35

Coexisting native and non-indigenous gammarideans in Lake Constance – Comparative morphology of mouthparts

(Crustacea, Amphipoda, Gammaridea)

Gerd Mayer, Andreas Maas & Dieter Waloszek

Mayer, G., Maas, A. & Waloszek, D. 2012. Coexisting native and non-indigenous gammarideans in Lake Constance – Comparative morphology of mouthparts (Crustacea, Amphipoda, Gammaridea). Spixiana 35(2): 269–285.

Over the past two decades the amphipod communities of German inland waters have changed dramatically. The Ponto-Caspian gammaridean Dikerogammarus villosus has severely impacted the biocoenosis of the concerned waters in a wide area of western and central Europe, by decreasing or even eliminating populations of native or earlier established gammarideans. In 2002 this invasive species was also recorded in Lake Constance, a prealpine lake in Germany, Austria and Switzerland. Within five years it has spread almost throughout the littoral zone of the entire lake, where it is now the dominant gammaridean species on hard substrates. However, in Lake Constance the coexistence between this so-called "killer-shrimp" and the native *Gammarus lacustris*, and the earlier established *G. roeselii* seems to be possible. Furthermore, a local population of another amphipod, Crangonyx pseudogracilis, has existed in Lake Constance since 2007 despite the presence of D. villosus. In our SEM study of the structures involved in food acquisition of the gammarideans inhabiting Lake Constance we discovered morphological differences that seem to enable these animals to feed on different kinds of food. D. villosus, despite its ecological impact, is not a specialized predator, but an opportunistic omnivore. The mouthparts of G. lacustris possess specializations for retaining very small food particles and those of G. roeselii for scraping periphyton off the substrates. By contrast, C. pseudogracilis seems to be specialized to feed on detritus and carrion. These different abilities to utilize food resources, as determined by morphology, may be a reason for the coexistence of the four gammaridean species in Lake Constance.

Gerd Mayer (corresponding author), Andreas Maas & Dieter Waloszek, Workgroup Biosystematic Documentation, University of Ulm, Helmholtzstr. 20, 89081 Ulm, Germany; e-mail: gerd.mayer@uni-ulm.de

Introduction

Since the opening of the Main-Danube canal in 1992 there is a continuous navigable connection between the Black Sea and the North Sea via the Rivers Danube, Main, and Rhine. Using ships as vectors or migrating actively, a great number of non-native aquatic species, especially from the Ponto-Caspian region, came through this waterway to these rivers and their tributaries (Tittizer 1996, 1997). Some Ponto-Caspian amphipod species were able to establish stable populations. Among these *Dikerogammarus villosus* Sowinsky, 1894 (Gammaridea, Pontogammaridae) was particularly successful. Known in the Austrian part of the Danube since 1989, this species was recorded for the first time in Germany in 1992 (Nesemann et al. 1995). In 1994 *D. villosus* reached the Rhine (Bij de Vaate & Klink 1995) and within a few years it spread into its tributaries in France, the Netherlands and Northern Germany (e.g. Devin 2001, Nehring 2003, Bollache et al. 2004, Mayer 2008). In 2010 it was recorded for the first time in waters of the British Islands (MacNeil et al. 2010). Furthermore, D. villosus was also found in isolated waters such as Lake Geneva in Switzerland (Bollache 2004) and Lake Garda in Italy (Casellato et al. 2006). D. villosus is very successful in many waters outside its native distribution area and often had, and still has, severe effects on the biocoenosis of the concerned waters. It spreads fast, occurs in high densities, and diminishes other macrozoobenthos organisms including other gammarideans, both native and earlier established species. D. villosus is now the dominant or only gammaridean species in many sections of the concerned waters (e.g. Dick & Platvoet 2000, Kley & Maier 2003, 2006, Devin et al. 2004, Pöckl 2007). Results from field observations and laboratory experiments suggest that D. villosus is a specialized predator, because, in comparison to related species, it captures more macrozoobenthos organisms and is superior in direct competition with related species (e.g. Dick et al. 1990, Dick et al. 1993, 1999, 2002, Kinzler & Maier 2003, Krisp & Maier 2005). As a result, this invasive species was even named the "killer-shrimp".

In Lake Constance, an oligotrophic pre-alpine lake with a surface area of about 536 km² in the triborder region of Germany, Austria and Switzerland, D. villosus was recorded for the first time in 2002 (Mürle et al. 2004, Rey et al. 2005). Within only a few years it spread through the littoral zone of nearly the entire lake and is now the dominant gammaridean species on hard substrates. However, in contrast to most other waters invaded by D. villosus (see above), in Lake Constance the coexistence of D. villosus with the native Gammarus lacustris Sars, 1863 and the earlier established G. roeselii Gervais, 1835 seems to be possible. Additionally, a local population of another non-native amphipod species, Crangonyx pseudogracilis Bousfield, 1958 (Crangonyctidae) was recorded in 2007 near the town of Hard in the Austrian part of Lake Constance (Hanselmann & Gergs 2008).

Dikerogammarus villosus is the largest of the four gammarideans inhabiting Lake Constance. In German waters males and females can reach a body length of up to 22 mm and 18 mm respectively (Kley & Maier 2003, Devin et al. 2004). Originally it was widely distributed in the lower reaches of large rivers of the Ponto-Caspian region. In the Netherlands Wijnhoven et al. (2003) found *D. villosus* in rivers, canals and lakes but not in brooks or trenches. *D. villosus* prefers hard substrates like gravel and boulders and avoids sandy or muddy substrates (e.g. Nesemann et al. 1995, Devin et al. 2003, Kley et al. 2009, Boets et al. 2010, Tricarico et al. 2010).

For Lake Constance, Hartmann (1977) was the

first to mention Gammarus roeselii in a publication on fish food. For his work Hartmann examined gut content of fishes sampled in 1974 and 1975. It is likely that this species arrived some years earlier, because it was already a considerable portion of the gut content of the fishes examined. The original distribution area of G. roeselii is Asia Minor, the Peloponnesos, the western Balkan Peninsula, the Hungarian Plain and the Danubian valley. G. roeselii was first described by Gervais (1835) from the vicinity of Paris and its spread from southeastern Europe westward is still ongoing. In middle Europe it is now well established and is the typical gammarid of large and medium sized lowland rivers with low current velocity and large lakes, but in France it is still increasing its range of distribution (e.g. Karaman & Pinkster 1977, Jazdzewski 1980, Jazdzewski & Roux 1988, Meijering 1991, Nesemann et al. 1995, Bollache et al. 2006). G. roeselii appears to show little preference for a particular substrate. In enclosure experiments there was little difference in preference for stones, leaf litter, stonewort and stones colonised by Dreissena polymorpha Pallas, 1771, and even sandy habitats were occupied (Hesselschwerdt et al. 2008). However, Kaldonski et al. (2008) reported that G. roeselii often hides in submersed vegetation and also in the Danube, where the specimens for this work were collected, G. roeselii was found mainly between the submersed macrophytes near the shoreline, but only a few could be found on stony substrates. In laboratory experiments G. roeselii clearly preferred aquatic weeds as substrate compared to stones and gravel (Kley et al. 2009).

