Research Article

Mouthpart Morphology of Three Sympatric Native and Nonnative Gammaridean Species: *Gammarus pulex*, *G. fossarum*, and *Echinogammarus berilloni* (Crustacea: Amphipoda)

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In the last 20 years several nonnative amphipod species have immigrated inland waters of Germany and adjacent central European countries. Some of them have been very successful and could establish stabile populations. In some places, they have even replaced native or earlier established species. The gammarid *Echinogammarus berilloni* originates from the Atlantic region of France and the north-western part of Spain and coexists in some central European waters with the native *Gammarus pulex* and *G. fossarum*. Here, we describe and compare the mouthparts and other structures involved in food acquisition of these three sympatric gammaridean species. Our hypothesis was that differences in the mode of feeding of the three species could be the reason for their coexistence and that these differences would be expressed in differences in mouthpart morphology. The results of our SEM study demonstrate that there are indeed interspecific differences in details of the morphology of the feeding structures. This is especially true for the setation of antennae, maxillulae, gnathopods, and third uropods, which can be interpreted as adaptations to special modes of feeding. Generally, all three species are omnivorous, but specializations in details point to the possibility to use some food resources in a special effective way.

1. Introduction

The gammaridean fauna of middle European inland waters has dramatically changed in the last two decades; particularly, Ponto-Caspian gammarideans arrived in middle European rivers, canals, and lakes [1–11]. Immigration has happened and is still ongoing via three main corridors: (i) along the Danube, Main-Donau Canal and Main into the Rhine system; (ii) via the Pipet-Bug connection from the east, and from the north and along the Baltic coast via ships [12]; (iii) also from the Mediterranean region, freshwater gammarideans have enlarged their range of distribution towards western and middle Europe [5, 13–16]. Some of these nonnative gammaridean species could establish stabile populations and occur in high densities, and several species have a severe impact on the ecology of the invaded regions by reducing and even eliminating native and earlier established gammaridean species (therefore, the immigrants are called invasive).

One well-examined example of such invasive species is *Dikerogammarus villosus* (Sowinsky, 1894) [17]. This species is now the dominant gammaridean species in many rivers, canals, and larger lakes all over central Europe, affecting also other members of the macrozoobenthos [1, 6, 18–20]. But not all nonnative species are invasive, and invasive species are, vice versa, not always able to eliminate native species in every habitat. Under certain conditions, coexistence of native and nonnative species may be possible. In some places, even the very successful invasive species *D. villosus* occurs together with other species in the same waters. In Lake Constance, Germany, for example, no less than four sympatric species can be found: the invasive *D. villosus*, the earlier established *Gammarus roeselii* Gervais, 1835 [21], the native *Gammarus lacustris* Sars, 1863 [22], and the recently discovered *Crangonyx pseudogracilis* Bousfield, 1958 [23]. In this lake, like in other waters with a diverse amphipod fauna, coexistence of these closely related species may be possible because it is rich in its ecological structure, that is,

by offering different microhabitats, which can be inhabited by different species according to their substrate preferences [10, 24–34]. But also different food preferences might be a factor, which enables individuals of these species to cooccur in the same habitat. If sympatric species are specialized to feed on different types of food, we hypothesize that such specializations should be expressed in the morphology of their mouthparts.

Therefore, we investigated the mouthparts and other structures involved in food acquisition of the three gammarideans *Gammarus fossarum* Koch in Panzer, 1836 [35], *G. pulex* (Linnaeus, 1758) [36], and *Echinogammarus berilloni* (Catta, 1878) [37] using scanning electron microscopy (SEM). These three species, the two native *Gammarus* species and *E. berilloni*, originating from the Atlantic region of France and Spain, occur sympatrically in some middle European rivers, such as the river Meuse in France and Belgium [9], the Viroin, Belgium [38], and in a karstic stream system in the Paderborn Plateau, Westphalia, Germany [39]. Moreover, *G. pulex* and *E. berilloni* are sympatric in a Rhine tributary near Iffezheim, Germany [30], in smaller rivers in Brittany, France [10], and in the Loire and its tributaries, Region Centre, France [40]. Sympatric occurrences of *G. pulex* and *G. fossarum* have been reported from some waters in Germany, for example, Fulda-Elder Basin [41], Schlitz [42], and from a forest brook, Rimbach [43]. However, in most waters, the populations of these two species live separately, with *G. fossarum* inhabiting springs and the upper reaches of small streams and rivers and tolerating high current and lower temperatures, whereas *G. pulex* prefers sections of brooks and smaller rivers with lower currents [44, 45].

Because these three species are closely related, we do not expect major differences in the morphology of their mouthparts, but more likely modifications in detail should be found, for example, size and shape of particular structures and, in particular, differences in limb setation as signs of specialization to a specific kind of food. Such morphological modifications of the mouthparts have already been demonstrated for *G. roeselii* and *D. villosus* [46]. We therefore aimed at investigating the mouthpart morphologies of the three mentioned species. We expect specific differences that enable the species to live sympatrically on an, at least, slightly different food source that would explain their coexistence.

2. Material and Methods

Specimens of *Gammarus pulex* were obtained from a spillway of a gravel pit filled with groundwater, draining into a side canal of the river Danube near Ulm (N 48° 18' 40.5'', E 9° 52' 9.9'') in 04/2007. Specimens of *G. fossarum* were collected from the river Nau near Langenau (N 48° 30' 3.4'', E 10° 8' 18.7'') in 07/2008. Specimens of *Echinogammarus berilloni* were obtained from the collection of Gerhard Maier, Senden, collected in 05/2004 from a Rhine tributary near Iffezheim (N 48° 50' 15'', E 8° 7' 11.9''). For identification of species, the taxonomic key of Eggers and Martens [47, 48], the original taxonomic descriptions, and redescrptions were used [14, 35–37, 49–51]. Macrophotographs of specimens

stored in 70% ethanol were taken with a Canon Macro Photo Lens EF-S 60 mm mounted on a Canon EOS 450D digital camera. Specimens were illuminated with cold-light lamps. For reducing reflections, both the lamps and the lens were equipped with polarizing filters.

For SEM studies, approximately 30 adult males of each species were anesthetized with carbon dioxide by adding a small amount of sparkling mineral water and fixed and stored in 70% ethanol. After dissection, debris was removed from the specimens by using an ultrasonic cleaner. The specimens were dehydrated in an alcohol series, critical-point dried, and sputter-coated with a mixture of gold and palladium. SEM work was performed with a Zeiss DSM 962 scanning electron microscope of the Central Unit Electron Microscopy at the University of Ulm. Digital images obtained from the SEM were trimmed in Adobe Photoshop, and plates were arranged using Adobe Illustrator.

