Review Article

Gammarus-Microbial Interactions: A Review

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Gammarus spp. are typically classified as shredders under the functional feeding group classification. In the wild and in the laboratory, *Gammarus* spp. will often shred leaves, breaking them down into finer organic matter fractions. However, leaf litter is a poor quality food source (i.e., high C : N and C : P ratios) and very little leaf material is assimilated by shredders. In freshwater habitats leaf litter is colonized rapidly (within ~1-2 weeks) by aquatic fungi and bacteria, making the leaves more palatable and nutritious to consumers. Several studies have shown that *Gammarus* spp. show preference for conditioned leaves over nonconditioned leaves and certain fungal species to others. Furthermore, *Gammarus* spp. show increased survival and growth rates when fed conditioned leaves compared to non-conditioned leaves. Thus, *Gammarus* spp. appear to rely on the microbial biofilm associated with leaf detritus as a source of carbon and/or essential nutrients. Also, *Gammarus* spp. can have both positive and negative effects on the microbial communities on which they fed, making them an important component of the microbial loop in aquatic ecosystems.

1. Introduction

The diets of amphipods in the genus *Gammarus* are variable [1]. For example, *Gammarus* spp. can serve as detritivores [2, 3], herbivores [4, 5], predators [6, 7], and even cannibals [2, 8, 9] in aquatic ecosystems. However, under the functional feeding group classification [10–12], *Gammarus* spp. are typically classified as shredders/facultative shredder collectors [1]. In the wild and in the laboratory, *Gammarus* spp. often function as shredders consuming leaves and other coarse particulate organic matter (CPOM), breaking it down into smaller fractions or fine particulate organic matter (FPOM). Microbes, such as bacteria and fungi, are often associated with particulate organic matter such as leaves and decaying wood [13, 14]. Leaf detritus, in particular, is an important carbon source for the microbial loop in aquatic ecosystems [13]. Leaf matter serves as a substrate for bacterial and fungal growth, while at the same time supplying the microbial community with carbon in the form of leached dissolved organic carbon (DOC) [13]. Along with physical abrasion and soluble organic matter leaching, microbial decomposition and invertebrate feeding interact to regulate leaf litter breakdown rate in aquatic

ecosystems [15]. Detritus-associated bacteria and fungi are responsible for detrital decomposition and its increase in palatability and nutritional quality to consumers [11, 16, 17]. Invertebrate consumers often rely on the microbial biofilm as a carbon source rather than on the detritus itself [11, 14, 18]. Cummins [2] refers to CPOM as a "cracker" and its associated microbes as "peanut butter." The CPOM (cracker) acts as a vessel, enabling the consumer to more easily ingest the more nutritious bacteria and fungi (peanut butter).

Over the years, research has shown that *Gammarus* spp. feed on conditioned or inoculated detritus (i.e., leaves, leaf discs, or sediment) with "suitable" microflora [17, 19–22]. In addition, research has shown higher survival and growth rates of *Gammarus* amphipods in the laboratory when they are fed leaves with fungal growth compared to unconditioned or sterile leaves [20, 23, 24]. Freshly shed and sterile leaves typically have low nutritive value (i.e., high C:N and C : P ratios) and contain high amounts of lignin and cellulose, which are virtually indigestible to most invertebrates [25]. Therefore, for shredders, the percentage of food ingested and converted into invertebrate biomass is typically very low. As a result, many shredders, including *Gammarus* amphipods, wait until microbes (which are

typically highly nutritious) colonize and build up on this poorly nutritious food before feeding.