Gammarus lacustris is widely distributed in Scandinavia, alpine regions of Asia, Russia, and northern America. In central Europe it is found in Poland, Austria, northern Italy, and Ireland. In Germany it only inhabits some Lakes in northern Germany and Lake Constance (Schellenberg 1934, Vornatscher 1969, Pinkster 1972, Karaman & Pinkster 1977). G. lacustris inhabits oligotrophic or mesotrophic stagnant waters where it can survive in low temperatures for a long time but it cannot stand water temperatures higher than 20 °C, therefore, it is mostly restricted to mountain or glacier lakes (Karaman & Pinkster 1977). It prefers waters with a high amount of organic sediment and a diverse and abundant macroflora (Karaman & Pinkster 1977, Costello 1993). According to Hargeby (1990) G. lacustris typically occurs in waters with stable conditions, where it can be found mainly in submersed vegetation, which does not die back in winter. The preferred water depth of adult G. lacustris is about 3-6 meters, whereas juveniles inhabit the vegetation of the littoral zone down to 1.5 meters (Yemelyanova et al. 2002, Mirzajani et al. 2011).

Crangonyx pseudogracilis is the smallest of the gammarideans inhabiting Lake Constance, its maximum length there is 10.5 mm (Hanselmann & Gergs 2008). It is originally a North American species, but has been known in Britain since 1936 and was first recorded in central Europe in 1979, in Dutch tributaries of the Rhine (Garland 1981, Costello 1993, Pinkster et al. 1980). In Lake Constance it was recorded for the first time in 2007 (Hanselmann & Gergs 2008). C. pseudogracilis prefers littoral habitats with soft sediments and rich submersed vegetation or reeds. Stony substrates are only inhabited if there are roots between the stones (Garland 1981). MacNeil (2001) found few C. pseudogracilis on gravel and sand, but found that they occurred in high densities on silt and mud. In northern Germany C. pseudogracilis was found in ditches, and southern Germany in pools and oxbow lakes of the floodplain of the river Rhine (Martens & Grabow 2006, Gerdes & Eggers 2007).

Our aim was to look for the reason behind the coexistence of the four gammaridean species in Lake Constance, besides spatial segregation due to different substrate preferences. In our earlier works (Mayer et al. 2008, 2009) we described the general morphology of the mouthparts and other structures involved in food acquisition of gammarideans. Subsequently, we documented differences in the morphology of the mouthparts of non-marine gammarideans, which indicate that these specializations enable the species to use different types of food (Mayer et al. 2009, 2012). In addition here we describe and illustrate the main differences between the parts of the bodies of the four species, which are supposed to be modifications for a special mode of food acquisition, in order to test our working hypothesis that different food preferences led to the coexistence.

Material and methods

Specimens of Gammarus roeselii were obtained from a branch of the Danube near Donaurieden, Ulm, Germany in December 2007. Specimens of the other three species were obtained from Lake Constance. Specimens of Crangonyx pseudogracilis were sampled in May 2010 at Grüner Damm near Hard, Austria, about 5 meters from the shoreline by kick-sampling on gravel in water of about 50 cm in depth. Specimens of Dikerogammarus villosus were collected in July 2010 from boulders of the shoreline stabilization near Langenargen, Germany and those of Gammarus lacustris were sampled in August 2011 by scuba diving from a depth of 2-5 meters near Allensbach, Germany. All specimens were fixed in 70 % ethanol. For determination of species, the taxonomic key of Eggers & Martens (2001, 2004) was used. For SEM studies about 20 fixed males of each species were dissected using watchmaker forceps under a stereomicroscope. For removing debris, the bodies parts obtained were stored in a dilute aqueous solution of a detergent for dental prostheses for five minutes at room temperature and treated for 30 seconds in an ultrasonic cleaner. Afterwards, the specimens were washed in demineralised water, dehydrated in an alcohol series, critical-point dried, and sputter-coated with a gold-palladium mixture. SEM work was performed with a Zeiss DSM 962 Scanning Electron Microscope. Digital images obtained from the SEM were trimmed in Adobe PhotoshopTM and arranged in plates using Adobe IllustratorTM.

Results

Gammarus lacustris

Antennae (Fig. 1A): Setation of flagellum sparse and short; flagellum consists of 12–14 annuli; annuli 1–10 slightly antero-posteriorly compressed; each portion bears one calceolus, an antennal receptor of gammaridean Amphipoda, on its median side and 4 groups of 3–4 simple setae, these are about half as long or as long as a flagellar annulus.

Mandibles (Fig. 2A,E): Right incisor process stout and 4-toothed. Right lacinia mobilis distally notched with two rows of irregularly arranged pointed and distally directed spines; articular condylus well developed. Distal half of setal row consists of densely set long and strong setae with bases broadened in anterior-posterior dimension; they bear setulae only on their distal end. Setae of setal row near molar process are densely set and pappose (= with setulae randomly arranged along the shaft of the seta) with cylindrical shafts. Molar processes are well developed; surface, in median view, ellipsoidal, with regularly arranged parallel ridges. Mandibular palp well developed; distal margin of its distal portion bears a straight row of densely set serrate setae. Left incisor process stout and five-toothed. Left lacinia mobilis blade-like, nearly as long as incisor process, broad and four-toothed. Articular condylus well developed. Setal row next to the lacinia mobilis consists of an alternating sequence of stiletto-shaped setae with very broad and flattened bases and pappose setae. Setae of setal row next to the molar process are shorter, pappose, with bases round in cross section. Surface of left molar triangular in median view, with parallel ridges.

Maxillulae: Inner plate (= coxal endite) (Fig. 3A) elongated, broad and remarkably flat in posterior view; median margin nearly straight, bearing a row of extremely densely set (about 22) medio-distally projected pappose setae with plenty of very thin and long setulae. Distal margin of outer plate (= basipodal endite) (Fig. 4A) bears 11 medio-distally directed cuspidate setae in two rows; each of these spine-like



Fig. 1. SEM images of antennae. A. Gammarus lacustris; B. G. roeselii; C. Dikerogammarus villosus; D. Crangonyx pseudogracilis.



Fig. 2. SEM images of surface of right mandibular molar in median view with signs of abrasion (left = distal) (A–D) and incisor process, lacinia mobilis, and setal row of left mandible in anterior view (E–H). **A,E.** *Gammarus lacustris;* **B,F.** *G. roeselii;* **C,G.** *Dikerogammarus villosus;* **D,H.** *Crangonyx pseudogracilis.* Abbreviations: **gbs**, gnathobasic seta; **ip**, incisor process; **Im**, lacinia mobilis; **sr**, setal row.

setae with a row of up to 11 medio-distally directed secondary spines. The number of secondary spines decreases from median to lateral, but the diameter of spines and secondary spines increases; therefore, setae on median part of distal margin look like coarse combs, but lateral four setae are distally flattened and laterally toothed. Maxillae (Fig. 4E): Inner plate with two rows of medially directed setae; one row direct along margin; setae here serrate. Second row on anterior side of inner plate near median margin; about 30 plumose (= with setulae in two opposing rows on the shaft of the seta) setae, medially directed, about as long as medio-lateral dimension of inner plate; setulae thin, long and very densely set, creating a dense net.



Fig. 3. SEM images of coxal endites (= inner plates) of maxillulae in situ in posterior view. **A.** *Gammarus lacustris*; **B.** *G. roeselii*; **C.** *Dikerogammarus villosus*; **D.** *Crangonyx pseudogracilis*. Abbreviations other than in previous figures: ipl, inner plate; opl, outer plate.

