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Review

The Ecological Importance of Amphipod–Parasite Associations for Aquatic Ecosystems

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Abstract: Amphipods are a key component of aquatic ecosystems due to their distribution, abundance and ecological role. They also serve as hosts for many micro- and macro-parasites. The importance of parasites and the necessity to include them in ecological studies has been increasingly recognized in the last two decades by ecologists and conservation biologists. Parasites are able to alter survival, growth, feeding, mobility, mating, fecundity and stressors' response of their amphipod hosts. In addition to their modulating effects on host population size and dynamics, parasites affect community structure and food webs in different ways: by increasing the susceptibility of amphipods to predation, by quantitatively and qualitatively changing the host diet, and by modifying competitive interactions. Human-induced stressors such as climate change, pollution and species introduction that affect host–parasite equilibrium, may enhance or reduce the infection effects on hosts and ecosystems. The present review illustrates the importance of parasites for ecosystem processes using examples from aquatic environments and amphipods as a host group. As seen from the literature, amphipod–parasite systems are likely a key component of ecological processes, but more quantitative data from natural populations and field evidence are necessary to support the results obtained by experimental research.

Keywords: parasitism; aquatic ecosystems; host manipulation; food webs; feeding ecology; competitive and predatory interactions; intraguild predation; climate change; biological invasions

1. Introduction

Understanding how parasites can affect biodiversity and ecosystem functionality is of increasing interest for both conservation biology and ecology [1–3]. Although in the last two decades the number of articles and reviews about the ecological implications of parasitism has increased, the knowledge on this topic remains in its infancy, waiting for an effective integration of expertise between parasitologists and ecologists.

The present review focuses on the aquatic environment for which many important host–parasite associations are known. Moreover, especially for parasites, aquatic habitats appear to provide ideal living conditions, as shown by Behringer et al. [4]. Water is a medium that ensures a good thermal stability and prevents desiccation, allowing parasite longevity outside their host, and represents an excellent vehicle of transport and spread largely exploited by parasites [4,5]. It is therefore not surprising that some parasite groups such as monogeneans, trematodes and acanthocephalans, as well as crustacean parasites, are much more common in aquatic habitats [6–8]. We used amphipods and their parasites as an example for the following reasons: firstly, this group of hosts is ecologically important in aquatic systems and secondly, they can be infected by a variety of parasites. Furthermore, some of these parasites can have substantial effects on their host that have been studied in detail [9].

The aim of this review was to use amphipod–parasite systems to shed light on how host–parasite interactions contribute to community structure and ecosystem regulation in aquatic environments. Particular attention was paid to the roles of amphipod infections during biological invasions. The following subsection of the introduction gives a short overview of the importance of parasitism, especially from an ecological perspective. Furthermore, Section 1.2 illustrates the role of amphipods as an important host group.

1.1. Ecological Importance of Parasites

The parasitic lifestyle is one of the most successful and widespread in nature [10,11]. Every ecosystem contains parasites and all organisms experience infection during their lifetime [11,12]. It is estimated that the proportion of parasite species ranges from 30% to over 50% of the species on our planet [7,12,13]. In addition, with regard to biomass, parasites can be relevant [14], reaching a comparable or higher biomass than certain groups of free-living species (e.g., top predators) in some ecosystems [15–17].

Some parasites have detrimental effects on the host (animal or human) health, and on economics. These negative effects are often the main aspect of why parasites become a focus of researchers and of public awareness [2,18–23]. However, when departing away from this medical or veterinarian perspective, parasites are involved in different ecological processes, drive ecosystem services, and may act as ecosystem engineers [24–26]. They regulate host population demographics, shape community structure affecting predation or the competitive interactions of their host populations, influence food web networks and consequently contribute to ecosystem stability and energy flow [25,27,28]. Within the food web, parasites can co-occur at different levels, depending on the trophic level of their host and their developmental stage, and play different roles: parasites can function as consumers [29,30], feeding on and acquiring energy from their hosts. Additionally, free living-stages or ectoparasites can be consumed by predators [31] and the infected prey can be consumed along with their parasites with two possible cases: the "concomitant predation" when the parasites die with the prey/host and the "trophic transmission" in which the parasites of prey infect the predator [32].

Many parasites are known to manipulate host behavior to increase the predation of infected prey hosts [33,34]. This shows that parasites are able to enhance existing trophic interactions and facilitate new ones [35–38]. The ecological consequences of parasitism are more evident and documented for the so called "manipulative parasites" and "keystone parasites" [26,39]. Manipulative parasites induce phenotypic or behavioral changes that can render their hosts easy prey for the next host [33,40,41]. As a result, parasites with complex life cycles using trophic transmission can increase their chances to complete the life cycle, with positive implications for their fitness, but can also alter host population structure, the outcome of competition between hosts, and predator–prey dynamics with considerable consequences for the ecosystem [39,42,43]. The wide ranges of manipulative parasites (from viruses to higher orders of metazoans) and of hosts susceptible to manipulation (plants, invertebrate and vertebrate species including humans) further emphasizes the ecological significance of this phenomenon [44–46]. Keystone parasites infect hosts that have essential roles in an ecosystem [27,47]. These parasites can act directly in regulating the host population density or indirectly through trait-mediated effects such as the reduction of feeding activity [43,48,49].

Parasites interact in complex ways with environmental stressors leading to different possible outcomes for hosts and ecosystems. Due to the variety of both parasites and stressors and the fact that each parasite can interact differently with each stressor, it is not possible to predict or generalize the effects of these interactions: some parasites may benefit from the concomitant action of stressors however, more often and especially when their life cycles are indirect and complex, they may decrease in abundance or diversity [50].