Gammarus spp. have also been shown to have both negative and positive effects on the microbial communities on which they feed, illustrating the importance of this genus to the microbial loop in lotic and lentic ecosystems. Most research investigating interactions between microbes and invertebrates has been focused on the role of microbes as a potential food source [26]. Although relatively little is known of the feedback effects that grazing invertebrates, such as *Gammarus* amphipods, can have on their microbial food [26], it has been demonstrated that microbial metabolism, production, and biomass can be influenced by both "bottom-up" and "top-down" controls [27–29]. Although invertebrate feeding can decrease microbial biofilm biomass, it has also been shown to stimulate microbial growth and activity [27, 30]. Thus, *Gammarus* spp. are often involved in a feedback loop with the microbial community on which they feed. In some cases, these feedbacks can be positive [28–30], while in others, they can be negative [29].

The specific objective of this review is to evaluate what is known regarding how microbes influence *Gammarus* spp. feeding preference, survival, and growth in the laboratory and aquatic habitats. In addition, it will be discussed how *Gammarus* spp. affect the microbial community on which they feed, either through ingestion or other types of interactions. Finally, the current state of research investigating *Gammarus*-microbial interactions will be reviewed and possible future research directions will be discussed.

2. Food Selection, Survival, and Growth

Quality of detritus is an important factor that determines food selection by shredders. Research has shown that shredders tend to prefer certain leaf species to others [31–33] and conditioned leaves over non-conditioned leaves [33–40]. Typically, shredders select food based on several characteristics of leaves, which include toughness, nutrient content, and the degree of conditioning by microbes [40]. *Gammarus* spp. are no exception [19, 20, 23, 31, 33, 41]. In some of the earliest laboratory experiments investigating food selection by *Gammarus* spp., Bärlocher and Kendrick [19] investigated food (leaf species) and fungi preference of *Gammarus pseudolimnaeus*. When very little microflora were present on leaf discs, *G. pseudolimnaeus* preferred ash to maple and maple to oak leaves. Bärlocher and Kendrick [19] then presented amphipods with pure colonies of ten different hyphomycetes along with maple leaf discs with very little associated microflora. *Gammarus pseudolimnaeus* always preferred the fungus to the leaf discs and in several cases the amphipods entirely ignored the leaves and consumed only the hyphomycetes.

As Bärlocher and Kendrick [19] demonstrated, *G. pseudolimnaeus* can exhibit preference for certain conditioned leaf species over others. Other *Gammarus* spp. have shown similar preferences. In the laboratory, the stygophilic *G. troglophilus* consumed conditioned oak if they were the only leaves presented to it [31]. However, if presented with conditioned oak and elm leaves simultaneously, *G.*

troglophilus ingested the elm leaves and ignored the oak. Pöckl [23] simultaneously offered *G. fossarum* and *G. roeseli* eight different naturally decaying (i.e., conditioned) leaf species. The most preferred and quickly eaten were leaf discs of lime, ash, and alder. Both species showed little interest in oak leaves, and beech leaf discs were nearly untouched [23]. This behavior most likely resulted from differences in toughness of the leaves, leaf thickness, and chemical constituents (e.g., phenols and tannins) [23].

To determine if *G. minus* could distinguish different foods and exhibit a preference for the different foods, Kostalos and Seymour [20] performed a series of laboratory and field experiments. They individually compared preference of five different foods against a control, which contained a microflora most similar to fresh stream leaves [20]. The five different foods consisted of elm leaves with no microflora (sterile), bacteria-enriched elm leaves, conditioned elm leaves with a reduced bacterial fauna (still containing fungi), fungus-enriched (*Tetrachaetum elegans*) elm leaves, and the fungus *T. elegans* alone. *Gammarus minus* most strongly preferred the fungus-enriched leaves and conditioned leaves with a reduced bacterial fauna to the control leaves. The sterile elm leaves were least preferred.