Maxillipeds (Fig. 5A,E): Basipodal endite slender, reaching about two-thirds of the carpus; distal margin bears a row of 6 cuspidate setae accompanied by a row of stout pappose setae with short serrate setulae. Endite of ischium well developed, reaching the mandibular incisor processes in its natural position; median margin bears a row of flattened cuspidate setae accompanied posteriorly by a row of distally flattened setae (Fig. 5E). Carpus bears postero-medially directed simple setae on its posteromedian surface.

There are only minor differences in the morphology of the first pair of gnathopods in the four species. Therefore, the first gnathopods are not described or illustrated here.

Second gnathopods (Fig. 6A): Carpus and propodus bear transverse rows of densely set serrate setae on their postero-median margins.

Third uropods (Fig. 7A): Endopod and exopod long and antero-posteriorly flattened. Endopod is three quarters the length of the exopod. Setae on medial and lateral margins of exopod and endopod plumose, building a broad fan-like net.

Gammarus roeselii

Antennae (Fig. 1B): Setation on distal two portions of peduncle and on flagellum more developed than in *G. lacustris;* simple setae in transverse rows; longer on postero-median side of antennae; no calceoli.

Mandible (Fig. 2B,F): Molar processes well developed; surfaces with distinct parallel ridges. Right incisor process four-toothed, slender. Right lacinia mobilis distally transversely notched, therefore, two distal margins with irregularly arranged distally pointing spines; base broad. Left incisor process fivetoothed, flat. Left lacinia mobilis four-toothed, flat. Setae of setal rows of both left and right mandible similar; setae next to lacinia mobilis with broadened plane shafts and setulae only on the side of the shaft facing the molar process; delicate pappose setae near molar process.

Maxillulae (Fig. 3B, 4B): Inner plate with a row of densely set pappose setae on median margin. Cuspidate setae on distal margin of outer plate dimorphic, setae on median part of row comb-like, those of lateral part of row distally flattened and



Fig. 4. SEM images of distal setation of basipodal endite (= outer plate) of left maxillula in posterior view (A-D) and right maxilla in anterior view (E-F). A, E. Gammarus lacustris; B, F. G. roeselii; C, G. Dikerogammarus villosus; D, H. Crangonyx pseudogracilis.

broadened like chisels (Fig. 4B).

Maxillae (Fig. 4F): Setation of median margin of inner plate very similar to that of *G. lacustris*, but anterior row consists of only about 20 plumose setae.

Maxillipeds (Fig. 5B,F): Median margins of endites of ischia recessed on their distal halves; posterior side of median margin of these endites bears a row of hook-shaped medio-distally directed cuspidate setae (Fig. 5F). Second gnathopods (Fig. 6B): Carpus and propodus bear transverse rows of simple and serrate setae on their postero-median margins.

Third uropods (Fig. 7B): Endopod and exopod long and antero-posteriorly flattened; endopod nearly reaches distal end of proximal portion of the exopod; plumose setae on medial and lateral margins of endopod and exopod, creating a broad fan-like net.



Fig. 5. SEM images of maxillipeds (= 1st thoracopods) in posterior view (A–D) and median setation of endopod of right ischium in posterior view (E–H). **A**, **E**. *Gammarus lacustris;* **B**, **F**. *G. roeselii;* **C**, **G**. *Dikerogammarus villosus;* **D**, **H**. *Crangonyx pseudogracilis.* Abbreviations other than in previous figures: **1**, ischium; **2**, merus; **3**, carpus; **4**, propodus; **5**, dactylus; **bas**, basipod; **cox**, coxa; **eb**, endite of basipod; **ei**, endite of ischium.

Dikerogammarus villosus

Antennae (Fig. 1C): Setation of peduncle sparse; annuli of flagellum with densely set groups of long simple setae on their posterior side, together creating a brush-like structure; no calceoli.

Mandibles (Fig. 2C,G): Incisor processes stout, left lacinia mobilis with well-developed articular condylus. Setal rows consist of several long pappose setae and few stiletto-shaped setae. Molar processes well developed; surfaces only little structured, without ridges.

Maxillulae (Fig. 3C, 4C): Inner plate with a row of 12–14 long pappose setae on median margin. Distal margin of outer plate with 9–11 spine-like cuspidate setae; secondary spines of these setae irregularly arranged and directed medio-posteriorly; setae on lateral end of row distally not flattened.

Maxillae (Fig. 4G): Inner plate with a row of serrate setae on median margin; another row of 13



Fig. 6. SEM images of right second gnathopod (= 3rd thoracopod) in anterior view. **A.** *Gammarus lacustris;* **B.** *G. roeselii;* **C.** *Dikerogammarus villosus;* **D.** *Crangonyx pseudogracilis.*

medially directed plumose setae begins proximally near median margin and curves distally onto the anterior face of the inner plate.

Maxillipeds (Fig. 5C,G): Median margin of endite of ischium straight; posterior side of median margin of this endite bears a row of medially directed cuspidate setae accompanied by two rows of distally flattened simple setae.

Second gnathopods (Fig. 6C): Merus with a row of medially directed long simple setae; carpus with long densely set setae, arranged in tufts, together creating a brush which is directed medio-ventrally in natural position of the gnathopods.

Third uropods (Fig. 7C): Endopod very short; exopod antero-posteriorly flattened, with densely set plumose setae on median and lateral margins; exopods of left and right third uropod together create a fan-like net.

Crangonyx pseudogracilis

Antennae (Fig. 1D): Setation sparse, only few short simple setae; flagellum consists of 6 portions; three elongated calceoli on median side of peduncular portions 4 and 5; proximal 3 annuli of flagellum each with one calceolus.

Mandibles (Fig. 2D,H): Incisor process of right mandible stout, four-toothed; right lacinia mobilis well developed, distally deeply notched, with two rows of irregularly arranged spines; articular condylus well developed. Setal row of right mandible near lacinia mobilis consists of an alternating sequence of four stout setae with broadened bases and pappose setae; setae of setal row near molar process are delicate and pappose. Incisor process of left mandible five-toothed; lacinia mobilis broad, five-toothed and as long as incisor process; articular condylus very well developed. Setal row of left mandible near lacinia mobilis consists of an alternating sequence of 6 stout setae with broadened bases and pappose setae; next to the molar process setae of setal row are again smaller and pappose. Molar processes elongated; surface of molar processes small, ellipsoidal, composed of separate columnar elements; without ridges.

Maxillulae (Fig. 3D, 4D): Inner plates short; medio-anteriorly oriented margin bears 5–7 pappose setae. Distal margin of outer plate bears 7 pointed spine-like cuspidate setae with up to 7 medio-distally directed secondary spines.

Maxillae (Fig. 4H): Inner plate with a row of short serrate setae on distal half of median margin;



Fig. 7. SEM images of uropods and telson in situ in dorsal view. A. *Gammarus lacustris*; B. *G. roeselii*; C. *Dikerogammarus villosus*; D. *Crangonyx pseudogracilis*. Abbreviations other than in previous figures: en, endopod; ex, exopod; te, telson; u1, first uropod; u2, second uropod; u3, third uropod.

another row of 5–7 medio-distally directed pappose setae begins proximally near the median margin, curving distally onto the middle of anterior face of inner plate.