3. Results

Besides the mouthparts (mandibles, maxillulae, maxillae, maxillipeds; also considered are the paragnaths), we also describe several more structures, which are involved in food acquisition and are of potential significance. These are the antennulae, the antennae, the third pair of uropods, and the first and second pairs of gnathopods. We start the description with the latter appendages. All specimens illustrated and described herein are adult males. Description is complete for the first species, while we applied an abbreviated style thereafter to focus on differences and cut descriptions short.

3.1. *Gammarus pulex* (Linnaeus, 1758) [36] (Figure 1(a)). The antennulae (Figure 2(a)) are about half as long as the body of the animal. They consist of a three-jointed peduncle and a 23-jointed flexible flagellum. In addition, a short five-part accessory flagellum is present at the junction of peduncle and flagellum. The proximal portion of the peduncle is the longest; the distal portion is slightly more than half as long as the second. Setation of both peduncle and flagellum is short and sparse.

The antennae (Figure 2(d)) are shorter than the antennulae. They consist of a two-part proximal section, the protopod with coxa and basipod, and a distal endopod. The endopod is made up of three long tubular portions and a flagellum consisting of 16 annuli. The annuli of the flagellum are anteroposteriorly flattened and broadened in mediolateral dimension. The posterior surface of the proximal 12 flagellar annuli is armed with a transverse row of about 12 long simple setae, together forming a kind of flag-like brush. Moreover, each flagellar annulus 2 to 11 bears one calceolus on their medioposterior margin (Figure 2(g)). The distal 4 annuli are only weakly setated. The (excretory) gland cone on peduncle segment 2 is rather long, nearly reaching the distal end of peduncle segment 3.

In contrast with the styliiform first and second pairs of uropods, those of the third pair (Figures 3(a) and 3(b)) are foliaceous and articulate more flexibly. The one-part endopod is shorter than the bipartite exopod with its small second distal part. In *G. pulex*, the endopod reaches about

FIGURE 1: Photographs of males of (a) *Gammarus pulex*; (b) *Gammarus fossarum*; (c) *Echinogammarus berilloni*.

3/4 of the length of the proximal part of the exopod (Figure 3(a)). Most of the setae on the median and lateral margin of endopod and exopod are plumose (with setulae in two opposing rows along the shaft of the seta) (Figure 3(b)). The two slender lobes of the deeply notched telson overhang the peduncles of the third uropods. Their distal ends are armed with two spines and about 5 long simple setae each (Figure 3(a)).

The first two pairs of pereopods (=2nd and 3rd pairs of thoracopods) are modified to subchelate gnathopods. Mainly because the ischium has the shape of an elbow, the gnathopods are flexed anteriorly, covering the mouthparts ventrally with their distal four podomeres. The propodus of the first gnathopods (Figure 4(a)) is piriform. The curved dactylus is slightly more than half as long as the propodus. The propodus of the second gnathopods (Figures 4(b) and 4(c)) is less piriform, nearly rectangular. The dactylus is arranged almost transverse. Setation of the second gnathopods is much denser and the setae are much longer than in the first gnathopods. Carpus and propodus bear many groups of long and distally curved setae on their margins. These setae are directed medioventrally in the natural position of the gnathopods.

The maxillipeds (=first pair of thoracopods) (Figures 5(a)–5(d)) are bent anteriorly in their natural position, covering most of the other mouthparts and the labrum (Figure 5(a)). Their coxae are fused medially, so that they act as one unit for feeding and handling food. The basipods stem from a triangular socket, built by the fused coxae. Each basipod is medially drawn out into a distally directed spatulate endite (Figure 5(b)). The five-partite

endopods are well developed. The first portion, the ischium, of each side also bears a distally directed spoon-shaped endite. The remaining four portions of each endopod build two opposing “palps.” Their distal portions, the dactyli, taper into medially directed claw-like spines.

Basipod, ischium, and merus of the maxilliped bear one group of six to seven simple setae on their posterior sides each. Several groups of medioposteriorly directed simple setae are sited on the posteromedian margins of carpus and propodus (Figure 5(a)). On their anterior sides, the median margins of the endites of the basipods are bent anteriorly, together forming a keel-like elevation. Here several long pappose setae (with setulae randomly arranged along the shaft) are sited, which are anteriorly directed (Figure 5(b)). The distal end of each basipodal endite is, on their anterior sides, armed with a row of distally directed short pappose setae (Figure 5(c)). In addition, four distally directed tooth-like cuspidate setae insert on the medial section of the distal margin of each endite. The endite of each ischium bears a row of mediolaterally directed, flattened, and hook-shaped cuspidate setae on the posterior side of its medial margin (Figure 5(d)). This row is accompanied by two rows of short, tape-like setae on each endite.

The small coxal elements of the maxillae (Figure 8) arise from a common sternal elevation (Figures 8(a) and 8(b)). The coxae are predominantly membranous and do not give rise to any enditic extensions. The basipod is medially drawn out into a distally pointing spatulate endite, the so-called “inner plate.” Additionally, the so-called “outer plate,” possibly representing the endopod, stems from the outer side of each basipod. The median margin of the inner plate

FIGURE 2: : SEM images of antennulae and antennae: (a–c) right antennula in median view of (a) *Gammarus pulex*, (b) *Gammarus fossarum*, and (c) *Echinogammarus berilloni*; (d–f) right antenna in median view of (d) *G. Pulex*, (e) *G. Fossarum*, and (f) *E. berilloni*; (g) proximal part of right antenna of *G. pulex* in posterior view; (h) proximal part of flagellum of right antenna of *G. fossarum* in median view; (i) flagellum of left antenna of *E. berilloni* in posterior view. af: accessory flagellum; bas: basipod; cal: calceolus; cox: coxa; f: flagellum; gc: gland-cone; 1, 2, 3, 4, 5: number of podomeres of peduncle.

carries three rows of setae. The anterior row of setae curves from the median margin onto the anterior surface of the inner plate towards the distal margin of the inner plate (Figure 8(b)). The shafts of these setae are on their lateral and posterior sides equipped with long thin setulae (Figure 8(d)). The medio-distally pointing setae of the posterior row are short, straight, and bear only scale-like setulae on one side of the distal third of their shafts. The median row comprises pappose setae. The median and posterior rows of setae follow the margin along the distal end of the inner plate. As a result of that, these setae change their shape. Those of the posterior row become more and more similar from proximal to distal to those of the other plate, those of the median row are only partly equipped with scale-like setulae. The outer plates are movable in the mediolateral plane and partly cover the

smaller inner plates posteriorly (Figure 8(a)). On their distal margin, each outer plate is armed with two rows of setae (Figure 8(c)). The setae of the anterior row are flattened and bear no setulae. The shafts of the setae of the posterior row are, on their distal third, flattened and equipped with closely arranged, triangular lobes.

