ. Pollut.* **180**, 173-179.
- Fuller, C. A., Rock, P. & Phillips, T. 2003: Behavior, color changes and predation risk induced by acanthocephalan parasitism in the Caribbean termite *Nasutitermes acajutlae*. *Caribb. J. Sci.* **39**, 128-135.
- Gaillard, M., Juillet, C., Cézilly, F. & Perrot-Minnot, M.-J. 2004: Carotenoids of two freshwater amphipod species (*Gammarus pulex* and *G. roeseli*) and their common acanthocephalan parasite *Polymorphus minutus*. *Comp. Biochem. Physiol. B* **139**, 129-136.
- Gismondi, E., Beisel, J.-N. & Cossu-Leguille, C. 2012c: *Polymorphus minutus* affects antioxidant responses of *Gammarus roeseli* exposed to cadmium. *PLoS ONE* **7**, e41475.
- Gismondi, E., Cossu-Leguille, C. & Beisel, J.-N. 2012a: Does the acanthocephalan parasite *Polymorphus minutus* modify the energy reserves and antioxidant defences of its intermediate host *Gammarus roeseli*? *Parasitology* **139**, 1054-1061.
- Gismondi, E., Cossu-Leguille, C. & Beisel, J.-N. 2012b: Acanthocephalan parasites: help or burden in gammarid amphipods exposed to cadmium? *Ecotoxicology* **21**, 1188-1193.
- Gotelli, N. J. & Moore, J. 1992: Altered host behaviour in a cockroach-acanthocephalan association. *Anim. Behav.* **43**, 949-959.
- Guinnee, M. A. & Moore, J. 2004: The effect of parasitism on host fecundity is dependent on temperature in a cockroach-acanthocephalan system. *J. Parasitol.* **90**, 673-677.
- Guler, Y. & Ford, A. T. 2010: Anti-depressants make amphipods see the light. *Aquat. Toxicol.* **99**, 397-404.
- Haine, E. R., Boucansaud, K. & Rigaud, T. 2005: Conflict between parasites with different transmission strategies infecting an amphipod host. *Proc. R. Soc. Lond. B* **272**, 2505-2510.
- Hasu, T., Benesh, D. P. & Valtonen, E. T. 2009: Differences in parasite susceptibility and costs of resistance between naturally exposed and unexposed host populations. *J. Evol. Biol.* **22**, 699-707.
- Hasu, T., Holmes, J. C. & Valtonen, E. T. 2007: Isopod (*Asellus aquaticus*) size and acanthocephalan (*Acanthocephalus lucii*) infections. *J. Parasitol.* **93**, 450-457.
- Hasu, T., Valtonen, E. T. & Jokela, J. 2006: Costs of parasite resistance for female survival and parental care in a freshwater isopod. *Oikos* **114**, 322-328.
- Haye, P. A. & Ojeda, F. P. 1998: Metabolic and behavioral alterations in the crab *Hemigrapsus crenulatus* (Milne-Edwards 1837) induced by its acanthocephalan parasite *Profilicollis antarcticus* (Zdzitowiecki 1985). *J. Exp. Mar. Biol. Ecol.* **228**, 73-82.
- Hechtel, L. J., Johnson, C. L. & Juliano, S. A. 1993: Modification of antipredator behavior of *Caecidotea intermedius* by its parasite *Acanthocephalus dirus*. *Ecology* **74**, 710-713.
- Helluy, S. & Holmes, J. C. 1990: Serotonin, octopamine, and the clinging behavior induced by the parasite *Polymorphus paradoxus* (Acanthocephala) in *Gammarus lacustris* (Crustacea). *Can. J. Zool.* **68**, 1214-1220.
- Hernandez, A. D. & Sukhdeo, M. V. K. 2008: Parasite effects on isopod feeding rates can alter the host's functional role in a natural stream ecosystem. *Int. J. Parasitol.* **38**, 683-690.
- Hindsbo, O. 1972: Effects of *Polymorphus* (Acanthocephala) on color and behavior of *Gammarus lacustris*. *Nature* **238**, 333.
- Hynes, H. B. N. 1955: The reproductive cycle of some British freshwater Gammaridae. *J. Anim. Ecol.* **24**, 352-387.
- Hynes, H. B. N. & Nicholas, W. L. 1963: The importance of the acanthocephalan *Polymorphus minutus* as a parasite of domestic ducks in the United Kingdom. *J. Helminthol.* **37**, 185-198.