The recently established research direction known as “Environmental Parasitology” investigates the different aspects of the interaction of parasitism and environmental stressors, including pollution, providing many studies from the aquatic environment [26,51–57]. Frequently, the combined effects of parasites and pollutants on host health are negative and could be additive or synergistic, increasing parasite occurrence and adverse effects [52,55,58,59]. However, effects are sometimes antagonistic, leading to an advantage for infected organisms in which parasites accumulate pollutants and thereby reduce the exposure concentration of the hosts [56,60,61].

In the Anthropocene Epoch, climate change emerges as one of the most important factors affecting the host–parasite equilibrium [62], but the knowledge of the joint effects of parasitism and climate change is limited [63,64]. Communities and ecosystems could be directly and indirectly affected by climatic conditions due to the influence that thermic variations exert on parasitism [65,66]. Climate change may modify the growth, development, metabolism and transmission rates of parasites and also the physiology, abundance and distribution of their hosts [66–68]. In aquatic environments, global warming is expected to enhance both disease transmission and virulence, to reduce the fitness and immune response of hosts, and to extend the geographical range of parasites [65,69,70]. However, Cizauskas et al. [71] underline that many parasites could be negatively impacted by climate change with a risk of decline and even extinction. Overall, it is expected that the effects of climate change on parasites can lead to cascading effects on food webs and ecosystem stability [71].

Invasion by exotic species is another phenomenon capable of profoundly altering both host–parasite interactions and ecosystems. Introduced animals may (i) bring their parasites and transfer them to native hosts (spill-over), intensifying the negative impact on native host populations and changing their parasite communities; (ii) lose all or most of their parasites (enemy release) and obtain an advantage over native species; and (iii) acquire local native parasites and induce a spillback or a dilution effect on native hosts [50,72–76]. In all the aforementioned scenarios, parasites may affect or even drive the invasion dynamics with repercussions on host and non-host species, and biodiversity in general [77–79].

1.2. *Ecological Role of Amphipods*

Amphipods are a major order of crustaceans that stands out for their local abundance (both in terms of density and biomass), diversity, ecological importance and role as hosts for parasites. More than 10,000 species are currently described [80] and colonize all aquatic ecosystems (freshwater, brackish and marine), including extreme habitats like groundwater, polar and hydrothermal sites [81,82], and to a lesser degree, some terrestrial ones [83]. Amphipods not only inhabit multiple habitats, but also fill different ecological niches and support several ecosystem services [9,84]. They are omnivorous, trophically versatile and opportunistic, having a great diet adaptability [85,86]. Many species are assigned to the functional feeding group of shredders, feeding mainly on leaf material, but some species are also predators of a wide range of invertebrates including conspecifics and congenerics (cannibalism) [87–89].

The success and global occurrence of amphipods are linked to their adaptability, resilience to changes of abiotic conditions and a wide range of feeding strategies [90]. Even species of the same genus can show different behavior patterns, physicochemical tolerances, invasive potentials, resistance to invasion and predatory tendencies [86].

Amphipods are keystone organisms, often representing the dominant component among benthic macroinvertebrates and they play crucial roles in aquatic food webs in which they act as secondary producers, consumers and a food source for various predators [84–86,91]. Through their shredding activity, amphipods recycle nutrients and provide processed material for microorganisms and other invertebrates; a function that is essential and accounts for 75% of the overall leaf-litter breakdown in some ecosystems. Additionally, their predatory activity influences the size, location, growth and reproduction of prey populations [88,89,92]. In many aquatic ecosystems, the diet of both macroinvertebrates (from flatworms to crabs) and vertebrates (especially fish and birds but also mammals) is composed of amphipods to a large extent [93–95]. In particular *Gammarus* spp., one of the most common and important genera within the Amphipoda, represent an essential food source for predators such as fish [86], and is available during the whole year, unlike many insect species [90,96]. In lakes and rivers, *Gammarus* spp. are important prey items for numerous fish species, some of which are of economic importance such as salmonids [86,97,98]. In lotic systems, amphipods can leave the benthos, enter the current, and drift downstream. This drift activity offers several advantages (e.g., the search of food resources, better abiotic conditions, mate encounter), but also increases the risk to be captured by predators [99]. Both selective predation on amphipods and their drift behavior are often linked to parasitism among other influencing factors [90].

Many aquatic ecosystems are inhabited by native and non-native amphipods and the former suffer the threat of replacement/displacement by non-native ones [100–103]. Due to their function as a food resource, many *Gammarus* spp. have been intentionally introduced to improve fish stocks since the 1950s: several cases of these deliberate introductions into freshwaters ecosystems are reported by MacNeil and collaborators [90]. Moreover, exotic amphipods have spread accidentally thanks to passages and distribution pathways (e.g., water ballast, cargo shipping, ship lifts, and canals) provided by anthropogenic actions [79,104]. A famous invader, the killer shrimp, *Dikerogammarus villosus*, moved from the Ponto–Caspian region, colonizing the main water systems of Western and Central Europe after the inauguration of the Rhine–Main–Danube canal in 1992 [105–107].