The maxillulae (Figure 11) consist of a coxa, inner plate, outer plate, and palp (Figures 11(a) and 11(b)). The spherical coxa inserts in an ample membrane on the cephalothorax with plenty of muscle fibres (Figure 11(b)). The distally directed coxal endite, the so-called “inner plate,” has the shape of an isosceles triangle in anterior and posterior perspective (Figure 11(c)). It stems from the coxa with a small and short connexion. It bears a row of medio-distally directed long pappose setae on its longer median margin. In

FIGURE 3: SEM images of telson and third uropods: (a) telson and third pair of uropods of *G. pulex* *in situ* in dorsal view; (b) exopod of left third uropod of *G. pulex* in anterior view; (c) telson and third pair of uropods of *G. fossarum* *in situ* in dorsal view; (d) exopod of left third uropod of *G. fossarum* in posterior view; (e) telson and third pair of uropods of *E. berilloni* *in situ* in dorsal view; (f) exopod of left third uropod of *E. berilloni* in anterior view. Arrows indicate presence or absence of plumose setae.

their natural position, the coxal endites of the two maxillulae look like two opposing hand brushes, building a dense net. The basipods are anteriorly directed in their natural position. The articulation with the coxa allows movement in medio-lateral plane. The basipod carries a broad spatulate endite medio-distally. The compound of basipod and its endite is traditionally termed “outer plate.” The latter is anteroposteriorly flattened with a concave anterior side and a convex posterior side. The distal margin of the basipodal endite is armed with 10 very robust, medio-distally directed cuspidate setae which are arranged in two rows (Figures 11(e) and 11(f)). Each of these setae, for their part, is armed with one row of up to 12 medio-posteriorly directed secondary spines. Along the distal margin of the outer plate, the number of secondary spines of the setae decreases from median to lateral of the row of setae. Therefore, the median setae look like coarsely elaborated combs with up to 12 prongs, whereas those of the lateral parts of the rows are equipped with three finger-like secondary spines (Figure 11(f)). The sockets of these robust cuspidate setae are

still membranous and therefore elastic. The maxillular palp, the endopod, consists of two portions (Figure 11(b)). The proximal portion is small and cylindrical, whereas the distal portion is nearly four times as long, flattened, and medially bent. The spatulate distal portions of the endopods of the left and right maxillulae are asymmetric. That of the right one is broader and its distal margin is armed with a row of six stout, triangular, tooth-like, cuspidate setae. They are accompanied by two conical setae on the anterior end of the row (Figure 11(e)). In contrast, on the left endopod, there is a row of eight robust, conical setae on the distal margin flanked by five simple setae posterodistally (Figure 11(f)).

The paragnaths (Figures 5(e) and 5(f)), traditionally often termed “lower lip,” are a pair of flap-like, medially fused extensions of the sternum of the mandibular segment. The paragnaths are the posterior limitation of the mouth area and they build, together with the labrum, the space in which the mandibles operate. There is a deep cut between the two flaps. In this region, the flaps are armed with a dense field of short, thin, and scaled setae. On the anterior

FIGURE 4: SEM images of distal part of gnathopods: (a) right first gnathopod of *G. pulex* in anterior view; (b) left second gnathopod of *G. pulex* in posterior view; (c) left second gnathopod of *G. pulex* in anterior view; (d) right first gnathopod of *G. fossarum* in anterior view; (e) left second gnathopod of *G. fossarum* in posterior view; (f) left second gnathopod of *G. fossarum* in anterior view; (g) right first gnathopod of *E. berilloni* in anterior view; (h) left second gnathopod of *E. berilloni* in posterior view; (i) left second gnathopod of *E. berilloni* in anterior view. Abbreviations other than in previous figures: c: carpus; d: dactylus; p: propodus.

side (Figure 5(f)), near the entrance to the oesophagus, there are two depressions, in which the molars of the mandibles fit, when these are adducted. On their posterior side (Figure 5(e)), the paragnaths are drawn out into a proximolaterally directed cusp on each side. The flaps of the paragnaths are asymmetric, with the left being slightly wider than the right in proximodistal extension. This corresponds with the asymmetry of the mandibles. In all three species investigated here, the paragnaths are very similar. In *G. pulex*, the proximo-laterally directed cusps are slender, elongated, and pointed. The distal and proximolateral margins of the paragnaths are curved.

The mandibles (Figure 14) comprise a prominent proximal portion, the coxa and a distal portion, the palp consisting of the basipod, and a two-segmented endopod (for overview see, Figure 16(a)). In their natural position, only the distal part of the coxa surmounts the labrum (Figures 14(a) and 14(b)). The coxa is medially drawn out into a proximodistally extending protrusion. This gnathal edge is divided into a distal pars incisiva (or incisor process), a lacinia mobilis, a spine row, and a proximal pars molaris (or molar process) (Figures 14(c) and 14(d)). There is a distinct asymmetry of left and right mandible and their components. On the right mandible, the whole coxal body as well as the gnathal

FIGURE 5: SEM images of maxillipeds and paragnaths of *Gammarus pulex*: (a) maxillipeds in posterior view; (b) maxillipeds in anterior view; (c) distal setation of endite of left basipod in anterior view (cf. eb in (b)); (d) median setation of endite of right ischium in posterior view (cf. ei in (a)); (e) paragnaths in posterior view; (f) paragnaths in anterior view. Abbreviations other than in previous figures: eb: endite of basipod; ei: endite of ischium; i: ischium; m: merus.