- Jacquin, L., Mori, Q. & Médoc, V. 2013: Does the carotenoid-based colouration of *Polymorphus minutus* facilitate its trophic transmission to definitive hosts? *Parasitology* **140**, 1310-1315.
- Jacquin, L., Mori, Q., Pause, M., Steffen, M. & Médoc, V. 2014: Non-specific manipulation of gammarid behaviour by *P. minutus* parasite enhances their predation by definitive bird hosts. *PLoS ONE* **9**, 101684.

- Kakizaki, T., Saito, T., Ohtaka, A. & Nagasawa, K. 2003: Effects of *Acanthocephalus* sp. (Acanthocephala: Echinorhynchidae) on the body size and reproduction of isopods (*Asellus hilgendorfi*). *Limnology* **4**, 43–46.
- Kaldonski, N., Perrot-Minnot, M.-J. & Cézilly, F. 2007: Differential influence of two acanthocephalan parasites on the antipredator behaviour of their common intermediate host. *Anim. Behav.* **74**, 1311–1317.
- Kaldonski, N., Perrot-Minnot, M.-J., Dodet, R., Martinaud, G. & Cézilly, F. 2009: Carotenoid-based colour of acanthocephalan cystacanths plays no role in host manipulation. *Proc. R. Soc. Lond. B.* **276**: 169–176.
- Kaldonski, N., Perrot-Minnot, M.-J., Motreuil, S. & Cézilly, F. 2008: Infection with acanthocephalans increases the vulnerability of *Gammarus pulex* (Crustacea Amphipoda) to non-host invertebrate predators. *Parasitology* **135**, 627–632.
- Kennedy, C. R., Broughton, P. F. & Hine, P. M. 1978: The status of brown trout and rainbow trout *Salmo trutta* and *Salmo gairdneri* as hosts of the acanthocephalan *Pomphorhynchus laevis*. *J. Fish Biol.* **13**, 265–275.
- Kolluru, G. R., Green, T. S., Vredevoe, L. K., Kuzma, M. R., Ramadan, S. N. & Zosky, M. R. 2011: Parasite infection and sand coarseness increase sand crab (*Emerita analoga*) burrowing time. *Behav. Process.* **88**, 184–191.
- Korkofigas, E., Park, T. & Sparkes, T. C. 2016: Acanthocephalan-related variation in the pattern of energy storage of a behaviorally and physiologically modified host: field data. *Parasitol. Res.* **115**, 339–345.
- Labaude, S., Cézilly, F. & Rigaud, T. 2017b: Temperature-related Intraspecific variability in the behavioral manipulation of acanthocephalan parasites on their gammarid hosts. *Biol. Bull.* (published online, DOI: 10.1086/692684).
- Labaude, S., Cézilly, F., Tercier, X. & Rigaud, T. 2015: Influence of host nutritional condition on post-infection traits in the association between the manipulative acanthocephalan *Pomphorhynchus laevis* and the amphipod *Gammarus pulex*. *Parasit. Vectors* **8**, 403.
- Labaude, S., Rigaud, T. & Cézilly, F. 2017a: Additive effects of temperature and infection with an acanthocephalan parasite on the shredding activity of *Gammarus fossarum* (Crustacea: Amphipoda): the importance of aggregative behavior. *Glob. Change Biol.* **23**, 1415–1424.
- Lackie, A. M. & Holt, R. H. F. 1989: Immunosuppression by larvae of *Moniliformis moniliformis* (Acanthocephala) in their cockroach host (*Periplaneta americana*). *Parasitology* **98**: 307–314.
- Lagrué, C., Güvenatam, A. & Bollache, L. 2013: Manipulative parasites may not alter intermediate host distribution but still enhance their transmission: field evidence for increased vulnerability to definitive hosts and non-host predator avoidance. *Parasitology* **140**, 258–265.
- Lagrué, C., Kaldonski, N., Perrot-Minnot, M.-J., Motreuil, S. & Bollache, L. 2007: Modification of hosts' behavior by a parasite: field evidence for adaptive manipulation. *Ecology* **88**, 2839–2847.
- La Sala, L. F., Perez, A. M. & Martorelli, S. R. 2012: Epidemiology of acanthocephalan infections in crabs from the Bahía Blanca Estuary, Argentina. *J. Helminthol.* **86**, 446–452.