2. Parasites of Amphipods

Amphipods are involved in the life cycles of an incredible variety of other organisms (mutualists, commensals, parasites), from viruses to metazoans, some of which have been found exclusively in amphipods [108–111]. A recent review by Bojko and Ovcharenko [112] describes all the micro- and macro-parasites recorded in amphipods and provides details of their systematics, pathology and effects on their host population. Nevertheless, only a few of these parasites have been studied in more detail [112]. Among the best studied parasite groups of amphipods are acanthocephalans and microsporidians [57,113]. Their known effects on the amphipod host include increased mortality, impaired reproduction, changed behavior (including parasitic host manipulation) and changed sex ratio [113–118].

Microsporidia are unicellular parasites that develop in various tissues inside the host cells. They are related to fungi [119] and are frequently detected in amphipods [120–125]. Their transmission can be directly from one host to the next via spores that are released into the environment upon host death or via cannibalism (horizontal transmission) or from infected mothers to offspring via developmental stages in cells of ovary and eggs (vertical transmission) [122,125]. Particularly, transovarially transmitted microsporidians can shift the sex ratio towards female-biased populations either by male-killing or the feminization of male individuals [126]. Furthermore, in some cases, infected females reproduce earlier and show a higher fecundity [127,128]. An effect on the sex ratio has also been found for another vertically transmitted and intracellular parasite group, the Paramyxea, which also occur in amphipods and sometimes as co-infections with microsporidians [129].

Acanthocephalans, or thorny-headed worms, are a phylum of metazoan endoparasites that need at least two hosts to complete their life cycle. Species with aquatic life cycles often use amphipods as intermediate hosts and fish or aquatic birds as definitive/final hosts [130]. Adult acanthocephalans, inhabiting the intestine of vertebrate hosts, release eggs in the water and the amphipod becomes infected by eating them. Inside the amphipod, the parasite completes its larval development from acanthor to acanthella and finally to the infective cystacanth stage. Infection of the definitive host occurs when the infected amphipod is consumed by the definitive host [130]. Often, the behavior of the intermediate host is manipulated by the parasite to increase the chance of trophic transmission as soon as the mature cystacanth stage is reached [41,131].

Amphipods are also hosts for several tapeworms [112]. Particularly well studied is the species *Cyathocephalus truncatus* that uses gammarids as an intermediate host. Fish are final hosts and become infected when feeding on infected gammarids. Several effects of *C. truncatus* on its intermediate host were reported, including parasitic manipulation [132] or the impairment of reproductive biology [133,134].

Additionally, infections with the metacercariae of trematodes (particularly *Maritrema* and *Microphallus* spp.) are frequently reported from amphipods. The amphipods serve as a second intermediate host and become infected by the cercariae that are released from infected snails. Birds that prey on infected amphipods are the final hosts. Several studies on the trematodes of amphipods include results on the ecological effects of the host–parasite relationship (e.g., [63,135–137]).

3. Ecosystem Effects of Amphipod Parasites

Parasites of amphipods often regulate host populations, but effects at higher levels (community, ecosystem) were reported only for a few examples. Table 1 provides a schematic overview of the amphipod–parasite systems for which a possible influence on ecosystems has been reported in the literature. Mostly, these effects become obvious, when ecosystems and host–parasite associations are impacted by (often anthropogenic) changes like biological invasions, climate change, or pollution that interrupt or enhance parasite life cycles and reveal the regulatory role of the parasite for the host population, for communities and sometimes the whole ecosystem.

Table 1. Effects and impacts of amphipod–parasite associations in aquatic ecosystems (the study cases are listed alphabetically for parasite group and then genus).

Amphipod Species (Host) (From L = Lake, R = River, S = Sea)	**Parasite Species (Group)**	**Effects on Host**	**Impact at Community and Ecosystem Levels (O = Observed, E = Expected/Predicted)**	**Reference (Type of Study: F = Field, L = Laboratory, M = Model)**
Gammarus pulex (R)	*Echinorhynchus truttae* (Acanthocephala)	No change in feeding rate on leaf and dead animals but decreased predation on *Asellus aquaticus*	Reduction of predation activity with possible community consequences (E)	[138] (L)
Gammarus pulex (R)	*Echinorhynchus truttae* (Acanthocephala)	Change in habitat usage; increased activity; preference for illumination	Modification of host communities structure through altered micro-distribution and increased vulnerability to predation (E)	[139] (F, L)
Gammarus pulex (R)	*Echinorhynchus truttae* (Acanthocephala)	Reduction of predatory behavior and predation ability on *G. d. celticus*	Alteration of intraguild predation (O): promotion of co-existence of the invading *G. pulex* and the native *G. d. celticus* with a slowing effect on invasion process (E)	[140] (F, L)
Gammarus pulex (R)	*Echinorhynchus truttae* (Acanthocephala)	Reduction of female fitness and higher consumption of the prey *Asellus aquaticus*	Increased feeding (predation) rates (O) and enhanced impact of the invader *G. pulex* in the community (E)	[141] (F, L)
Gammarus pulex (R)	*Echinorhynchus truttae* (Acanthocephala)	Increased predation rates on chironomid larvae, with further increase due to raising temperatures	Enhanced impact of the invader *G. pulex* thanks to the synergy between infection and temperature (E)	[142] (L)
Gammarus duebeni celticus (R)	*Polymorphus minutus* (Acanthocephala)	Altered micro-distribution, increased phototropism and drifting activity	Greater predation on *G. d. celticus* than on the invasive *G. tigrinus* by shared fish predators (E)	[143] (F, L)
Gammarus roeseli (R)	*Polymorphus minutus* (Acanthocephala)	Preference for floating materials rather than benthic substrates	Habitat shift (O) with probable effects both at lower and upper trophic levels (E)	[144] (F)
Gammarus roeseli (R)	*Polymorphus minutus* (Acanthocephala)	Changes in diet composition; in laboratory: less live isopods and less leaf material In the field: less perilithon and more leaf material	Modified trophic ecology (O) with possible top-down effects (E)	[145] (L, F)
Gammarus pulex (R)	*Pomphorhynchus laevis* (Acanthocephala)	Depressed feeding rate and increased mortality when exposed to Cd	Enhanced vulnerability of *G. pulex* populations to Cd pollution (E)	[146] (L)
Gammarus pulex (R)	*Pomphorhynchus laevis* (Acanthocephala)	Reduced feeding rate on eggs of *Artemia salina*	Modified trophic ecology: decreased predatory impact (E)	[147] (L)
Gammarus pulex and *G. roeseli* (R)	*Pomphorhynchus laevis* (Acanthocephala)	Induced photophilia with increased vulnerability to predators only in *G. pulex*	Possible shaping action on amphipod communities: more predation on *G. pulex* than on the non-manipulated invasive *G. roeseli* (E)	[148] (F, L)
Gammarus pulex and *G. roeseli* (R)	*Pomphorhynchus laevis* (Acanthocephala)	Manipulation of drifting behavior and consequent parasite-induced mortality only in *G. pulex*	Higher predation rates on the native *G. pulex* than on the non-manipulated invasive *G. roeseli* (O)	[116] (F)
Gammarus pulex and *Gammarus roeseli* (R)	*Pomphorhynchus laevis* (Acanthocephala)	Immune depression, lower bacterial resistance, energetic budget modification in the native *G. pulex* but not in the invader *G. roeseli*	Potential advantage for the invader *G. roeseli* due to the differential alterations (E)	[149] (F)