edge is smaller in proximo-distal extension than on the left mandible. Also the angles, in which the molar surfaces are oriented, are different, being nearly rectangular on the left, but about 60° on the right mandible (Figure 14(b)). The left incisor is stout and five toothed. The well-developed stout and broad left lacinia mobilis is blade shaped and four toothed. The base of the lacinia mobilis is slightly protruded against the incisor. This so-called articular condylus reaches into a cavity on the base of the incisor (Figure 14(b)). On the posterior side of the lacinia, the articular condylus is well developed, whereas on the anterior side, it cannot be detected, when the lacinia mobilis is in its upright position parallel to the incisor (Figures 14(c) and 14(d)). The right incisor is stout and four toothed. The right lacinia mobilis is smaller than the left, and its articular condylus is poorly developed and visible only in posterior aspect. The right lacinia mobilis is distally notched, therefore divided into

two distal parts which are arranged parallel to the incisor (Figure 14(d)). The part adjacent to the incisor is slightly bent inwards; its distal edge consists of 3–5 small spines flanked by two somewhat longer lateral spines. The other part is longer and nearly straight; its edge consists of 4–6 spines which are homogeneous in size. The setae of the spine rows are directed mediodorsally *in situ* (Figure 14(b)). Each spine row directly starts at the molar with a group of short pappose setae, together building a tuft of fine hair-like setae. Towards the incisor, the setae of the spine row successively change from pappose to setulae on the entire shaft to spinelike with only few setulae on the distal end of their shafts. These setulae are located on the proximal side of the shaft facing the molar and are distally directed. All setae of the spine row are, at least their proximal part, flattened and therefore band shaped. This shape only allows deflexion of the setae in the plane between incisor and molar

FIGURE 6: SEM images of maxillipeds and paragnaths of *Gammarus fossarum*: (a) maxillipeds in posterior view; (b) maxillipeds in anterior view; (c) distal setation of endite of left basipod in anterior view (cf. eb in (b)); (d) median setation of endite of right ischium in posterior view (cf. ei in (a)); (e) paragnaths in posterior view; (f) paragnaths in anterior view.

(Figures 14(c) and 14(d)). The succession of setae is more distinct on the spine row of the right mandible. Here, some of the setae are stiletto shaped with very broad bases.

The anterior side of each molar bears a single gnathobasic seta pointing anteromedially into the oesophagus in the live animal (Figures 14(c) and 14(d)). The left molar area is kite shaped in median view, whereas the right is more ellipsoidal. The molar surface is slightly concave with parallel edges, which are arranged vertically to the gnathal edge (Figure 14(e)). These edges are probably built by laterally conjoined feathered setae with free setulae only on one side. Therefore, an alternating sequence of hard compact cuticular mass and flexible separate setulae together builds the rasplike structure of the surface of the molars (Figure 14(f)). On the surface of the right molar, these free setulae are directed proximally, those of the left molar distally. The short first portion of the mandibular palp, the basipod, is cylindrical and bears no setae. The mediolaterally compressed proximal portion of the endopod is about three times as long as the basipod. It is armed with a row of simple setae on the lateral side of its posterior margin. These setae are becoming longer

towards the distal end of this row. The distal portion of the palp is also medio-laterally compressed and has about two-thirds of the length of the second portion. Its tip is armed with a group of simple setae, the longest being nearly as long as the distal portion. The posterior margin of the distal portion bears a regular row of setae. These setae are adorned with medio-distally directed setulae on their distal halves. On the lateral and median surface of the distal portion of the palp, there is one, in some of the investigated specimens two, groups of up to five simple setae and a dense field of short hair-like setae near its posterodistal margin of the lateral surface (compare Figures 16(g) and 16(h)).

3.2. *Gammarus fossarum* Koch in Panzer, 1836 (Figure 1(b)). Antennulae (Figure 2(b)): almost half as long as body; second portion of peduncle about twice as long as distal portion, proximal portion nearly as long as second and third portion together; flagellum 29-partite; accessory flagellum consisting of 4 annuli; setation of flagellum and peduncle poorly developed.

FIGURE 7: SEM images of maxillipeds and paragnaths of *Echinogammarus berilloni*: (a) maxillipeds in posterior view *in situ*; (b) maxillipeds in anterior view; (c) distal setation of endite of left basipod in anterior view (cf. eb in (b)); (d) median setation of endite of right ischium in posterior view (cf. ei in (a)); (e) paragnaths in posterior view demonstrating also the position against labrum and mandibles *in situ*; (f) paragnaths in anterior view. Abbreviations other than in previous figures: lbr: labrum; md: mandible.

Antennae (Figure 2(e)): shorter than antennulae; gland-cone pointed, nearly reaching the distal end of peduncle segment 3; flagellum slender, consisting of 13 tubular annuli; each annulus with two transversely arranged groups of 2–5 simple setae on median and lateral side, respectively; one calceolus present on median side of each flagellar annulus 1–7 (Figure 2(h)).

Third uropods: endopod about half as long as exopod (Figure 3(c)); most of the setae on the median margin of both endopod and exopod plumose; lateral margin of exopod bears simple setae; here, if any, only scattered plumose setae (Figure 3(d)); lobes of telson only little longer than peduncles of third uropods (Figure 3(c)).

Gnathopods (Figures 4(d)–4(f)): propodus of first gnathopod (Figure 4(d)) very similar to that of *G. pulex*; dactylus not as strongly curved as in *G. pulex*, more than half as long as propodus; shape and setation of second gnathopod (Figures 4(e) and 4(f)) closely resemble those of *G. pulex*.

Maxillipeds (Figures 6(a)–6(d)): in shape and setation very similar to those in *G. pulex*.

Maxillae (Figure 9): very similar to those of *G. pulex*, differences exist in details of setation; setae of posterior row of inner plate with short scale-like setulae on two opposing sides (Figure 9(d)); some setae on distal margin of inner plates with broad rounded scale-like setulae all around their shafts.

Maxillulae (Figure 12): shape of inner and outer plate (Figures 12(a)–12(c)) very similar to those of *G. pulex*, but distinct differences in setation of distal margin of outer plates (Figures 12(a) and 12(e)); two to three setae on lateral end of the two rows medially bent, overhanging the other comb-like setae posteriorly (Figure 12(a)); these two setae distally flattened and broadened, like chisels with three humps on distal edge (Figure 12(e)). In some of the specimens investigated, clear signs of abrasion on these two and adjacent

FIGURE 8: SEM images of maxillae of *Gammarus pulex*: (a) maxillae *in situ* in posterior view; (b) maxillae in anterior view; (c) distal setation of outer plate of left maxilla in posterior view; (d) median setation of inner plate of left maxilla in posterior view. Abbreviations other than in previous figures: ipl: inner plate; mxl: maxillula; opl: outer plate; ste: sternite.

setae were found. The setae are abraded to more than half of their length (Figure 12(f)).

Paragnaths (Figures 6(e) and 6(f)): very similar to those in *G. pulex*; proximo-laterally cusps not as slender and pointed as in *G. pulex*; distal margins medially edged.