Maxillipeds (Fig. 5D,H): Setation sparse; endite of ischium barely reaching half the length of carpus, its median margin bears irregularly arranged short setae with flattened distal ends, but no cuspidate setae.

Second gnathopods (Fig. 6D): Setation sparse; only a few serrate setae on carpus and propodus, which are directed medio-ventrally in natural position.

Third uropods (Fig. 7D): styliform, similar to the first and second uropods. Endopods very short, hardly overhanging the telson; each endopod bears one pointed cuspidate seta. Exopods short, bearing only pointed cuspidate setae on median and lateral margin.

Discussion and conclusions

When Mürle et al. (2004) reported that Dikerogammarus villosus was found in Lake Constance, it was assumed that this invasive species could have serious impact on the biocoenosis of this lake, comparable to the impact it had in many rivers and lakes in western and central Europe. Furthermore, it was feared that D. villosus could have negative effects on fisheries, not only because it leads to changes or reduction of fish prey but also because it is known to feed on fry (Casellato et al. 2007). Moreover, Kinzler & Maier (2006) demonstrated that the risk of predation by fish is lower in D. villosus compared to native or earlier established gammarideans, e.g. G. roeselii, because D. villosus is less active and has a high affinity to hard substrate, where it can hide and is scarcely accessible for predators. Indeed, D. villosus was able to spread in the littoral zone of almost the whole lake and is now the dominant species on hard substrates, but coexistence with native and earlier established gammaridean species seems to be possible. This can be inferred from the fact that since the occurrence of D. villosus in 2002, there was no obvious decline

of populations of *G. lacustris* and *G. roeselii* and a population of *C. pseudogracilis* was able to establish in spite of the presence of *D. villosus*.

Competition for food is often a reason for displacement of one species by another. For a long time it was assumed that non-marine gammarideans feed mainly on plant material (e.g. Haeckel et al. 1973, Kostalos & Seymour 1976). Consequently, they have been assigned to the functional feeding group of shredders (Cummins & Klug 1979). At least since the impact of *D. villosus* was documented and results of laboratory studies on its predation were published, it was clear that limnic gammarideans not only feed on plant material but on a wide variety of food sources, some of them are even effective predators (e.g. MacNeil et al. 1997, Dick & Platvoet 2000, Dick et al. 2002, Kinzler & Maier 2003, Kinzler et al. 2009). In non-marine gammarideans the existence of morphological modifications and specializations of the mouthparts and other structures involved in specialized food acquisition has been documented in earlier publications by the authors of the present work (Mayer et al. 2008, 2009, 2012). Direct observation of movements and interactions of the mouthparts during feeding is not possible in amphipods, because the anteriorly directed mouthparts cover each other at least partially. Therefore, the information on the feeding actions given in the following chapters are interpretations of the morphology of the structures involved in food acquisition based on the results of our SEM examination.

Gammarus lacustris

Gammarus lacustris performs diurnal vertical migration. During the day it is epibenthic and feeds on sediment, at night it migrates into the pelagic zone and predates on zooplankton. In enclosure experiments G. lacustris was able to change the plankton community in fish-free alpine lakes (Wilhelm & Schindler 1999, Wilhelm et al. (1999). Yemelyanova et al. (2002) even stated that plankton is the most important food resource for *G. lacustris* and that it is a top-predator in fish free lakes, with highest growth rates when feeding on lake plankton. Copepods respond to different concentrations of kairomones from G. lacustris with corresponding predator avoidance reactions. The coevolution of this predator-prey relationship is further evidence that *G. lacustris* is an active predator on zooplankton (Gubanov et al. 2010). Gut content analysis revealed that G. lacustris primarily ingested fresh seston including a considerable amount of microalgae (Gladyshev et al. 2000). Berezina (2007) observed a shift in feeding during ontogenesis, with juveniles preferably feeding on detritus and adults on zooplankton. When the availability of zooplankton is low, adults will also feed on detritus and macrophytes. Such flexibility in feeding according to the availability of food is also reported by Skoptsov (1980) who found remains of zooplankton, macrophytes like stonewort (Characeae), pondweeds (*Potamogeton* sp.), cattail (*Typha* sp.), watermilfoil (*Myriophyllum* sp.), larvae of chironomids, and detritus in the foregut of specimens of *G. lacustris*.

In *G. lacustris* the setation of the antennae is sparse (Fig. 1A). Therefore, the antennae are suited for collecting detritus, but not for sieving particles out of the respiration current. According to Read & Williams (1990) the calceoli on the antennae are mechanoreceptors, which may help to detect zooplankton. However, it must be taken into account that only the antennae of males bear calceoli. We found no information in the literature about genderspecific differences in feeding of *G. lacustris*.

The stout incisor processes together with the broad left lacinia mobilis with its well-developed articular condylus seem to be well suited for biting. For that, the right incisor process glides into the gap between the left incisor process and the left lacinia mobilis, which is stabilized in its position parallel to the adjacent incisor process by its well-developed articular condylus. Thus, these structures can act as double-edged scissors with one blade on the right mandible and two blades on the left. The mandibular setal rows consist of both long stiletto-shaped setae and pappose setae (Fig. 2E). This combination seems to enable them to push larger as well as very fine food particles towards the molars. In G. lacustris the surfaces of the well-developed molar processes are equipped with ridges, but these are not as regular and distinct as in G. roeselii (Fig. 2A). Nevertheless, they seem to be suitable for grinding hard food items. The inner plates of the maxillulae completely fill the space between the outer plates. They are remarkably flat and their median margins are very densely set with pappose setae (Fig. 3A). Compared to those of the other species, the inner plates of the maxillulae in *G. lacustris* create the most effective sieve to retain small particles. This also applies for the inner plates of the maxillae that have densely set plumose setae on their median margins (Fig. 4E). It seems that fine particulate organic matter is an important component of food in G. lacustris. The comb-like cuspidate setae on the distal margin of the outer plates of the maxillulae (Fig. 4A) seem to be suited to remove periphyton from substrates. The latter is also true for the maxillipeds, with their medially directed flattened cuspidate setae on the endites of the ischia (Fig. 5E). The fan like net, created by the third uropods with their plumose setae on the median and lateral margins of the endopods and the exopods (Fig. 7A), is well suited for sieving particles out of the respiration current.

Gammarus roeselii

In gut content analyses Ponyi (1961) found exclusively plant remains in two-thirds of the specimens he had examined, but only a minority had solely animal remains in their foregut. Willer (1922) observed G. roeselii preferably feeding on parts of submerged macrophytes that are exposed to light and concluded that periphyton is an important component in the nutrition of G. roeselii. In laboratory experiments G. roeselii also fed on animal food like larvae of Chironomidae and Simulidae, Tubifex sp. and Asellus aquaticus (Linnaeus, 1758) (Krisp & Maier 2005). Growth rates in *G. roeselii* are higher when feeding on chironomid larvae compared to conditioned leaf litter. However, its long-term survival rate is higher when feeding on conditioned leaf litter (Gergs & Rothhaupt 2008). According to Pöckl (1995) G. roeselii can also feed on fresh macrophytes with good growth rates, but again long term survival rate is higher when feeding on conditioned leaf litter. In summary it can be stated that G. roeselii preferably feeds on fresh or decaying plant material including macrophytes and on periphyton, but also on macrozoobenthic organisms if available.