Table 1. *Cont.*

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G. fossarum/G. pulex cryptic lineages and *G. roeseli* (R)	*Pomphorhynchus laevis, Pomphorhynchus tereticollis and Polymorphus minutus* (Acanthocephala)	Differences in infection levels and parasite-induced mortality among cryptic lineages of the native *G. fossarum/G. pulex* and compared to the invasive *G. roeseli*	Potential strong influence on inter-lineages interactions of native amphipods and on invasion success of *G. roeseli* that does not suffer acanthocephalan-induced mortality (E)	[150] (F)
Gammarus fossarum (R)	*Pomphorhynchus tereticollis* (Acanthocephala)	Reduction of leaf consumption in infected amphipods; increase in leaf consumption at low and medium temperatures and decrease at high temperature	Negative impact on shredding activity due to additive effects of parasitism and raising temperature (E)	[151] (L)
Dikerogammarus villosus (R)	*Cucumispora dikerogammari* (Microsporidia)	Reduced predatory behavior on Chironomids	Diminished predation pressure of this invader amphipod within colonized ecosystems (E)	[152] (L)
Crangonyx pseudogracilis (R and L)	*Fibrillanosema crangonycis* (Microsporidia)	Sex ratio distortion with overproduction of female offspring	Invasion success facilitated by the parasite-induced feminization and consequent increased population growth rate (E)	[153] (F)
Gammarus duebeni celticus (R)	*Pleistophora* sp. (Microsporidia)	No direct effect on survival, size or fecundity, but reduction of host fitness in presence of other species populations	Alteration of intraguild predation between the native *G. d. celticus* and invading amphipods (*G. pulex, G. tigrinus, Crangonyx pseudogracilis*) (O) with a favoring action on biological invasions (E)	[154] (F, L)
Gammarus duebeni celticus (R)	*Pleistophora mulleri* (Microsporidia)	Influence on spatial distribution (infected in slower-flowing pool patches and uninfected in fast-flowing riffle patches) and on intraguild predation; reduction of survivor in presence of the invader *G. pulex* (not subject to the parasite)	Increased chances of invasion for *G. pulex* and of replacement of *G. d. celticus* (E)	[155] (F, L, M)
Gammarus duebeni celticus (R)	*Pleistophora mulleri* (Microsporidia)	Reduction of host motility, activity level, reproduction fitness, predation on the isopod *Asellus aquaticus* and aggression towards precopula pairs *G. pulex*	Reduced predatory pressure on the invader *G. pulex* with disadvantage for the native *G. d. celticus* (O)	[156] (F, L)
Gammarus duebeni celticus and *Gammarus pulex* (R)	*Pleistophora mulleri* (Trematoda) and *Polymorphus minutus* (Acanthocephala)	Decreased predation of infected *G. d. celticus* and *G. pulex* on *C. pseudogracilis*	Parasite-mediated interspecific interaction contributing to the co-existence of *Gammarus* sp. and the invader *C. pseudogracilis* (O)	[157] (F, L)
Gammarus duebeni, G. pulex, G. tigrinus (R)	*Embata parasitica* (Rotifera) and *Epistylis* (Protozoa)	Higher parasite burden in the native *G. duebeni* than in the invading *G. pulex* and *G. tigrinus*	Influence on host invasion and species distribution (E)	[158] (F)
Gammarus fasciatus and *Echinogammarus ischnus* (R)	Oomycete belonging to Saprolegnacee	Higher prevalence and intensity of infection in the exotic *E. ischnus* than in the native *G. fasciatus*	Possible co-existence of the two amphipod species thanks to the reduced abundance of *E. ischnus* otherwise dominant (E)	[159] (F, L)