Mandibles (Figure 15): incisors and left lacinia mobilis slender in posterior aspect but broad in anteroposterior dimension; left incisor five-toothed; right incisor four-toothed; left lacinia mobilis four-toothed, with well-developed articular condylus; right lacinia mobilis distally notched, spines on the two edges longer and more pointed than in *G. pulex*; articular condylus on right lacinia mobilis short but stout (Figure 15(b)); spine row of right mandible (Figure 15(d)) with one or two stiletto-shaped setae without any setulae, other setae of spine rows like in *G. pulex*; molar surfaces rasp-like, with regularly arranged edges (Figures 15(e) and 15(f)); lateral surface of distal portion of mandibular palp with dense field of hair-like setae which extends as long as adjacent row of setae on posterior margin.

3.3. *Echinogammarus berilloni* (Catta, 1878) [37] (Figure 1(c)). Antennulae (Figure 2(c)): more than half as long as the body of the animal; proximal and second portion of peduncle about twice as long as distal portion; flagellum 38-partite, annuli of flagellum slightly flattened anteroposteriorly; accessory flagellum consisting of 5 annuli; setation of flagellum and peduncle poorly developed.

Antennae (Figure 2(f)): peduncle segments 4 and 5 slender and elongate; gland-cone short; flagellum (Figure 2(i)) 20-partite, flagellum distinctly anteroposteriorly flattened

and therefore broadened; setae on flagellum and peduncle short; calceoli absent.

Third uropods (Figures 3(e) and 3(f)): endopod very short compared to exopod (Figure 3(e)); exopod with groups of simple setae on median and lateral margin, those on median margin longer than laterally located ones (Figure 3(f)); distal portion of exopod short, about as long as terminal spines of proximal portion; lobes of telson compressed, little shorter than peduncle of third uropods (Figure 3(e)).

Gnathopods (Figures 4(g)–4(i)): propodus of first gnathopods (Figure 4(g)) slender; dactylus only slightly bent, with nearly straight median part; propodus of second gnathopods (Figures 4(h) and 4(i)) piriform; setae on carpus and propodus less numerous and shorter than on those of *G. pulex* and *G. fossarum*.

Maxillipeds (Figures 7(a)–7(d)): in shape and setation very similar to those of *G. pulex*.

Maxillae (Figure 10): very similar to those of *G. pulex* and *G. fossarum*; differences in details of setation; setae on lateral section of distal margin of inner plate correspond to those of outer plate with shafts flattened and equipped with closely arranged, triangular lobes on their distal third (Figure 10(c)); setae of median section of distal margin of inner plate with broad, rounded, scale-like setulae all around their shafts.

Maxillulae (Figure 13): inner plates (Figure 13(c)) more oblong than triangular; median margin of outer plates (Figure 13(a)) straight; basipodal endites not as strongly bent medially as in *G. pulex*, 10–11 setae on distal margin of outer plate (Figure 13(d)), lateral 4 of these setae with markedly

FIGURE 9: SEM images of maxillae of *Gammarus fossarum*: (a) maxillae *in situ* in posterior view; (b) maxillae in anterior view; (c) distal setation of outer plate of left maxilla in posterior view; (d) median setation of inner plate of left maxilla in posterior view; (e) distal setation of outer plate of left maxilla in posterior view; (f) median setation of inner plate of left maxilla in anterior view.

thickened shafts, distal end flattened and broadened, distal edge blunt with 2-3 humps; shafts of these 4 setae without secondary spines laterally; in some specimen, these setae display signs of abrasion (Figure 13(f)); setae of median part of distal row of setae on outer plate with up to 15 medio-posteriorly directed, pointed secondary spines (Figures 13(d) and 13(f)); the latter arranged nearly rectangular to shaft of setae and are longer than those in *G. pulex*; distal margin of left palp (Figure 13(e)) with 8 robust conical setae, flanked by a posterior row of 5 setae; these distally angled, with posterodistally directed setulae; distal margin of right palp (Figure 13(d)) with a row of 4-5 very robust triangular cuspidate setae; additionally on anterolateral end of row there is one conical seta and one seta which is distally provided with setulae.

Paragnaths (Figures 7(e) and 7(f)): more angular in shape; distal margins with hump; proximo-distally pointing cusps broader than in the two *Gammarus* species.

Mandibles (Figure 16): incisors and left lacinia mobilis very slender in posterior aspect; left incisor five-toothed; left lacinia mobilis four-toothed, with well-developed articular condylus (Figures 16(c) and 16(d)); right incisor four-toothed; right lacinia mobilis distally notched, both distal parts straight with pointed spines of different length; articular condylus on right lacinia mobilis well developed, its cavity on the base of the incisor small but well elaborated (Figures 16(b) and 16(e)); setae of spine rows (Figures 16(b) and 16(c)) comparable to those of *G. pulex*; molar surfaces (Figure 16(f)) rasp-like, with regularly arranged edges; distal portion of mandibular palp (Figures 16(g) and 16(h)) with 3 groups of up to 4 simple setae, distal half of posterior margin with a row of serrate setae, tip armed with group of long serrate setae; field of dense hair-like setae on lateral side of distal portion about half as long as row of setae on posterior margin; setae on posterior margin of second portion of palp also serrated.

FIGURE 10: SEM images of maxillae of *Echinogammarus berilloni*: (a) maxillae *in situ* in posterior view; (b) maxillae in anterior view; (c) distal setation of outer plate of left maxilla in posterior view; (d) median setation of inner plate of left maxilla in posterior view.

The main differences between the three species in morphology of mouthparts and other structures involved in food acquisition are listed in Table 1.

4. Discussion

Specialization on a certain kind of food such as carrion, sponges, algae, or periphyton is mainly known from marine amphipods. The mouthparts of these nutrition specialists exhibit morphological adaptation for collecting, handling, processing, and ingestion of this specific kind of food [52–60].

In context with the dramatic change of the nonmarine gammaridean fauna in central Europe, several investigations on the ecology of native and invasive species were performed. The results of these field and laboratory experiments changed our view on the feeding habit of non-marine gammarideans. It was demonstrated that these animals, formerly presumed to feed mainly on dead plant material and therefore assigned to the functional feeding group of shredders [43, 61, 62], are, in fact, able to use a much wider variety of food [63–72].

For the very successful invasive species *Dikerogammarus villosus*, the following feeding-related activities were identified: detritus feeding, coprophagy, grazing, particle feeding, predation on free-swimming animals, benthic animals, and fish eggs and feeding on byssus threads of zebra mussels (*Dreissena polymorpha* Pallas, 1771) [73]. However, morphological investigations demonstrated that also the mouthparts of several non-marine gammarideans possess morphological adaptations, which enable the animal to use a certain food resource in an especially effective manner [46, 74, 75].