There are more and longer setae on the posterior side of the antennae in G. roeselii than in G. lacustris (Fig. 1B). Hence, the antennae of *G. roeselii* seem to be suitable for collecting detritus and, in a limited amount, for sieving particles out of the respiration current. The latter is also true for the third uropods with plumose setae on the median and lateral margin of both endopods and exopods (Fig. 7B). The incisor processes and the left lacinia mobilis are well developed so that the mandibles are suited for biting (Fig. 2F). The surfaces of the molar processes, with their distinct parallel ridges, are rasp-like (Fig. 2B), therefore enabling grinding of hard food items like parts of macrophytes or leaf litter. Compared to G. lacustris there are fewer setae on the median margins of the inner plates of maxillulae (Fig. 3B) and maxillae (Fig. 4F) in G. roeselii. Nevertheless, the nets created by these setae still appear to be well suited for retaining small food particles.

As described in Mayer et al. (2009), peculiar features of *G. roeselii* are the cuspidate setae on the distal margin of the maxillular outer plates (Fig. 4B). Some of them are distally broadened and flattened and thus chisel-like so that the outer plates of the maxillulae are modified as tools for scraping off periphyton from substrates. The recessed median margins of the endites of the maxillulaes (Fig. 5B) enable the cuspidate setae of the maxillular inner

plates to reach the substrate more easily. Also the medio-distally directed cuspidate setae on the posterior side of the median margin of the maxillipedal ischia (Fig. 5F) can be used for scraping and for removing particles from the antennae, which are collected by the latter.

Dikerogammarus villosus

The severe impact of D. villosus on the macrozoobenthos community, when it occurs in waters outside its natural distribution area, led to the conclusion that it is a specialized predator. In fact, in laboratory experiments D. villosus fed on larvae of Chironomidae and Ephemeroptera, on Asellus aquaticus, and Tubifex sp. (Krisp & Maier 2005). Under equal conditions D. villosus captured more individuals of Asellus aquaticus than G. roeselii did (Bollache et al. 2008). It also feeds on individuals of closely related species, e.g. Gammarus pulex (Linnaeus, 1758), G. tigrinus Sexton, 1939, and Crangonyx pseudogracilis (Boets et al. 2010). In laboratory experiments on intraguild predation D. villosus was the superior predator compared to G. fossarum Koch in Panzer, 1835 and G. roeselii (Kinzler & Maier 2003) or compared to Gammarus duebeni Liljeborg, 1852 (Dick & Platvoet 2000). However, predation is not the only mode of feeding in D. villosus. As a result of their video study Platvoet et al. (2009) described the following feeding activities for D. villosus: 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). Additionally it was demonstrated that D. villosus is able to incorporate and digest micro-algae (Platvoet et al. 2006). The long-term survival rate of *D. villous* in the laboratory was comparable when fed with either larvae of Chironomidae, conditioned leaf litter or detritus (Gergs & Rothhaupt 2008). This supports the view that D. villous is not a specialized predator but an opportunistic omnivore (for details see Mayer et al. 2008, 2009).

The antennae of *D. villosus* are equipped with a postero-ventrally directed flag-like brush of densely set long setae on the flagella (Fig. 1C). With these, *D. villosus* is able to sieve suspended particles out of the respiration current and collect detritus. Moreover, as Platvoet et al. (2009) described, *D. villosus* can catch zooplankton organisms with the aid of a water current which is created when the antennae are rapidly moved towards the ventral side of the animal. Organisms transported towards the mouth area by this water current are grabbed by the gnathopods. The second gnathopods, with their long and densely set setae (Fig. 6C), can build a basket

to prevent escape of small mobile organisms. In addition, with these setae the gnathopods can be used for sweeping food particles from the substrates. The stout incisor processes and the well-developed left lacinia mobilis (Fig. 2G) are well suited for biting and cutting. With the long pappose setae of the mandibular setal rows, fine-particulate food items can also be transported towards the molars. The molar processes are well developed, but their surfaces are without any parallel ridges (Fig. 2C) and therefore, not well suited for grinding hard plant material. Nevertheless, there are no modifications of the mandibles of D. villosus, which are, according to Watling (1993) typical for specialized carnivorous amphipods, such as broadened incisor processes, reduced setal rows or reduced molar processes. Although there are a relatively small number of setae on the median margin of the inner plates of the maxillulae (Fig. 3C), these opposing rows of pappose setae create a net, which still seems to be suited for retaining small particles. This is also true for the inner plates of the maxillae (Fig. 4G). The cuspidate setae on the distal margin of the maxillular outer plates are without any comb-like or chisel-like modifications (Fig. 4C). The medio-distally directed cuspidate setae on the posterior side of the median margin of the maxillipedal ischia (Fig. 5G) are suited for removing food particles from the setae of the antennae and the second gnathopods. The endopods of the third uropods are very small, but the long and flattened exopods with long and densely set plumose setae on their median and lateral margins together build a fan-like net (Fig. 7C), well suited for sieving particles out of the respiration current.

Crangonyx pseudogracilis

We found only little information on nutrition in *C. pseudogracilis* in literature. In aquaria it survives several weeks when fed with leaf litter, *Phragmites* sp., *Lemna trisulcata*, and carrion (Martens & Grabow 2006). It may also be possible to draw conclusions from the nature of its preferred habitats. *C. pseudogracilis* prefers habitats with soft fine-particulate sediments and rich vegetation. Therefore, detritus and remains of plants should at least be part of its preferred food.

The antennae of *C. pseudogracilis* bear only a few short setae, but many calceoli are present, which make the antennae a mechanosensitive organ (Fig. 1D). The stout and broad incisor processes together with the broad left lacinia mobilis seem to be well suited for cutting (Fig. 2H). The mandibular setal rows, which consist of only 4–6 stout setae and some pappose setae (Fig. 2H), appear to be reduced compared to those of the other three species inves-

tigated. The elongated molar processes with their small surfaces composed of columnar elements (Fig. 2D) appear not to be suitable for grinding hard plant material, but for softer food items. With these modifications of their main coxal elements, the mandibles of C. pseudogracilis are somewhat similar to those amphipods specialized in feeding on carrion (Watling 1993, Mekhanikova 2010). The inner plates of both the maxillulae (Fig. 3D) and maxillae (Fig. 4H) bear only few setae on their median margins. Therefore, they can hardly be an effective net for retaining fine particulate organic matter. The few cuspidate setae of the distal margin of the maxillular outer plates bear only few and mostly short secondary spines (Fig. 4D) and therefore, they seem to be suitable only for handling bigger food items. There are no cuspidate setae on the median margins of the maxillipedal ischia (Fig. 5H). This is further evidence that periphyton seems to play a minor role in the nutrition of C. pseudogracilis. The same is true for fine particulate matter collected as well as sieved out of the respiration current, because there are only few setae on the second gnathopods (Fig. 6D) and the styliform uropods bear only spiky cuspidate setae (Fig. 7D). Summarizing, it seems that C. pseudogracilis is specialized to mainly feed on carrion of small organisms and on larger particles of detritus.