Table 1. *Cont.*

Amphipod Species (Host) (From L = Lake, R = River, S = Sea)	**Parasite Species (Group)**	**Effects on Host**	**Impact at Community and Ecosystem Levels (O = Observed, E = Expected/Predicted)**	**Reference (Type of Study: F = Field, L = Laboratory, M = Model)**
Paracalliope fluviatilis and *Paracorophium excavatum* (L)	*Coitocaecum parvum* and *Maritrema poulini* (Trematoda)	Differential effects of the same parasites on the two amphipod species: reduced survival only in *P. fluviatilis*	Possible community effects due to the strong impact on *P. fluviatilis* population and the absence of impact on *P. excavatum* population (E)	[160] (L)
Paracalliope novizealandiae (S)	*Maritrema novaezealandensis* (Trematoda)	Increased parasite-induced mortality with increasing temperature (transmission and development of the parasite positively affected between 20 and 25 °C)	Predicted massive infection events and parasite-induced mortality leading to a reduction in intertidal amphipod populations under global warming (E)	[161] (L)
Paracalliope novizealandiae (S)	*Maritrema novaezealandensis* (Trematoda)		High vulnerability and collapse of the amphipod host population with temperature increases (E)	[162] (M)
Paracalliope novizealandiae, Paramoera chevreuxi, Heterophoxus stephenseni, Paracorophium lucasi, Aora sp., *Lembos* sp. (S)	*Maritrema novaezealandensis* (Trematoda)	Elevation of mortality with raising temperature in a species-specific manner; low impact of parasite at 17 °C and strong at 21 °C	Drastic reduction of amphipod species richness (especially of the epibenthic ones) triggered by the synergism of temperature and parasitism (E)	[136] (L, F)
Paracalliope fluviatilis (L)	*Maritrema poulini* (Trematoda)	Reduced survival and recruitment of *P. fluviatilis* compared to other four crustacean host species included in the study	Influence on relative abundances of the four crustaceans studied and shaping the effect on community structure (O) with a risk for the long-term persistence of *P. fluviatilis* (E)	[137] (L)
Corophium volutator (S)	*Maritrema subdolum* (Trematoda)	Anemia; reduction of survival at increasing temperatures	Temperature-mediated additive mortality in host populations (O)	[163] (L)
Corophium volutator (S)	*Maritrema subdolum* (Trematoda)	Increase in parasite-induced mortality under increased temperature	Parasite-induced collapse of the amphipod population with impact on the coastal ecosystem (E)	[63] (M)
Gammarus insensibilis and *Gammarus aequicauda* (S)	*Microphallus papillorobustus.* (Trematoda)	Differential tolerance (lower for *G. insensibilis*) to the parasite	Parasite regulation of *G. insensibilis* density versus *G. aequicauda* leading to a parasite-mediated coexistence of the two amphipod species (O)	[135] (F)
Corophium volutator and *C. arenarium* (S)	Microphallid species (Trematoda)	Higher sensitivity and mortality in *C. volutator* (superior competitor) than in *C. arenarium*	Collapse of *C. volutator* (triggered by increased temperature) and parasite-mediated competitive release of *C. arenarium* (O)	[164] (F)
Corophium volutator (S)	Species not reported (Trematoda)	Mass mortality event	Host population decline (O) with consequences on sediment stability (increased sediment size) and primary production (E)	[165] (F)

Here, we aim to show examples that illustrate the potential effects of amphipod parasites on ecological communities and beyond. Parasites can influence interspecific interactions and consequently shape the communities in complex ways, both directly by affecting the host population size (see Section 3.1) and indirectly through induced trait-mediated effects (see Sections 3.2 and 3.3). As described by Hatcher et al. [166], there are different possible scenarios depending on the position and the role of the hosts in the community. A parasite can infect two host species that are true competitors, apparent competitors (i.e., interacting only via the effects of the parasite), intraguild predators, prey and predator, or a parasite can infect only a specific host species limiting its competitive or predator capacity against a non-host species.

The differential occurrence and/or effects of parasites in host species with different susceptibility is a crucial factor determining the ecosystem impact of parasitism [167]. Different prevalence levels (or absence) and the more or less severe virulence of parasites in different amphipod species may mediate interspecific interactions, allowing the coexistence of species or favoring the success of some species at the expense of others [158,168]. Native and non-native hosts, even if they are congeneric, can vary greatly in their vulnerability to infection and in the pathogenic effects imposed by parasites [149]. This phenomenon has been shown to influence the biological invasions of exotic amphipods (generally suffering less from parasitism than native ones) with significant consequences for biodiversity and community structure.

3.1. Direct Regulation of Host Population Size

Debilitation and the induced death of a host is the most apparent structuring force a parasite can exert [169]. However, the impairment of host fecundity and/or sex ratio imposed by some parasites (for example the microsporidian *Octosporea effeminans* in *Gammarus duebeni* [120,170]) could also affect host population size. All these direct impacts on host abundance, especially if it is a key species, can modify the competitive or predator–prey interactions with other species [171].

In French marine ecosystems, two congeneric and sympatric amphipods, *Gammarus insensibilis* and *G. aequicauda*, show different reproductive success (higher in *G. insensibilis*), infection patterns and parasite-induced mortality [135]. The trematode *Microphallus papillorobustus* limits *G. insensibilis* density, favoring the coexistence of *G. aequicauda* that is less susceptible to infection [135]. In this situation *M. papillorobustus* appears to act as a keystone parasite [135].