Until now, detailed descriptions of mouthparts and other structures involved in food acquisition of non-marine gammarideans are scarce. In taxonomic descriptions, mouthparts have often been neglected, possibly because preparation is necessary. The structures are also often very small, and differences can only be found in details. This is likewise true for the descriptions of the three species investigated herein. The original taxonomic description of *Gammarus pulex* by Linnaeus [36] is so short that Sars [76] questioned whether Linnaeus had actually described specimens of *G. pulex*. Pinkster [49] redescribed *G. pulex*, but did not describe the mouthparts except for the mandibular palp. In their redescription of *G. pulex*, Karaman and Pinkster [51] described all mouthparts, but also this description lacks enough details to detect functional relevant differences between the mouthparts of the various species. The latter is also true for the work of Agrawal [77], who described and illustrated the feeding appendages and the digestive system of *G. pulex*. Lastly, the original descriptions as well as the redescriptions of *Gammarus fossarum* [35, 50, 51] and of *Echinogammarus berilloni* [14, 37] give comparably little information on details of the morphology of the mouthparts.

The mouthparts of specimens of the three species investigated herein are very similar, but nevertheless various fine-graded differences could be found between these species.

Gammarus pulex is the most widespread freshwater amphipod in mainland Europe as well as the most widespread and abundant freshwater amphipod in Britain [78, 79] and is regarded as one of the most important invertebrate species in chalk streams in terms of biomass and food for fish [80]. It predominantly occurs in middle

FIGURE 11: SEM images of maxillulae of *Gammarus pulex*: (a) maxillulae *in situ* in posterior view; (b) left maxillula in anterior view; (c) inner plates of maxillulae *in situ* in posterior view; (d) median setation of inner plate of left maxillula in medio-posterior view; (e) outer plate and palp of right maxillula in anteromedian view; (f) outer plate and palp of left maxillula in posterior view. Abbreviations other than in previous figures: md plp: palp of mandible; mxl plp: palp of maxillula.

TABLE 1: Main differences in morphology of mouthparts and other structures involved in food acquisition.

Structure	<i>Gammarus pulex</i>	<i>Gammarus fossarum</i>	<i>Echinogammarus berilloni</i>
Antennal flagellum	Annuli medio-laterally broadened; each with a row of 12 posteriorly directed setae together building a flag-like brush	Each annulus with a group of 2–5 simple setae on median and lateral side	Antero-posteriorly flattened and therefore broadened; setation sparse; setae short
Cuspidate setae on distal margin of basipodal endites of maxillula	Lateral setae with three finger-like secondary spines	2–3 lateral setae distally flattened and broadened like chisels with three humps on distal edge	4 lateral setae with thickened shafts, distally flattened; distal margin blunt with 2–3 humps
Setation of carpus and propodus of 2nd gnathopod	Long and closely arranged setae with curled distal ends	Long and closely arranged setae with curled distal ends	Less numerous and shorter setae than in <i>G. pulex</i> and <i>G. fossarum</i>
Third uropod	Endopod 3/4 as long as exopod; plumose setae on medial and lateral margins of endopod and exopod	Endopod half as long as exopod, plumose setae on median margin of endopod and exopod; simple setae on lateral margin of exopod	Endopod very short; only simple setae on lateral and median margin of exopod

FIGURE 12: SEM images of maxillulae of *Gammarus fossarum*: (a) maxillulae *in situ* in posterior view; (b) left maxillula in anterior view; (c) inner plates of maxillulae *in situ* in posterior view; (d) median setation of inner plate of left maxillula in posterior view; (e) distal setation of outer plate of left maxillula in posterior view; (f) distal setation of outer plate of right maxillula in posterior view. Arrows indicate signs of abrasion.

and lower reaches of streams and rivers, lowland lakes, ponds, and brooks [51]. In some publications, the limit of distribution is stated to be at about 450 m altitude [41, 81, 82], but when competing species are absent, it can be found in all sections of the waters [51]. Dusauguey [83] and Goedmakers [84] have found the species at 1340 and 1200 m, respectively. In Ireland, *G. pulex* is an invasive species where it replaces the native *G. duebeni* Liljeborg, 1852 in rocky parts of lakes, rivers, and along canals [78] and has a great impact on native macroinvertebrate community composition [85]. Microdistribution of *G. pulex* seems to be size assortative, with large animals being associated with large substrate particles like pieces of wood or accumulated fallen leaves and macrophytes [10, 77, 86, 87]. In running waters, *G. pulex* prefers sections with lower velocity [88, 89]. According to Piscart et al. [24], its preferred substratum is vegetation and leaf litter.

Agrawal [77] investigated gut contents and concluded that *G. pulex* mainly feeds on algal filaments and other

vegetable matter. Also laboratory experiments indicate that plant material is an important food source, because specimens of *G. pulex* also shredded leaf material in the presence of animal prey [67]. Graca et al. [90, 91] reported that *G. pulex* feeds preferentially on conditioned rather than on unconditioned leaf material, although no significant effect of conditioning on growth was observed. Also Welton and Clarke [92] observed feeding on both decaying leaves and fresh green leaves. Investigations on the enzymes of the midgut glands yielded that *G. pulex* produces both cellulose and phenol oxidase by itself and is therefore adapted to digest plant material [93]. However, laboratory experiments show that *G. pulex* is also an effective predator on *Asellus aquaticus* Linnaeus, 1758 [94], Copepoda [95], mayfly nymphs [67], larvae of Chironomidae, Simuliidae, Ephemeroptera [68], Enchytraeidae [96], and on *Tubifex* sp. [68]. Moreover, experiments on intraguild predation demonstrated that *G. pulex* also preys on other gammarideans such as *G. tigrinus* Sexton 1939, *G. duebeni* Liljeborg, 1852, and *Crangonyx*

FIGURE 13: SEM images of maxillulae of *Echinogammarus berilloni*: (a) maxillulae *in situ* in posterior view; (b) maxillulae in anterior view; (c) inner plates of maxillulae *in situ* in posterior view; (d) distal setation of outer plates and palps of maxillulae in anterior view; (e) distal part of palp of left maxillula in medio-posterior view; (f) distal setation of outer plate of right maxillula in posterior view. Arrows indicate signs of abrasion.

pseudogracilis Bousfield, 1958 [27, 97]. Also analyses of stable C and N isotopes highlighted that *G. pulex* is able to feed on a broad spectrum of food sources [24].

The results of our investigation on the morphology of the mouthparts and other structures involved in food acquisition correspond with findings of the investigations mentioned above.