Apparently, the four gammaridean species inhabiting Lake Constance have different food preferences and these differences are expressed in modifications and specializations of the morphology of mouthparts and other structures involved in food acquisition. For Gammarus lacustris, besides zooplankton, fine particulate organic matter from detritus, collected using the extremely tight sieve-apparatus built by the inner plates of the maxillulae and maxillae, is also an important food source. This is either sieved out of the respiration current with the aid of the third uropods or removed from the substrate by the aid of the comb-like cuspidate setae of the maxillular outer plates. Gammarus roeselii, with the chisel-like cuspidate setae on the maxillular outer plates, possesses specializations for scraping off periphyton from substrates. Dikerogammarus villosus is omnivorous without any morphological specializations and Crangonyx pseudogracilis seems to be specialized for feeding on carrion and on larger particles of detritus. These differences in food acquisition are an important factor, which enable coexistence of these four gammaridean species.

Besides feeding, competition for habitat is an important factor for coexistence. Lake Constance consists of two parts, the smaller western part called Untersee ("lower lake"; 63 km²; mean depth 13 m) and the larger part called Obersee ("upper lake"; 473 km²; mean depth 101 m). The two parts are connected by a small stretch called the Seerhein. In most parts of the lower lake the bottom is covered with fine-grained soft sediments. Bigger stones without mud are only available directly on the shoreline. Therefore, most of the littoral zone in the lower lake is only suitable to a limited extent as a habitat for Dikerogammarus villosus, and individuals of this species can be found crowded together under such stones near the shoreline (own observation). There is an extensive stonewort stand (Chara sp.) in the lower lake. This seems to be a suitable habitat for Gammarus roeselii and G. lacustris. G. roeselii inhabits the submerged vegetation here (own observation). The lower lake, with its soft sediments and plenty of submerged vegetation, also meets the requirements as a habitat for G. lacustris, which can mostly be found in stonewort stands at a depth of 2-6 m. Until now Crangonyx pseudogracilis has not been reported in the lower lake, although this section of the lake with muddy bottom, rich submerged vegetation, and reed beds should be a suitable habitat for this species.

In most parts of the upper lake hard substrates in the form of coarse to medium gravel or boulders are dominant in the littoral zone. Here D. villosus occurs in high densities, whereas the other gammarideans are mostly missing. G. roeselii, which until 2002 also inhabited these sections of the littoral zone, is now restricted to submerged vegetation (Mürle et al. 2004; Rey et al. 2005). C. pseudogracilis was first recorded in Lake Constance in 2007 near Hard. Austria on a section of the littoral zone with coarse and medium gravel at a depth of about 0.5 m (Hanselmann & Gergs 2007). This habitat does not meet the requirements of C. pseudogracilis as they are described in literature (see above). Possibly C. pseudogracilis migrated via the groundwater from the adjacent inland basin or pools into Lake Constance. Such subterraneous migrations between waters are reported for C. pseudogracilis in literature (Harris et al. 2002).

There are diverse types of substrate and vegetation in Lake Constance. Hence, it offers suitable habitats for all of the four gammaridean species so that coexistence is possible. Although *D. villosus* occupied parts of the habitat of *G. roeselii* and displaced it from hard substrates the competition for habitat seems to be tolerable, because submersed vegetation is an alternative habitat for *G. roeselii* (Hesselschwerdt et al. 2008). *G. lacustris* as well as *G. roeselii* have affinities to macrophytes, but they occur at different water depths. Since substrate preferences of *G. lacustris* and *C. pseudogracilis* do not meet those of *D. villosus*, there is no concurrence for habitat between these species. A similar situation was described by Kley & Maier (2005) from a natural tributary of the Rhine, with diverse substrates and food resources, where *D. villosus* coexists with two other gammarideans.

Acknowledgements

We are grateful to John Hesselschwerdt who provided us with specimens of *Gammarus lacustris*, and to the staff of the Central Facility for Electron Microscopy, University of Ulm, for their continuous support. The study material is stored at the University of Ulm. Special thanks to Amaia Green Etxabe, Institute of Marine Sciences, University of Portsmouth for improving the English of the paper.

References

- Berezina, N. A. 2007. Food spectra and consumption rates of four amphipod species from the North-West of Russia. Fundamental and Applied Limnology – Archiv für Hydrobiologie 168: 317–326.
- Bij de Vaate, A. & Klink, A. G. 1995. *Dikerogammarus villosus* Sowinsky (Crustacea: Gammaridae) a new immigrant in the Dutch part of the Lower Rhine. Lauterbornia 20: 51–54.
- Boets, P., Lock, K., Messiaen, M. & Goethals, P. L. M. 2010. Combining data-driven methods and lab studies to analyse the ecology of *Dikerogammarus villosus*. Ecological Informatics 5: 133–139.
- Bollache, L. 2004. *Dikerogammarus villosus* (Crustacea: Amphipoda): another invasive species in Lake Geneva. Revue Suisse de Zoologie 111: 309–313.
- -- , Devin, S., Wattier, R., Chovet, M., Beisel, J.-N., Moreteau, J.-C. & Rigaud, T. 2004. Rapid range extension of Ponto-Caspian amphipod *Dikerogammarus villosus* in France: potential consequences. Fundamental and Applied Limnology – Archiv für Hydrobiologie 160: 57-66.
- , Dick, J. T. A., Farnsworth, K. D. & Montgomery, W. I. 2008. Comparison of the functional responses of invasive and native amphipods. Biology Letters 4: 166–169.
- -- , Kaldonski, N., Troussard, J.-P., Lagrue, C. & Rigaud, T. 2006. Spines and behaviour as defences against fish predators in an invasive freshwater amphipod. Animal Behaviour 72: 627–633.
- Casellato, S., La Piana, G., Latella, L. & Ruffo, S. 2006. *Dikerogammarus villosus* (Sowinsky, 1894) (Crustacea, Amphipoda, Gammaridae) for the first time in Italy. Italian Journal of Zoology 73: 97–104.
- -- , Visentini, A. & La Pianna, G. 2007. The predatory impact of *Dikerogammarus villosus* on fish. Pp. 495–506 in: Gherardi, F. (ed.). Biological invaders in inland waters: profiles, distribution, and threats. Berlin, New York (Springer).