Two trematodes, *Coitocaecum parvum* and *Maritrema poulini*, occur in two amphipod hosts, *Paracorophium excavatum* and *Paracalliope fluviatilis*, but decrease the survival only in the latter. Due to the higher tolerance, *P. excavatum* exhibits higher levels of prevalence and abundance of *M. poulini*. Therefore, they act as a "reservoir" of the parasite and increase the parasite load for the more susceptible *P. fluviatilis*, which, as a result, can be outcompeted by *P. excavatum* [160]. In the same way, Microphallid trematodes cause a reduction in the abundance of the intertidal amphipod *Corophium volutator*. As a consequence, the abundance of the amphipod *C. arenarium* increases, as this species is less sensitive to the parasite. The parasite weakens the stronger competitor *C. volutator* and thus facilitates the coexistence between the two competing host species. This phenomenon is further enhanced by increased temperature [164]. This is a field example of parasite-mediated competition and of the important role of environmental parameters, in this case, the temperature, that have consequences for the whole community structure.

In the context of biological invasions, parasitism often provides a competitive advantage to the non-native amphipods but there are also cases in which parasites limit the success of invaders avoiding the replacement of the native amphipod species [172]. When parasitized by the acanthocephalan *Pomphorhynchus laevis*, the immune system of the native *Gammarus pulex* is impaired and resource storage is decreased whilst the invader *G. roeseli*, infected with the same parasite, is not affected [149]. The immune depression of *G. pulex* constitutes a parasite-mediated disadvantage towards *G. roeseli*. Moreover, *G. roeseli*, being less damaged by and more tolerant to *P. laevis*, contributes to maintain the parasite population acting as a reservoir [173]. Additionally, Galipaud et al. [150] suggest a contribution of parasitism to the invasion success of *G. roeseli* that, unlike the native gammarids (*G. fossarum*/*G. pulex*), is not affected by acanthocephalan-induced mortality.

In contrast to the previous example, a parasitic water mold provides an advantage to the native amphipod host toward the exotic one in the St. Lawrence River [159]. The oomycete parasite infects both gammarid species but reduces the abundance of the invasive *Echinogammarus ischnus*, by causing mortality in this species [159]. The authors hypothesize that the parasite pressure prevents *E. ischnus* from becoming dominant and to replace the native *Gammarus fasciatus* as occurred in many other locations.

The effects of non-native parasites can be severe, if they are able to infect native host species (parasite spill-over). This was shown for the microsporidian *Cucumispora ornata*, a parasite of the invader *Dikerogammarus haemobaphes*. This microsporidian was also found in native *Gammarus pulex* and reduced the survival of both the invader and the native amphipod [111]. Parasites that have been introduced and retained in their invading amphipod, can contribute to the invasion success of their host. This may be the case of a sex ratio distorter microsporidian parasite that induces feminization in *Crangonyx pseudogracilis* [153]. The high number of females may increase host population growth [174] and thus favor the invasion process of *C. pseudogracilis* [153].

In one of the few experimental studies available to date that focuses on the effects of parasites on communities of different crustacean species, Friesen et al. [137] showed that a trematode parasite selectively reduced the survival of one of the tested amphipod species and that it influenced the overall abundances of the amphipod and isopod species used in this experiment. In another study, the parasite-induced mortality of acanthocephalan parasites was found to be different between "cryptic" amphipod lineages. This also indicates the structuring role of parasites in amphipod populations [150].

The mortality rate due to infection per se can significantly increase when parasites act in presence of other environmental stressors such as climate change and pollution [146,163]. This was reviewed recently for amphipods infected with microsporidians and/or acanthocephalans [57].

An additive effect of temperature and parasitism has been reported in intertidal trematode–amphipod systems [136,161,163,175]. Under the conditions of increasing temperature due to global warming, trematodes could cause increased parasite-induced mortality and a substantial reduction in amphipod populations, with ecosystem-wide consequences [63,136]. Both laboratory experiments [163] and a model study [63] on *Corophium volutator* indicate that this amphipod host suffers a harmful additive mortality due to increased temperature. The ecosystem effects linked to the parasite-induced decline of this amphipod population were observed after mass mortality events that occurred in 1990 in the Danish Wadden Sea [165]: both the topography and the sediment characteristics of the intertidal flat were affected underlying the ecological role of this amphipod as a stabilizer of the sediment and the great importance of the equilibrium with its parasites. Moreover, Studer et al. [161,162] documented a higher vulnerability and reduced survival in the presence of increased temperature in *Paracalliope novizealandiae* infected with the trematode *Maritrema novaezealandensis*. The positive influence of a temperature between 20 and 25 °C on the transmission rate and the development of the parasite accounts for the predicted massive infection and mortality of the host and the possible collapse of the *P. novizealandiae* population due to global warming [161,162]. Mouritsen et al. [136] showed in a mesocosm experiment that temperature alone was not sufficient to cause population effects, while the combination of increased temperature and parasitism (*M. novaezelandensis*) led to a decline of the amphipod community richness in the system. In contrast, temperature did not enhance infection or impact of another trematode (*Gynaecotyla adunca*) in *C. volutator* [176] and this suggests that not all the amphipod/parasite systems react in the same way to the same perturbing factor.