In another laboratory study, Friberg and Jacobsen [41] examined the feeding preferences of *G. pulex*. Overall, *G. pulex* preferred conditioned alder leaves over five other food items which included conditioned beech leaves, fresh beech leaves, Sitka spruce needles, a fresh macrophyte, and a fresh filamentous green algae. The authors found no linear relationships between food preference and fiber content, toughness, phosphorous content, nitrogen content, and C:N ratio, leading them to believe that bacterial or fungal coating was responsible for the preference patterns. In another study using *G. pulex*, Graça et al. [42] demonstrated that when offered a choice between unconditioned leaf discs of elm, leaf discs of elm inoculated with the fungus *Anguillospora longissima*, or *A. longissima* mycelia, *G. pulex* was able to discriminate between the different foods and concentrated its feeding on the inoculated leaf discs, and to a lesser extent, on the unconditioned leaf discs. The *A. longissima* mycelia were ignored by *G. pulex*. Because food preference was not correlated with fungal biomass, leaf disc toughness, leaf decomposition, or nitrogen content, Graça et al. [42] concluded that other unmeasured factors could have affected food preference by *G. pulex*. These could include the fungal synthesis of micronutrients or the differential ability of fungi to eliminate plant allelochemicals among others [42].

Gammarus spp. have also been shown to prefer particular fungal species to others. When offered leaves colonized separately by one of eight species of aquatic hyphomycetes, Arsuffi and Suberkropp [17] found *Gammarus* amphipods to be highly selective feeders. Leaves colonized by the fungus *Alatospora acuminata* were the most preferred, but *Gammarus* also fed on leaves colonized by *Clavariopsis aquatica* and *Flagellospora curvula*. Feeding on other aquatic hyphomycetes was negligible [17]. Aquatic hyphomycetes produce secondary metabolites that function in microbe-microbe interactions and may also defend the fungi from invertebrate feeding. Arsuffi and Suberkropp [17] suggest

that secondary metabolites from fungi are responsible for the variation observed in feeding preferences, growth rates, and survivorship of shredders consuming leaves colonized by different fungi [17].

The combination of leaf and fungal species has also been shown to influence selection by *Gammarus* spp. In a laboratory study, individuals of *G. tigrinus* were given a choice between six different leaf/fungus combinations [21]. The leaf discs were conditioned with single species of aquatic hyphomycetes and their concentrations of proteins, lipids, and ergosterol (an indicator of fungal biomass) were measured. Although total consumption was not correlated to the lipid or protein content of the leaves or the fungal biomass, *G. tigrinus* showed a slight preference for some leaf/fungal combinations over others [21]. The authors then extracted fungal mycelia and applied the extracts to unconditioned leaf discs. *Gammarus tigrinus* preferred naturally conditioned leaf discs to the extract-coated leaf discs, suggesting that natural colonization over time makes the leaf/fungi combination more attractive compared to a rapid assembly of the parts.

In a more recent study, Assmann and Elert [22] examined the role of fungal attractants and repellents in food preference of the amphipod *G. roeseli*. Because both attractants and repellents seemed to act on *G. roeseli* feeding preference, the authors suggest that the relative ratios of repellents and attractants might determine consumption of fungi by *Gammarus*. Furthermore, changes in the environment could lead to changes in the relative ratio of attractants to repellents [22]. Thus, food preference may be governed by environmental conditions rather than being fixed in the consumer.

Amphipods fed conditioned leaves and/or fungi have increased assimilation efficiencies. Low assimilation efficiency results in less matter and energy available for maintenance, growth, and reproduction [43], thus compromising performance. Bärlocher and Kendrick [44] compared the assimilation efficiencies of *G. pseudolimnaeus* fed elm leaves, maple leaves, or the mycelium of one of ten fungi (5 aquatic hyphomycetes and 5 terrestrial hyphomycetes). Although the amount of food consumed was ten times greater in all of the leaf diets than in the fungi diets, the highest assimilation efficiencies were found for those individuals fed four of the ten fungi. Only 10% of the dry mass, 14–18% of the protein, and 17–19% of the energy of either elm or maple leaves were assimilated by the amphipods. However, *G. pseudolimnaeus* assimilated approximately 43–76% of the dry mass, 73–96% of the protein, and 70–83% of the energy when fed fungal mycelium commonly found in streams [44].