- Costello, M. J. 1993. Biogeography of alien amphipods occurring in Ireland and interactions with native species. Crustaceana 65: 287–299.
- Cummins, K. W. & Klug, M. J. 1979. Feeding ecology of stream invertebrates. Annual Review of Ecology and Systematics 10: 147–172.
- Devin, S., Beisel, J. N., Bachmann, V. & Moreteau, J.-C. 2001. *Dikerogammarus villosus* (Amphipoda: Gammaridae): another invasive species newly established in the Moselle River and French hydrosystems. Annals of Limnology 37: 21–27.
- -- , Piscart, C., Beisel, J.-N. & Moreteau, J.-C. 2003. Ecological traits of the amphipod invader *Dikero-gammarus villosus* on a mesohabitat scale. Archiv für Hydrobiologie 158: 43–56.
- Piscart, C., Beisel, J.-N. & Moreteau, J.-C. 2004. Life history traits of the invader *Dikerogammarus villo*sus (Crustacea: Amphipoda) in the Moselle River, France. International Review of Hydrobiology 89: 21–34.
- Dick, J. T. A., Irvine, D. E. & Elwood, R. W. 1990. Differential predation by males on moulted females may explain the competitive displacement of *Gammarus duebeni* by *G. pulex* (Crustacea: Amphipoda). Behaviour Ecology and Sociobiology 26: 41–45.
- -- , Montgomery, I. & Elwood, R. W. 1993. Replacement of the indigenous amphipod *Gammarus duebeni celticus* by the introduced *G. pulex*: differential cannibalism and mutual predation. Journal of Animal Ecology 62: 79–88.
- -- , Montgomery, W. I. & Elwood, R. W. 1999. Intraguild predation may explain an amphipod replacement: evidence from laboratory populations. Journal of Zoology 249: 463–468.
- & Platvoet, D. 2000. Invading predatory crustacean Dikerogammarus villosus eliminates both native and exotic species. Proceedings of the Royal Society of London B 267: 977–983.
- , Platvoet, D. & Kelly, D. W. 2002. Predatory impact of the freshwater invader *Dikerogammarus villosus* (Crustacea: Amphipoda). Canadian Journal of Fisheries and Aquatic Sciences 59: 1078–1084.
- Eggers, T. O. & Martens, A. 2001. Bestimmungsschlüssel der Süßwasser-Amphipoda (Crustacea) Deutschlands. Lauterbornia 42: 1–68.
- & Martens, A. 2004. Ergänzungen und Korrekturen zum "Bestimmungsschlüssel der Süßwasser-Amphipoda (Crustacea) Deutschlands". Lauterbornia 50: 1–13.
- Garland, E. M. 1981. The colonization of Windermere by *Crangonyx pseudogracilis*. Freshwater Biological Association Occasional Publication 12: 1–13.
- Gerdes, G. & Eggers, T. O. 2007. First record of *Crangonyx* pseudogracilis (Crustacea: Amphipoda) in the northern part of Germany. Lauterbornia 61: 141–144.
- Gergs, R. & Rothhaupt, K.-O. 2008. Feeding rates, assimilation efficiencies and growth of two amphipod species on biodeposited material from zebra mussels. Freshwater Biology 53: 2494–2503.

- Gervais, M. 1835. Note sur deux espèces de Crevettes qui vivent aux environs de Paris. Annales des Sciences Naturelles (Zool.) 2: 127–128.
- Gladyshev, M. I., Emelianova A. Y., Kalachova, G. S., Zotina, T. A., Gaevsky, N. A. & Zhilenkov, M. D. 2000. Gut content analysis of *Gammarus lacustris* from a Siberian lake using biochemical and biophysical methods. Hydrobiologia 431: 155-163.
- Gubanov, M. V., Zadereev, E. S. & Degermenzhy, A. G. 2010. Chemical interactions between two dominant species in Lake Shira: *Gammarus lacustris* Sars (Crustacea: Amphipoda) and *Arctodiaptomus salinus* Daday (Crustacea: Copepoda). Doklady Biological Sciences 434: 318–321.
- Haeckel, J.-W., Meijering, M. P. D. & Rusetzki, H. 1973. *Gammarus fossarum* Koch als Fallaubzersetzer in Waldbächen. Freshwater Biology 3: 241–249.
- Hanselmann, A. J. & Gergs R. 2008. First record of *Crangonyx pseudogracilis* Bousfield 1958 (Crustacea: Amphipoda) in Lake Constance. Lauterbornia 62: 21–25.
- Hargeby, A. 1990. Macrophyte associated invertebrates and the effect of habitat permanence. Oikos 57: 338-346.
- Harris, P. M., Roosa, B. R. & Norment, L. 2002. Underground dispersal by amphipods (*Crangonyx pseudogracilis*) between temporary ponds. Journal of Freshwater Ecology 17: 589–594.
- Hartmann, J. 1977. Die Trüsche (*Lota Lota*) im eutrophierten Bodensee. Archiv für Hydrobiologie 80: 360–374.
- Hesselschwerdt, J., Necker, J. & Wantzen, K. M. 2008. Gammarids in Lake Constance: habitat segregation between the invasive *Dikerogammarus villosus* and the indigenous *Gammarus roeselii*. Fundamental and Applied Limnology 173: 177–186.
- Jazdzewski, K. 1980. Range extensions of some gammaridean species in European inland waters caused by human activity. Crustaceana Supplement 6: 84–107.
- -- & Roux, A. L. 1988. Biogeographie de *Gammarus* roeseli Gervais en Europe, en particulier repartition en France et en Pologne. Crustaceana Supplement 13: 272-277.
- Kaldonski, N., Lagrue, C., Motreuil, S., Rigaud, T. & Bollache, L. 2008. Habitat segregation mediates predation by the benthic fish *Cottus gobio* on the exotic amphipod species *Gammarus roeseli*. Naturwissenschaften 95: 839–844.
- Karaman, G. S. & Pinkster, S. 1977. Freshwater Gammarus species from Europe, North Africa, and adjacent regions of Asia (Crustacea – Amphipoda) Part I. Gammarus pulex-group and related species. Bijdragen tot de Dierkunde 47: 1–97.
- -- & Pinkster, S. 1977. Freshwater Gammarus species from Europe, North Africa, and adjacent regions of Asia (Crustacea – Amphipoda) Part II. Gammarus roeseli-group and related species. Bijdragen tot de Dierkunde 47: 165–196.

- Kley, A. & Maier, G. 2003. Life history characteristics of the invasive freshwater gammarids *Dikerogammarus villosus* and *Echinogammarus ischnus* in the river Main and the Main-Donau canal. Archiv für Hydrobiologie 156: 457–469.
- -- & Maier, G. 2005. An example of niche partitioning between *Dikerogammarus villosus* and other invasive and native gammarids: a field study. Journal of Limnology 64: 85–88.
- -- & Maier, G. 2006. Reproductive characteristics of invasive gammarids in the Rhine-Main-Danube catchment, South Germany. Limnologica 36: 79–90.
- -- , Kinzler, W., Schank, Y., Mayer, G., Waloszek, D. & Maier, G. 2009. Influence of substrate preference and complexity on co-existence of two non-native gammarideans (Crustacea: Amphipoda). Aquatic Ecology 43: 1047–1059.
- Kinzler, W. & Maier, G. 2003. Asymmetry in mutual predation: possible reason for the replacement of native gammarids by invasives. Archiv für Hydrobiologie 157: 473–481.
- -- & Maier, G. 2006. Selective predation by fish: a further reason for the decline of native gammarids in the presence of invasives? Journal of Limnology 65: 27-34.
- -- , Kley, A., Mayer, G., Waloszek, D. & Maier, G. 2009. Mutual predation between and cannibalism within several freshwater gammarids: *Dikerogammarus villosus* versus one native and three invasives. Aquatic Ecology 43: 457–464.
- Kostalos, M. & Seymour, R. L. 1976. Role of microbial enriched detritus in the nutrition of *Gammarus* minus (Amphipoda). Oikos 27: 512–516.
- Krisp, H. & Maier, G. 2005. Consumption of macroinvertebrates by invasive and native gammarids: a comparison. Journal of Limnology 64: 55–59.
- MacNeil, C., Dick, J. T. A. & Elwood, R. W. 1997. The trophic ecology of freshwater *Gammarus* spp. (Crustacea: Amphipoda): problems and perspectives concerning the functional feeding group concept. Biological Reviews 72: 349–364.
- -- , Platvoet, D., Dick, J. T. A., Fielding, N., Constable, A., Hall, N., Aldridge, D., Renals, T. & Diamond, M. 2010. The Ponto-Caspian "killer-shrimp", *Dikerogammarus villous* (Sowinsky, 1894), invades the British Isles. Aquatic Invasions 5: 441–445.
- Martens, A. & Grabow, K. 2006. Crangonyx pseudogracilis am Oberrhein (Crustacea: Amphipoda): ein Neozoon besiedelt erfolgreich Gewässer abseits der ausgebauten Fahrrinne. Lauterbornia 58:131–137.
- Mayer, G., Maier, G., Maas, A. & Waloszek, D. 2008. Mouthparts of the Ponto-Caspian invader *Dikero-gammarus villosus* (Amphipoda: Pontogammaridae). Journal of Crustacean Biology 28: 1–15.
- -- , Maier, G., Maas, A. & Waloszek, D. 2009. Mouthpart Morphology of *Gammarus roeselii* compared to a successful invader, *Dikerogammarus villosus* (Amphipoda). Journal of Crustacean Biology 29: 161–174.