The impact of pollutants on amphipods may vary if the population is infected. Experimental exposure of gammarids (*G. pulex*) to cadmium showed a decreased feeding rate and an increased mortality rate in the specimens infected with an acanthocephalan [146]. No detrimental effects were seen in parasites whilst parasitized *G. pulex* were two to three times more sensitive to Cd (nominal concentration of 2.1 µg/L) than uninfected ones [146]. These results raise concern about the enhanced vulnerability of populations of *G. pulex* harboring the parasite and naturally exposed to a low concentration of this metal. Another study, investigating the influence of microsporidians (genus *Dictyocoela*) in *G. roeseli*, revealed that the parasites were able to reduce the host fitness (by weakening energy reserves and defense response and by increasing the cellular damages) only under cadmium stress [177]. However, parasitism is not necessarily a factor increasing the sensitivity and mortality in polluted conditions [56]. Amphipods may benefit from the ability of their parasites (especially acanthocephalans) to accumulate pollutants and so to reduce their concentrations in the tissues of infected hosts as reported by Gismondi et al. [178] and Chen et al. [179]. Although contrasting results emerge from studies on infected gammarids exposed to pollutants, at the ecosystem level the joint effect of pollution and parasitism could have important implications for contaminant dynamics within food webs and the health of the interacting organisms [26,56].

3.2. Increase in Vulnerability to Predators

Selective predation on infected amphipods is another subtle but important factor driving both population dynamics and community structure through an alteration of competition and effects on upper trophic levels. The increased vulnerability to predation is often linked to parasite manipulation, although rarely demonstrated, it is a phenomenon frequently reported in amphipods.

Due to changes in morphology, physiology and behavior, infected amphipods may show an increased attractiveness, high activity levels [180], propensity to drift in the river [116,143,181,182], reverse of phototaxis/geotaxis [148,181,183], an altered perception of predation risk and anti-predator behavior [180,184–188], and a different spatial distribution (micro habitat) [139,144,182] with respect to their uninfected counterparts. All these parasite-induced traits render the infected amphipod individuals more prone to predation by host and non-host species [189].

Increased susceptibility to shared predators of an infected host relative to its uninfected competitors and the differential impact of the same infection on the behavior of different competing host species are parasite-mediated factors that can affect community composition [143,148].

The native *Gammarus duebeni celticus* and the non-native *G. tigrinus,* co-occurring in freshwaters in North Ireland, share predators but differ in susceptibility to them. This is caused by a parasite mediation: the acanthocephalan *P. minutus* infects *G. d. celticus* but not *G. tigrinus* that, free from the parasite and its manipulative effects, is less vulnerable to predation and has a competitive advantage compared to the native amphipod [143]. Field and laboratory studies show that another acanthocephalan, *Pomphorhynchus laevis*, uses both the native *G. pulex* and the introduced *G. roeseli* as intermediate hosts. However, the parasite manipulates only the behavior of *G. pulex*, enhancing its drifting and phototropism [116,148]. This interspecific difference in manipulation leads to increased predation rates and parasite-induced mortality only in the native amphipod species, which is shaping the community and favors the invasion success of *G. roeseli* [150].

G. pulex individuals infected with another acanthocephalan, *E. truttae*, prefer to stay in the water column and the water surface, instead of more safe locations under stones or in contact with macrophytes [139]. The subtle but relevant modification in micro habitat use and distribution induced by the parasite increases the vulnerability of *G. pulex* to fish predation. This in turn may impact the whole community and generate cascade effects, since *G. pulex* is either a major predator or a major prey within the ecosystem [86,90]. The importance of habitat shift as a way by which parasites can structure communities and influence energy flow is also suggested by Médoc and Beisel [144] that discuss the possible effects both on upper and lower trophic levels according to the example of *G. roeseli* infected by the manipulative acanthocephalan *P. minutus*.

3.3. Changes in Feeding Ecology

Alteration of diet composition, predation activity and feeding rate could lead to modified competition, top-down effects on amphipod prey populations and on the recycling of nutrients [140,141,144,145,151,154].

Dianne et al. [190] found that amphipods (*Gammarus pulex*) infected with an early stage (acanthella) of the acanthocephalan *Pomphorhynchus laevis* feed less and show increased refuge use to avoid premature predation by fish. The ecological consequences were not examined and might be compensated by the increased predation of amphipods infected with a later parasite stage [184,191].

Labaude et al. [151] assessed the effect of parasitism in combination with temperature on the feeding of the freshwater gammarid *Gammarus fossarum*. Infection with the acanthocephalan *Pomphorhynchus tereticollis* led to a significant reduction of leaf consumption exacerbated by the highest temperature tested (additive effects). The negative impact on shredding activity could have obvious ecological consequences, but are difficult to predict because several other abiotic and biotic factors can interact, influencing the feeding efficiency of this keystone amphipod [151]. Additionally, Médoc et al. [145] documented a reduced consumption of leaf material, together with other changes in diet composition, in infected gammarids (*G. roeseli* parasitized by *P. minutus*) in comparison to uninfected conspecifics but this result was found only in laboratory conditions and not confirmed by the stable isotope analysis of carbon in the field. Overall, the study clearly indicates a modified trophic ecology of *G. roeseli* induced by the acanthocephalan and calls for caution in predicting the possible top-down effects [145].

Parasitism may significantly enhance the predation rate of amphipods and thus their impact on prey populations [141] and climate change may act synergistically on this phenomenon [142]. *G. pulex* infected with *E. truttae* exhibit a higher (30%) consumption of isopods than uninfected conspecifics. This increase is probably linked to the metabolic demand and behavioral manipulation of the parasite [141]. Increased temperature, like that expected under global warming conditions, may further exacerbate the predation pressure and the impact of *G. pulex* in the invaded community [142].