The antennae of *Gammarus pulex* with their rows of long and posteriorly directed setae on each medio-laterally broadened annulus of the flagellum forming a flag-like brush (Figures 2(d) and 2(g)) are well suited to collect fine particular detritus and to sieve particles out of the respiratory water current. In addition, these setae can help to create a water current for capturing free-swimming organisms when the antennae are bent towards the ventral side of the cephalothorax in a sudden movement. Such a mode of catching free-swimming organisms has been described by Platvoet et al. [73] for the pontogammarid *D. villosus*. The

antennal flagellae of this species have similar setation [74]. The endopods of the foliaceous third uropods of *G. pulex* are relatively long (Figure 3(a)). Both endopod and exopod bear plumose setae on their median and lateral margins building a broad fan (Figure 3(b)). Therefore, the third uropods are also well suited to sieve particles out of the respiratory water current and it seems possible that they are used for guiding faeces anterior toward the gnathopods (coprophagy). The closely arranged long setae of the second gnathopods with their curled distal ends (Figures 4(b) and 4(c)) together are again a structure which is suited for sieving particles out of the respiratory water current. They can also be used for cleaning the antennae and for sweeping periphyton from the substratum. Furthermore, the two opposing gnathopods with their ventromedially directed setae build a space in which food particles and organisms can be held captive and guided to the mouthparts. The maxillipeds (Figures 5(a)–5(d)) with their medially directed setae and the two claw-like

FIGURE 14: SEM images of mandibles of *Gammarus pulex*: (a) ventral view of head with exposed mandibles; maxillulae, maxillae, maxillipeds, and gnathopods removed; (b) coxa of mandibles *in situ* in posterior view; (c) coxa of left mandible in anterior view; (d) coxa of right mandible in anterior view; (e) molar of right mandible in median view; rectangle indicates close-up image in (f); (f) closeup of molar surface of right mandible in median view (cf. (e)). Abbreviations other than in previous figures: ant: antenna; gbs: gnathobasic seta; gnp1: first gnathopod; ip: incisor process; lm: lacinia mobilis; mp: molar process; sr: setal row.

setae on the distal end of the endites seem to be useful for combing out particles from the setae of the gnathopods and antennae and for transferring them to the mandibles.

The basipodal endites of the maxillae (Figures 8(a)–8(d)) with their medially directed plumose setae build a dense net for preventing food from being washed away from the mouth region and for concentrating food. The coxal endites of the maxillulae with their medially directed pappose setae (Figure 11(c)) may have the same function. The comb-like cuspidate setae on the distal margin of the basipodal endites of the maxillulae (Figures 11(e) and 11(f)) seem to be well suited for combing out particles from the setae of the antennae and gnathopods. The use of these setae for detaching periphyton from the substrate might be possible, but there are no specializations for this purpose as it could be shown for *G. roeselii* [46], and on those specimens we investigated, we did not find distinct signs of abrasion. Left and right incisors and the left lacinia of

the mandibles (Figures 14(a)–14(d)) of *G. pulex* are broad and well developed and therefore seem to be well suited for cutting off pieces of bigger food items. The rasp-like surface of the molars (Figures 14(e) and 14(f)) seems to be well suited for grinding hard plant material, although these parallel edges are not as well developed as in *G. roeselii* [46].

Gammarus fossarum is widely distributed in central Europe, the Balkan Peninsula, and Asia minor [45, 51]. It inhabits springs, brooks, and upper reaches of smaller rivers with low content of nutrients and low conductivity [44, 81, 98, 99]. It tolerates and prefers low temperature and high currents [45, 82, 100–104]. In gut contents of *G. fossarum*, Helesic et al. [105] found filamentous algae and cyanobacteria, parts of leaves, moss, plankton organisms, and macroinvertebrates living in periphyton. If no other food is available, *G. fossarum* also feeds on fresh leaves [43]. However, in laboratory experiments, growth was best with decaying leaves of lime and elm, whereas growth and survival

FIGURE 15: SEM images of mandibles of *Gammarus fossarum*: (a) incisor processes, lacinia mobiles, and setal rows of mandibles *in situ* in posterior view; (b) incisor processes and lacinia mobiles of mandibles *in situ* in posterodorsal view; (c) coxa of left mandible in anterior view; (d) coxa of right mandible in anterior view; (e) molar of right mandible in medioanterior view, rectangle indicates close-up image in (f); (f) closeup of molar surface of right mandible in median view (cf. (e)). Abbreviations other than in previous figures: ac, articular condylus.

rate was significantly lower with fresh macrophytes and algae [106]. Pieper [107] observed that adult specimens mainly feed on dead leaves. In their natural habitats, specimens of *G. fossarum* were most abundant in accumulations of leave litter and other dead plant material [43, 108, 109]. Gut content analyses performed by Felten et al. [72] showed that the investigated individuals of *G. fossarum* fed on detritus, diatoms, filamentous algae, leaf litter, woody debris, and animal matter.

The setation of the slender antennal flagellum (Figures 2(e) and 2(h)) of *G. fossarum* is sparse and therefore not as effective for sieving particles out of the respiratory water current and for catching free-swimming organisms as in *G. pulex*. The endopods of the third uropods (Figure 3(c)) are not as long as those in *G. pulex*, and there are plumose setae only on the median margin of the exopods (Figure 3(d)). Therefore, the third uropods of *G. fossarum* seem to be not as well suited for sieving particles out of the respiratory water current as those of *G. pulex*.

Coprophagy in the same manner as in *G. pulex* seems also to be possible in *G. fossarum*. The long and closely arranged distally curved setae of the second gnathopods (Figures 4(e) and 4(f)) closely resemble those in *G. pulex*. Therefore, the second gnathopods of *G. fossarum* are also suited for cleaning the antennae and for sweeping periphyton from the substratum. Maxillipeds (Figures 6(a)–6(d)) and maxillae (Figures 9(a)–9(f)) of *G. fossarum* are very similar to those in *G. pulex*, so we expect no functional differences. In contrast, clear differences can be observed in the setation of the maxillulae (Figures 12(a)–12(f)). The lateral two or three setae of the row of setae on the distal margin of the basipodal endopods are distally flattened like chisels overhanging the other comb-like setae posteriorly (Figure 12(e)). With these setae, the maxillulae seem to be well suited for scraping off periphyton from the substratum. Signs of abrasion on these setae support this conclusion (Figure 12(f)). In contrast, Felten et al. [72] calculated from their results of gut content analyses that the investigated *G. fossarum* population