Research has shown higher survival and growth rates when *Gammarus* spp. are fed conditioned leaves compared to non-conditioned or sterile leaves. In addition to their experiments on food preference, Kostalos and Seymour [20] experimentally tested the survival of *G. minus* on ten different diets. These experiments showed significant differences in survivorship over a ten-week period, with the highest survivorship (45–88%) occurring on fungus-enriched leaves [20]. Intermediate survival rates (36–63%) occurred on leaves with a viable bacterial flora while the lowest survivorship (~3%) occurred on leaves that had no

or a reduced microflora [20]. Other *Gammarus* spp. have shown higher growth rates when fed conditioned leaves. Graça et al. [33] found that conditioning had a significant effect on the growth of *G. pulex*. Similarly, Pöckl [23] found that neonates, juveniles, and early adults of *G. fossarum* and *G. roeseli* fed leached and decaying leaves of lime, elm, and hornbeam with surface growth of aquatic fungi and bacteria had higher growth rates than amphipods fed fresh, growing leaves. These studies suggest that microbes, particularly fungi, confer an advantage to *Gammarus* spp. by positively influencing survival, growth rates, or both.

In contrast, Graça et al. [24] found no significant increase in the survival of *G. pulex* on fungally conditioned leaf material when compared to unconditioned food. In general, survival of *G. pulex* was low on both conditioned and unconditioned leaves [24]. Although growth rates were higher on conditioned leaf material, the difference was not significant [24]. The authors offered an explanation for this lack of significance, using the results of an energy budget study. Individuals of *G. pulex* feeding on unconditioned leaves had a significantly lower respiration rate than those individuals feeding on conditioned leaves. The authors hypothesized that the lower metabolic demands as a result of a lower respiration rate compensated for the reduced energy intake. Thus, *G. pulex* is able to maintain a constant growth rate, even when food quality is poor.

3. Effects of Feeding on the Microbial Community

The effect *Gammarus* spp. have on microbial communities is not well known. Obviously, *Gammarus* amphipods can influence microbial biomass and production through mechanical removal (i.e., direct consumption). Direct consumption of biofilms by invertebrates has been shown to decrease microbial biomass and alter microbial community composition [45–49], however, consumption has also been shown to stimulate microbial growth [27, 30]. Shredding of leaves by *Gammarus* spp. may enhance microbial respiration by increasing the surface area of the leaf, which can lead to higher microbial respiration per unit mass of leaves [30]. In addition, increased fragmentation of leaves and excretion by *Gammarus* amphipods may lead to an increase in the availability of DOC and inorganic nutrients [30]. Thus, if a biofilm is nutrient limited, leaf shredding by *Gammarus* spp. can possibly relieve nutrient limitation constraints. Direct consumption by *Gammarus* spp. can not only directly decrease microbial biomass, but it can also change biofilm architecture, thus altering the delivery of inorganic nutrients and energy to the biofilm [29, 49]. Morrison and White [27] showed that microbial biomass was higher on detritus (conditioned oak leaves) that had been grazed by *G. mucronatus* than on ungrazed detritus. In addition to increasing microbial biomass, grazing by *G. mucronatus* increased metabolic activity and changed microbial community structure [27]. As amphipods grazed, microbial community structure shifted from one with both prokaryotes (bacteria) and microeukaryotes (fungi) to one dominated by bacteria [27]. Because microbial biofilms are

important mediators of energy flux and nutrient transformation in aquatic habitats, changes in microbial biomass, community composition, and biofilm architecture may have profound effects on aquatic ecosystem functioning [50, 51].