- Latham, A. D. M. & Poulin, R. 2001: Effect of acanthocephalan parasites on the behaviour and coloration of the mud crab *Macrophthalmus hirtipes* (Brachyura: Ocypodidae). *Mar. Biol.* **139**, 1147–1154.
- Latham, A. D. M. & Poulin, R. 2002a: Field evidence of the impact of two acanthocephalan parasites on the mortality of three species of New Zealand shore crabs (Brachyura). *Mar. Biol.* **141**, 1131–1139.
- Latham, A. D. M. & Poulin, R. 2002b: Effect of acanthocephalan parasites on hiding behaviour in two species of shore crabs. *J. Helminthol.* **76**, 323–326.
- Lavery, C., Brenner, D., McIlwaine, C., Lennon, J. J., Dick, J. T. A., Lucy, F. E. & Christian, K. A. 2017: Temperature rise and parasitic infection interact to increase the impact of an invasive species. *Int. J. Parasitol.* **47**, 291–296.
- Lewis, S. E., Freund, J. G., Wankowski, J. L. & Baldrige, M. G. 2016: Correlations between estrogen and testosterone concentrations, pairing status and acanthocephalan infection in an amphipod. *J. Zool.* **298**, 2241–248.
- Lewis, S. E., Hodel, A., Sturdy, T., Todd, R. & Weigl, C. 2012: Impact of acanthocephalan parasites on aggregation behavior of amphipods (*Gammarus pseudolimnaeus*). *Behav. Process.* **91**, 159–163.
- Libersat, F. & Moore, J. 2000: The parasite *Moniliformis moniliformis* alters the escape response of its cockroach host *Periplaneta americana*. *J. Insect Behav.* **13**, 103–110.
- MacNeil, C., Fielding, N. J., Hume, K. D., Dick, J. T. A., Elwood, R. W., Hatcher, M. J. & Dunn, A. M. 2003: Parasite altered micro-distribution of *Gammarus pulex* (Crustacea: Amphipoda). *Int. J. Parasitol.* **33**, 57–64.
- Marriott, D. R., Collins, M. L., Paris, R. M., Gudgin, D. R., Barnard, C. J., McGregor, P. K., Gilbert, F. S., Hartley, J. C. & Behnke, J. M. 1989: Behavioural modifications and increased predation risk of *Gammarus pulex* infected with *Polymorphus minutus*. *J. Biol. Educ.* **23**, 135–141.
- Maynard, B. J., DeMartini, L. & Wright, W. G. 1996: *Gammarus lacustris* harboring *Polymorphus paradoxus* show altered patterns of serotonin-like immunoreactivity. *J. Parasitol.* **82**, 663–666.
- Maynard, B. J., Wellnitz, T. A., Zanini, N., Wright, W. G. & Dezfuli, B. S. 1998: Parasite-altered behavior in a crustacean intermediate host: Field and laboratory studies. *J. Parasitol.* **84**, 1102–1106.
- Mazzi, D. & Bakker, T. C. M. 2003: A predator's dilemma: prey choice and parasite susceptibility in three-spined sticklebacks. *Parasitology* **126**, 339–347.
- McCahon, C. P., Brown, A. F. & Pascoe, D. 1988: The effect of the Acanthocephalan *Pomphorhynchus laevis* (Müller 1776) on the acute toxicity of cadmium to its intermediate host, the amphipod *Gammarus pulex* (L.). *Arch. Environ. Contam. Toxicol.* **17**, 239–243.
- McCahon, C. P., Brown, A. F., Poulton, M. J. & Pascoe, D. 1989: Effects of acid, aluminium and lime additions on fish and invertebrates in a chronically acidic Welsh stream. *Water Air Soil Pollut.* **45**, 345–359.
- McCahon, C. P., Maund, S. J. & Poulton, M. J. 1991: The effect of the acanthocephalan parasite (*Pomphorhynchus laevis*) on the drift of its intermediate host (*Gammarus pulex*). *Freshw. Biol.* **25**, 507–513.

- McCahon, C. P. & Poulton, M. J. 1991: Lethal and sub-lethal effects of acid, aluminium and lime on *Gammarus pulex* during repeated simulated episodes in a Welsh stream. *Freshw. Biol.* **25**, 169-178.