Contrary to these findings, Fielding et al. [138], working on the same amphipod–parasite system (*G. pulex*–*E. truttae*) reported a decreased predation of the infected gammarids on *Asellus aquaticus*. A similar decrease was observed when the parasite was a microsporidian species (*Pleistophora muelleri*) [156]. Moreover, the predatory activity of *G. pulex* on the eggs of *Artemia salina* and of *G. roeseli* on isopod live prey were found to be reduced by the acanthocephalans *P. laevis* and *P. minutus*, respectively [145,147].

Dikerogammarus villosus is a recently introduced amphipod that has successfully established and strongly impacts the communities of many European rivers thanks to its high trophic position and high predatory activity [103,152]. The functional response (attack rate and handling time) and the predatory behavior of this invasive amphipod decreases when it is infected with the co-introduced microsporidian parasite *Cucumispora dikerogammari* [152,192]. Therefore, this infection may mitigate the ecological impact of *D. villosus* in the invaded communities.

Another important impact of parasites is represented by the modification of intraguild predation (IGP) i.e., the predation among potential competitors [193,194]. Frequently, IGP involves closely related amphipod species that prey on each other and could rapidly cause species replacement [101]. Altered IGP is able to affect predator–prey dynamics within a community, to change species dominance in IGP hierarchies and consequently to influence the outcome of invasions [155,166]. In a guild of native and invasive amphipods, the impact of parasites on IGP may drive the success of introduced species [154–157] or enable their containment, favoring the coexistence with and avoiding the extirpation of native species [140]. Several studies were conducted by MacNeil's group on *Gammarus duebeni celticus*, native to Ireland freshwaters, and on invader species (*Gammarus pulex, G. tigrinus, Crangonyx pseudogracilis*) looking at the influence exerted on IGP by the microsporidian *Pleistophora* or the acanthocephalans *Echinorhynchus truttae* and *Polymorphus minutus*.

The decreased predation of infected *G. d. celticus* on *G. pulex* [156] and on *C. pseudogracilis* [157] appears to favor these two invaders. In microcosm experiments with different levels of *Pleistophora muelleri* prevalence in *G. d. celticus*, MacNeil et al. [155] found that, in the presence of the invader *G. pulex*, the survival of infected *G. d. celticus* declined near to the total elimination. They suggest, among other factors, the differential IGP, which is enhanced by the parasite, as a mechanism making invasion by *G. pulex* more likely.

When parasitized by the microsporidian, the native amphipod not only reduces its predation pressure on the smaller invaders *G. tigrinus* and *C. pseudogracilis,* but also increases its vulnerability to predation by the large invader *G. pulex* [154]. Therefore, *G. d. celticus*, which is the only one of the four species that is susceptible to *Pleistophora* sp. infection, has the double disadvantage of being a less efficient intraguild predator and of becoming a more vulnerable intraguild prey. This case is also an example of the so called "cryptic virulence": the negative impact of the parasite is evident only if *G. d. celticus* interacts with the other amphipod species, otherwise no direct effects on the survival or fecundity of the host population occur. On the contrary, when both the native and the invasive amphipod share the parasite *E. truttae* and its prevalence is higher in the invader, *G. d. celticus* benefit from the reduction in IGP ability of the exotic competitor. The final result is the slowdown of invasion and replacement [140].

IGP is often associated with cannibalism, a trophic interaction very common in amphipods [101,193]. Parasites can enhance the rate of cannibalism among host individuals, potentially due to the increased energy demand of the infected hosts. Such an increase in cannibalistic tendency, mainly of uninfected juveniles, was found in the amphipod *Gammarus duebeni celticus* infected with the microsporidian *Pleistophora muelleri* [195].

Overall, the examples reported in Sections 3.2 and 3.3 clearly suggest that parasitism in amphipods has important consequences on trophic interactions, food webs and thus potentially on energy flow. Especially the impact of parasites on the outcome of species invasions and thus on amphipod community has the potential to influence ecosystem processes since native and invasive amphipods differ greatly in two keystone activities, i.e., predation and detritus processing [196].

4. Conclusions and Perspectives

Parasitism should be taken into consideration when evaluating biodiversity, health and ecosystem function. Including parasites when studying the biology of amphipods is mandatory to have a complete picture of community dynamics and can be precious from an ecosystem perspective, especially in biological invasion contexts [112,137,197]. Parasites of amphipods play an important but often still overlooked role in aquatic ecosystems. Some parasites of amphipods not only impair their host (population) but also have consequences on higher levels (community, whole ecosystem). These effects become obvious when drastic changes occur (e.g., disturbances such as temperature increase or drought due to climate change, pollution, introduction of species) that alter the species' interactions and impair the functioning of ecosystems. Parasitological monitoring and the inclusion of parasites in the analyses of community structures are necessary to understand the strength of host–parasite interaction at the ecosystem scale. Parasitism effects on ecological processes could probably be evident and determinant only when the prevalence of the parasite reaches a considerable level [144,198]. Moreover, the effects of parasites on host interactions have been studied mostly on smaller and less complex scales (generally two host species and one shared parasite) instead of natural ecosystems, therefore the real influence of parasitism within a community remains largely unexplored and difficult to predict. Recent papers (see for example [137,160]) attempted to tackle this problem by analyzing different parasite and host species in the same community. Most of the available knowledge on the ecological importance and implications of amphipod–parasite systems come from laboratory experimental studies but there is a need of field evidence and of quantitative data to draw solid conclusions. Therefore, research effort should proceed in this direction.

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