More recently, Kinsey et al. [30] compared the influence of feeding by cave and surface forms of *G. minus* on microbial biofilms and found that both forms increased the respiration rate of leaf-associated microbes by 32–52%. However, the cave form had a 15% greater stimulatory effect on microbial respiration. Kinsey et al. [30] concluded that their results may have been due to an attraction of *G. minus* to leaves with greater microbial growth or due to the amphipods stimulating microbial respiration by (1) increasing the availability of DOM and inorganic nutrients through fragmentation and excretion, (2) increasing water flow over the microbial biofilm, thus reducing boundary layer effects and increasing diffusion rates of nutrients and oxygen into biofilms, or (3) increasing leaf surface area, thereby increasing microbial respiration per unit mass of leaves. Cooney and Simon [29] then used microcosm experiments to examine how bacterial production on rocks and fine sediments from cave streams responded to amendments of dissolved organic matter (DOM) and to the cave form of *G. minus*. Interestingly, feeding by *G. minus* strongly suppressed bacterial production on rocks but had no effect on bacterial production on fine sediments. In addition, microbial production on rocks was stimulated by DOM amendments but production on sediments was not. Their results indicate that both resources and consumers play important roles in regulating microbial activity, particularly on rocky substrates.

4. Conclusions

This paper illustrates the importance of bacteria and fungi in the diet of *Gammarus* amphipods. It has been shown that *Gammarus* spp. frequently prefer certain leaf species to others and conditioned leaves to unconditioned leaves. Conditioning of detritus often enhances survival and even growth of *Gammarus* amphipods. Furthermore, *Gammarus* can have a significant influence on microbial communities through consumption of microbially enriched detritus, particularly fallen leaves. Although there is a body of literature on the interactions between *Gammarus* spp. and microbes, the full story is not complete. As important as *Gammarus* spp. are to detrital processing and nutrient cycling in aquatic ecosystems, there seems to be a decrease in interest in their interactions with microbes. Given the general paucity of recent information on *Gammarus* performance (e.g., survival, growth, and fecundity) after being fed bacteria and/or fungi, there should be a renewed interest in research on *Gammarus*-microbial interactions. More specifically, stoichiometric theory and unsaturated fatty acid analysis have been used by researchers to examine energy flow and growth efficiency in a number of aquatic consumers [52–55].

Future research should address stoichiometric relationships between *Gammarus* spp. and "conditioned" detritus. Colonization by microbes influences C:N and C:P ratios of leaf litter [56]. Furthermore, consumers often have lower C:N and C:P ratios than their food, thus elemental imbalances between detritivores (e.g., shredders) and their food can be common [53, 56–58]. An inadequate supply of one or more nutrients can constrain animal growth and alter their life history [57]. One way in which to examine the nutrient deficiency in consumers is the threshold elemental ratio (TER). Threshold elemental ratios are elemental ratios at which growth limitation of a consumer switches from one element to another [52, 57]. Calculation of TERs (C:N and C:P) requires estimates of assimilation efficiencies for C, N, and P, ingestion rates, respiration rates, and %C, %N, and %P of consumers. When the TER of the consumer is equal to the C:nutrient ratio of the consumer's food, animal growth is limited by both C and the nutrient [53]. When the TER of the consumer deviates from the C:nutrient ratio of the food, either C or the nutrient is limiting [53]. Further elucidation of the importance of highly nutritious microbes in *Gammarus* diets could be provided by identifying the critical C:N or C:P ratios of detritus and microbes and the TERs of *Gammarus* spp.

Fatty acids (e.g., polyunsaturated fatty acids (PUFAs) and highly unsaturated fatty acids (HUFAs)) are critical biological compounds in aquatic food webs [58, 59]. Some fatty acids are critical for growth and reproduction while others are thought to maintain membrane fluidity at low temperatures [59]. However, little is known about the fatty acid requirements for *Gammarus* spp. in lakes and streams. *Gammarus* spp., like other invertebrates, have fatty acid requirements that must be filled through their diet as evidence for synthesis *de novo* has not been found. Future research should address the trophic transfer of essential fatty acids from microbes to *Gammarus* amphipods, as this research could make important contributions to *Gammarus*-microbe food web ecology and to our understanding of the microbial loop.

Acknowledgments

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