- Médoc, V. & Beisel, J.-N. 2008: An acanthocephalan parasite boosts the escape performance of its intermediate host facing non-host predators. *Parasitology* **135**, 977-984.
- Médoc, V. & Beisel, J.-N. 2009: Field evidence for non-host predator avoidance in a manipulated amphipod. *Naturwissenschaften* **96**, 513-523.
- Médoc, V., Bollache, L. & Beisel, J.-N. 2006: Host manipulation of a freshwater crustacean (*Gammarus roeselii*) by an acanthocephalan parasite (*Polymorphus minutus*) in a biological invasion context. *Int. J. Parasitol.* **36**, 1351-1358.
- Médoc, V., Rigaud, T., Bollache, L. & Beisel, J.-N. 2009: A manipulative parasite increasing an antipredator response decreases its vulnerability to a nonhost predator. *Anim. Behav.* **77**, 1235-1241.
- Moore, J. 1983a: Responses of an avian predator and its isopod prey to an acanthocephalan parasite. *Ecology* **64**, 1000-1015.
- Moore, J. 1983b: Altered behavior in cockroaches (*Periplaneta americana*) infected with an archiacanthocephalan, *Moniliformis moniliformis*. *J. Parasitol.* **69**, 1174-1176.
- Moore, J., Freehling, M. & Gotelli, N. J. 1994: Altered behavior in two species of blattid cockroaches infected with *Moniliformis moniliformis* (Acanthocephala). *J. Parasitol.* **80**, 220-223.
- Moore, J. & Gotelli, N. J. 1992: *Moniliformis moniliformis* increases cryptic behaviors in the cockroach *Supella longipalpa*. *J. Parasitol.* **78**, 49-53.
- Moret, Y., Bollache, L., Wattier, R. & Rigaud, T. 2007: Is the host or the parasite the most locally adapted in an amphipod-acanthocephalan relationship? A case study in a biological invasion context. *Int. J. Parasitol.* **37**, 637-644.
- Munro, W. R. 1953: Intersexuality in *Asellus aquaticus* L. parasitized by a larval acanthocephalan. *Nature* **172**, 313.
- Muzzall, P. M. & Rabalais, F. C. 1975a: Studies on *Acanthocephalus jacksoni* Bullock, 1962 (Acanthocephala: Echinorhynchidae). II. An analysis of the host-parasite relationship of larval *Acanthocephalus jacksoni* in *Lirceus lineatus* (Say). *P. Helm. Soc. Wash.* **42**, 35-38.
- Muzzall, P. M. & Rabalais, F. C. 1975b: Studies on *Acanthocephalus jacksoni* Bullock, 1962 (Acanthocephala: Echinorhynchidae). III. The altered behavior of *Lirceus lineatus* (Say) infected with cystacanths of *Acanthocephalus jacksoni*. *P. Helm. Soc. Wash.* **42**, 116-118.
- Oetinger, D. F. 1987: Effects of *Acanthocephalus dirus* (Acanthocephala) on morphometrics and reproduction of *Caecidotea intermedius* (Crustacea: Isopoda). *T. Am. Microsc. Soc.* **106**, 240-248.
- Oetinger, D. F. & Nickol, B. B. 1981: Effects of acanthocephalans on pigmentation of freshwater isopods. *J. Parasitol.* **67**, 672-684.
- Oetinger, D. F. & Nickol, B. B. 1982a: Developmental relationships between acanthocephalans and altered pigmentation in freshwater isopods. *J. Parasitol.* **68**, 463-469.
- Oetinger, D. F. & Nickol, B. B. 1982b: Spectrophotometric characterization of integumental pigments from uninfected and *Acanthocephalus dirus*-infected *Asellus intermedius*. *J. Parasitol.* **68**, 270-275.
- Outreman, Y., Cézilly, F. & Bollache, L. 2007: Field evidence of host size-dependent parasitism in two manipulative parasites. *J. Parasitol.* **93**, 750-754.
- Pascoe, D., Kedwards, T. J., Blockwell, S. J. & Taylor, E. J. 1995: *Gammarus pulex* (L.) feeding bioassay—effects of parasitism. *Bull. Environ. Contam. Toxicol.* **55**, 629-632.
- Perrot-Minnot, M.-J. 2004: Larval morphology, genetic divergence, and contrasting levels of host manipulation between forms of *Pomphorhynchus laevis* (Acanthocephala). *Int. J. Parasitol.* **34**, 45-54.