FIGURE 16: SEM images of mandibles of *Echinogammarus berilloni*: (a) left mandible in median view; (b) incisor process, lacinia mobilis, and setal row of right mandible in posterior view; (c) incisor process, lacinia mobilis, and setal row of left mandible in posterior view; (d) coxa of left mandible in anterior view; (e) coxa of right mandible in anterior view; (f) molar of left mandible in median view; (g) distal portion of left mandibular palp in median view; (h) distal portion of left mandibular palp in lateral view.

could be considered as 48% collector, 43% shredder, 8.3% predator, and only 1.3% scraper. The reason for the marginal importance of scraping in the investigated population might be the abundant supply of leave litter and bryophytes in this particular stream. In waters with less availability of these food resources, as is often the case in headwaters, scraping might play a more important role in the nutrition of *G. fossarum*. Furthermore, a point to be taken into account is that *G. fossarum* can live in the hyporheic interstitial where biofilm represents a very important portion of food available. This might be important especially in winter when water level and temperature is low. The mandibles (Figures 15(a)–15(f)) of *G. fossarum* are similar to those of *G. pulex* and seem also to be well suited for cutting off pieces of bigger food items and to grind hard plant material.

Catta [37] described *Echinogammarus berilloni* from a spring of a brook on the Mandarin mount, Atlantic Pyrenean mountains. This species originates from the Atlantic region of France and the north-western part of Spain [14, 16] and

extended its area of distribution to the middle and lower reaches of larger streams, channels, and rivers of the north of France [10], the Channel Islands [110], Luxembourg, Belgium, the southern part of the Netherlands [13], and local populations exist in Germany [5, 14]. Kley and Maier [30] found specimens associated with near-shore submersed macrophytes in a tributary of the river Rhine. According to Piscart et al. [10, 24], *E. berilloni* shows strong preference for vegetation and leaf litter as substratum when existing in single-species populations, but there is a shift to a more diverse use of substrates including pebbles when it coexists with *G. pulex*. *E. berilloni* is salt tolerant and eurythermous and can withstand a high amount of organic pollution [2, 39]. Since the invasion of *Dikerogammarus villosus*, there has been a dramatic reduction of the relative abundance of *E. berilloni* [6].

In *Echinogammarus berilloni*, the antennae with their sparse and short setation (Figures 2(f) and 2(i)) are not suited for sieving particles out of the respiratory water

current and for catching free-swimming organisms. However, with their anteroventrally flattened and mediolaterally broadened flagellum, the antennae might be dedicated to collect food particles and move them into the reaching area of the gnathopods. Also the morphology of the third uropods indicates that sieving does not play a great role in the nutrition of *E. berilloni*, because their endopods are very short (Figure 3(e)), and there are only simple setae on the median and lateral margins of the exopods (Figure 3(f)). Also the setae on the second gnathopods (Figures 4(h) and 4(i)) are sparser and shorter, and therefore they seem to be less suitable for sieving and for sweeping periphyton from the substratum. Such constraints in the ability to use these food resources correlates with findings of Piscart et al.: "... their isotopic signatures highlighted a broader spectrum of food sources and a broader diversity of carbon sources assimilated by *G. pulex* than by *E. berilloni*" [24].

Maxillipeds (Figures 7(a)–7(d)) and maxillae (Figures 10(a)–10(d)) of *E. berilloni* are very similar to those of *G. pulex* and *G. fossarum* so we expect no functional differences. Again, there are differences in the morphology of the setae on the distal margin of the basipodal endites of the maxillulae. In *E. berilloni*, the lateral four of these setae are stout and do not bear lateral secondary spines, but end in a broadened distal margin with two or three humps (Figures 13(e) and 13(f)). Also here we found signs of abrasion, so it is likely that these setae are used to scrape off periphyton from the substratum. This adaptation of setae on the basipodal endite of the maxillulae with no lateral secondary spines and a broadened distal margin is comparable with the situation in *G. roeselii* [46]. However, in the latter, the distal margin of these setae is sharper, and therefore the adaptation to scraping seems to be even more effective as in *E. berilloni*. The mandibles (Figure 16(a)–16(f)) of *E. berilloni* are similar to those of *G. pulex* and *G. fossarum*. Therefore, they likewise seem to be well suited for cutting off pieces of bigger food items and to grind hard plant material.

5. Conclusions

The morphology of the mouthparts and structures involved in food acquisition indicate that *Gammarus pulex* is able to feed on a wide variety of food sources including sieving suspended organic particles out of the respiratory water current, coprophagy, collecting detritus, catching free-swimming organisms, removing periphyton from the substratum, biting off pieces from bigger food items, and grinding hard plant material. Therefore, this species can be characterized as omnivorous. Compared to *G. pulex*, in *G. fossarum* the structures investigated here indicate that these two species have very similar feeding habits. However, the setation of the maxillulae of *G. fossarum* and the severe abrasion of these structures indicate that feeding on periphyton removed from hard substratum plays a greater role in the nutrition of the latter. This coincides with the finding that *G. fossarum* typically inhabits the upper reaches of brooks and rivers, where periphyton on hard substratum is the most relevant food resource. The results of our work suggest that the ability to sieve particles out of the respiratory

water current and to catch free-swimming organisms is limited in *Echinogammarus berilloni*. This species seems to be adapted to collect food items with the antennae and to remove periphyton from the substratum with the maxillulae. Therefore, the ability to use different food sources seems to be restricted in *E. berilloni* compared to *G. pulex*.

Arndt et al. [60] hypothesised that "mouthpart morphology differs little between related amphipod species, but greater changes are encountered in the morphology of accessory feeding appendages as a consequence of trophic specialization." This is generally also true for the species investigated here, but we also found differences in the morphology of the maxillulae. These findings correspond with the situation in *Gammarus roeselii* and *Dikerogammarus villosus* where we, in an earlier study, also found differences in the morphology of the antennae, gnathopods, maxillipeds, maxillulae, and mandibles [46, 74].

Abbreviations

1, 2, 3, 4, 5:	Number of podomeres of antennulae and antennae
ac:	Articular condylus
af:	Accessory flagellum of antennula
ant:	Antenna
bas:	Basipod
cal:	Calceolus
cox:	Coxa
eb:	Endite of basipod
ei:	Endite of ischium
f:	Flagellum of antennula and antenna
gc:	Gland conus
gnp1:	First gnathopod
ip:	Incisor process
ipl:	Inner plate
lbr:	Labrum
lm:	Lacinia mobilis
md:	Mandible
md plp:	Mandibular palp
mp:	Molar process
mxl:	Maxillula
mxl plp:	Maxillular palp
mxp:	Maxilliped
opl:	Outer plate
sr:	Setal row
ste:	Sternite.

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