- Perrot-Minnot, M.-J., Dion, E. & Cézilly, F. 2013: Modulatory effects of the serotonergic and histaminergic systems on reaction to light in the crustacean *Gammarus pulex*. *Neuropharmacology* **75**, 31–37.
- Perrot-Minnot, M.-J., Gaillard, M., Dodet, R. & Cézilly, F. 2011: Interspecific differences in carotenoid content and sensitivity to UVB radiation in three acanthocephalan parasites exploiting a common intermediate host. *Int. J. Parasitol.* **41**, 173-181.
- Perrot-Minnot, M.-J., Kaldonski, N. & Cézilly, F. 2007: Increased susceptibility to predation and altered anti-predator behaviour in an acanthocephalan-infected amphipod. *Int. J. Parasitol.* **37**, 645-651.
- Perrot-Minnot, M.-J., Maddaleno, M., Balourdet, A. & Cézilly, F. 2012: Host manipulation revisited: no evidence for a causal link between altered photophobia and increased trophic transmission of amphipods infected with acanthocephalans. *Funct. Ecol.* **26**, 1007-1014.
- Perrot-Minnot, M.-J., Sanchez-Thirion, K. & Cézilly, F. 2014: Multidimensionality in host manipulation mimicked by serotonin injection. *Proc. R. Soc. B* **281**, 20141915.
- Pilecka-Rapacz, M. 1984: Cystacanths of *Polymorphus contortus* (Bremser, 1821) (Acanthocephala, Polymorphidae) in *Asellus aquaticus* L. *Acta Parasitol. Pol.* **29**, 107-110.
- Pilecka-Rapacz, M. 1986: On the development of acanthocephalans of the genus *Acanthocephalus* Koelreuther, 1771, with special attention to their intermediate host, *Asellus aquaticus* L. *Acta Parasitol. Pol.* **30**, 233–250.
- Piscart, C., Webb, D. & Beisel, J. N. 2007: An acanthocephalan parasite increases the salinity tolerance of the freshwater amphipod *Gammarus roeselii* (Crustacea: Gammaridae). *Naturwissenschaften* **94**, 741-747.
- Plaistow, S. J., Troussard, J. P. & Cézilly, F. 2001: The effect of the acanthocephalan parasite *Pomphorhynchus laevis* on the lipid and glycogen content of its intermediate host *Gammarus pulex*. *Int. J. Parasitol.* **31**, 346-351.
- Poulton, M. & Pascoe, D. 1990: Disruption of precopula in *Gammarus pulex* (L.) – development of a behavioural bioassay for evaluating pollutant and parasite induced stress. *Chemosphere* **20**, 403-415.
- Poulton, M. J. & Thompson, D. J. 1987: The effects of the acanthocephalan parasite *Pomphorhynchus laevis* on mate choice in *Gammarus pulex*. *Anim. Behav.* **35**, 1577–1579.
- Prenter, J., MacNeil, C., Dick, J. T. A., Riddell, G. E. & Dunn, A. M. 2004: Lethal and sublethal toxicity of ammonia to native, invasive, and parasitised freshwater amphipods. *Water Res.* **38**, 2847-2850.
- Pulgar, J., Aldana, M., Vergara, E. & George-Nascimento, M. 1995: Behavior of the estuarine crab *Hemigrapsus crenulatus* (Milne-Edwards 1837) in relation to the parasitism by the acanthocephalan *Proflicollis antarcticus* (Zdzitowiecki 1985) in southern Chile. *Rev. Chil. Hist. Nat.* **68**, 439-450.
- Rauque, C. A., Patterson, R. A., Poulin, R. & Tompkins, D. M. 2011: Do different parasite species interact in their effects on host fitness? A case study on parasites of the amphipod *Paracalliope fluviatilis*. *Parasitology* **138**, 1176-1182.
- Rauque, C. A. & Semenas, L. 2009: Effects of two acanthocephalan species on the reproduction of *Hyalella patagonica* (Amphipoda, Hyalellidae) in an Andean Patagonian Lake (Argentina). *J. Invertebr. Pathol.* **100**, 35–39.
- Rigaud, T. & Moret, Y. 2003: Differential phenoloxidase activity between native and invasive gammarids infected by local acanthocephalans: differential immunosuppression? *Parasitology* **127**, 571–577.

- Rojas, J. M. & Ojeda, F. P. 2005: Altered dopamine levels induced by the parasite *Proflicollis anartcticus* on its intermediate host, the crab *Hemigrapsus crenulatus*. *Biol. Res.* **38**, 259-266.
- Rumpus, A. E. & Kennedy, C. R. 1974: The effect of the acanthocephalan *Pomphorhynchus laevis* upon the respiration of its intermediate host, *Gammarus pulex*. *Parasitology* **68**, 271-284.
- Seidenberg, A. J. 1973: Ecology of the acanthocephalan, *Acanthocephalus dirus* (Van Cleave, 1931), in its intermediate host, *Asellus intermedius* Forbes (Crustacea: Isopoda). *J. Parasitol.* **59**, 957-962.
- Seppälä, O., Valtonen, E. T. & Benesh, D. P. 2008: Host manipulation by parasites in the world of dead-end predators: adaptation to enhance transmission? *Proc. R. Soc. Lond. B* **275**, 1611-1615.
- Sparkes, T. C., Weil, K. A., Renwick, D. T. & Talkington, J. A. 2006: Development-related effects of an acanthocephalan parasite on pairing success of its intermediate host. *Anim. Behav.* **71**, 439-448.
- Sparkes, T. C., Wright, V. M., Renwick, D. T., Weil, K. A., Talkington, J. A. & Milhalyov, M. 2004: Intra-specific host sharing in the manipulative parasite *Acanthocephalus dirus*: does conflict occur over host modification? *Parasitology* **129**, 335-340.
- Stone, C. F. & Moore, J. 2014: Parasite-induced alteration of odour responses in an amphipod-acanthocephalan system. *Int. J. Parasitol.* **44**, 969-975.
- Sures, B. & Radszwejt, H. 2007: Pollution-induced heat shock protein expression in the amphipod *Gammarus roeseli* is affected by larvae of *Polymorphus minutus* (Acanthocephala). *J. Helminthol.* **81**, 191-197.
- Tain, L., Perrot-Minnot, M.-J. & Cézilly, F. 2006: Altered host behaviour and brain serotonergic activity caused by acanthocephalans: evidence for specificity. *Proc. R. Soc. Lond. B* **273**, 3039-3045.
- Tain, L., Perrot-Minnot, M.-J. & Cézilly, F. 2007: Differential influence of *Pomphorhynchus laevis* (Acanthocephala) on brain serotonergic activity in two congeneric host species. *Biol. Lett.* **3**, 68-71.
- Thünken, T., Baldauf, S. A., Bersau, N., Bakker, T. C. M., Kullmann, H. & Frommen, J. G. 2010: Impact of olfactory non-host predator cues on aggregation behaviour and activity in *Polymorphus minutus* infected *Gammarus pulex*. *Hydrobiologia* **654**, 137-145.
- Thünken, T., Baldauf, S. A., Bersau, N., Frommen, J. G. & Bakker, T. C. M. 2017: Parasite-induced colour alteration of intermediate hosts increases ingestion by suitable final host species. (unpublished data).
- Uznanski, R. L. & Nickol, B. B. 1980: Parasite population regulation – lethal and sublethal effects of *Leptorhynchoides thecatus* (Acanthocephala, Rhadinorhynchidae) on *Hyalella azteca* (Amphipoda). *J. Parasitol.* **66**, 122-126.
- van Maren, M. J. 1979: The amphipod *Gammarus fossarum* Koch (Crustacea) as intermediate host for some helminth parasites, with some notes on their occurrence in the final host. *Bijdr. Dierk.* **48**, 97-110.
- Ward, P. I. 1986: A comparative field study of the breeding behaviour of a stream and pond population of *Gammarus pulex* (Amphipoda). *Oikos* **46**, 29-36.
- Wellnitz, T. A., Giari, L., Maynard, B. J. & Dezfali, B. S. 2003: A parasite spatially structures its host population. *Oikos* **100**, 263-268.
- Wilson, K. & Edwards, J. 1986: The effects of parasitic infection on the behaviour of an intermediate host, the American cockroach, *Periplaneta americana*, infected with the acanthocephalan, *Moniliformis moniliformis*. *Anim. Behav.* **34**, 942-944.
- Zohar, S. & Holmes, J. C. 1998: Pairing success of male *Gammarus lacustris* infected by two acanthocephalan: a comparative study. *Behav. Ecol.* **9**, 206-211.