- -- , Maas, A. & Waloszek, D. 2012. Mouthpart morphology of three sympatric native and nonnative gammaridean species: *Gammarus pulex, G. fossarum,* and *Echinogammarus berilloni* (Crustacea: Amphipoda). International Journal of Zoology Volume 2012, Article ID 493420, 23 pp.
- Meijering, M. 1991. Lack of oxygen and low pH as limiting factors for *Gammarus* in Hessian brooks and rivers. Hydrobiologia 223: 159–169.
- Mekhanikova, I. V. 2010. Morphology of mandible and lateralia in six endemic amphipods (Amphipoda, Gammaridea) from Lake Baikal, in relation to feeding. Crustaceana 83: 865–887.
- Mirzajani, A. R., Heidari, O. & Khodaparast S. H. 2011. Some biological aspects of *Gammarus lacustris* Sars, 1863 in Neur Lake Ardabeel province, Iran. Iranian Journal of Fisheries Sciences 10: 242–253.
- Mürle, U., Becker, A. & Rey, P. 2004. *Dikerogammarus villosus* (Amphipoda) new in Lake Constance. Lauterbornia 49: 77–79.
- Nehring, S. 2003. Alien species in German waters a risk for biodiversity. Schriftenreihe des BMVEL "Angewandte Wissenschaft", Heft 498 "Bedrohung der biologischen Vielfalt durch invasive gebietsfremde Arten": 40–52.
- Nesemann, H., Pöckl, M. & Wittmann, K. J. 1995. Distribution of epigean Malacostraca in the middle and upper Danube (Hungary, Austria, Germany). Miscellanea Zoologica Hungarica 10: 49–68.
- Pinkster, S. 1972. On members of the *Gammarus pulex*group (Crustacea – Amphipoda) from Western Europe. Bijdragen tot de Dierkunde 42: 164–191.
- -- , Dieleman, J. & Platvoet, D. 1980. The present position of *Gammarus tigrinus* Sexton, 1939 in The Netherlands, with the description of a newly discovered amphipod species, *Crangonyx pseudogracilis* Bousfield, 1958 (Crustacea, Amphipoda). Bulletin Zoologisch Museum Universiteit van Amsterdam 7: 33–45.
- Platvoet, D., Dick, J. T. A., Konijendijk, N. & Van der Velde, G. 2006. Feeding on micro-algae in the invasive Ponto-Caspian amphipod *Dikerogammarus villosus* (Sowinsky, 1894). Aquatic Ecology 40: 237-245.
- -- , Van der Velde, G., Dick, J. T. A. & Li, S. 2009. Flexible omnivory in *Dikerogammarus villosus* (Sowinsky, 1894) (Amphipoda) – Amphipod pilot species project (AMPIS) Report 5. Crustaceana 82: 703– 720.
- Pöckl, M. 1995. Laboratory studies on growth, feeding, moulting and mortality in the freshwater amphipods *Gammarus fossarum* and *G. roeseli*. Archiv für Hydrobiologie 134: 223–253.
- -- 2007. Strategies of a successful new invader in European fresh waters: fecundity and reproductive potential of the Ponto-Caspian amphipod *Dikerogammarus villosus* in the Austrian Danube, compared with the indigenous *Gammarus fossarum* and *G. roeseli*. Freshwater Biology 52: 50–63.

- Ponyi, J. E. 1961. Über die Ernährung einiger Amphipoden (Crustacea) in Ungarn. Annales Instituti Biologici (Tihany) Hungaricae 28: 117–123.
- Read, A. T. & Williams, D. D. 1990. The role of the calceoli in precopulatory behaviour and mate recognition of *Gammarus pseudolimnaeus* Bousfield (Crustacea, Amphipoda). Journal of Natural History 24: 351–359.
- Rey, P., Mürle, U., Ortlepp, J. 2005. Wirbellose Neozoen im Bodensee. Landesanstalt für Umweltschutz Baden-Württemberg, 1–44.
- Schellenberg, A. 1934. Der Gammarus des deutschen Süßwassers. Zoologischer Anzeiger 108: 209–217.
- Skoptsov, V. G. 1980. Feeding of *Gammarus lacustris* Sars under different conditions of habitation. Pp. 94–98 in: Vinberg, G. G. (ed.). Troficheskie svyazi presnovodnykh bespozvonochnykh. Leningrad (Zoologicheski Institute AN SSSR).
- Tittizer, T. 1996. Vorkommen und Ausbreitung aquatischer Neozoen (Makrozoobenthos) in den Bundeswasserstraßen. Pp. 49–86 in: Gebhardt, H., Kinzelbach, R. & Schmidt-Fischer, S. (eds). Gebietsfemde Tierarten. Landsberg (Ecomed).
- 1997. Ausbreitung aquatischer Neozoen (Makrozoobenthos) in den europäischen Wasserstraßen, erläutert am Beispiel des Main-Donau-Kanals. Schriftenreihe des Bundesamtes für Wasserwirtschaft 4: 113–134.
- Tricarico, E., Mazza, G., Orioli, G., Rossano, C., Scapini, F. & Gherardi, F. 2010. The killer shrimp, *Dikerogammarus villosus* (Sowinsky, 1894), is spreading in Italy. Aquatic Invasions 5: 211–214.

- Vornatscher, J. 1969. Gammarus (Rivulogammarus) lacustris G. O. Sars (Amphipoda) in Österreich. Mitteilungen des Naturwissenschaftlichen Vereins Steiermark 99: 123–129.
- Watling, L. 1993. Functional morphology of the amphipod mandible. Journal of Natural History 27: 837-849.
- Wijnhoven, S., van Riel, M. C. & van der Velde, G. 2003. Exotic and indigenous freshwater gammarid species: physiological tolerance to water temperature in relation to ionic content of the water. Aquatic Ecology 37: 151–158.
- Wilhelm, F. M. & Schindler, D. W. 1999. Effect of *Gammarus lacustris* (Crustacea: Amphipoda) on plankton community structure in an alpine lake. Canadian Journal of Fisheries and Aquatic Sciences 56: 1401–1408.
- -- , Hudson, J. J. & Schindler, D. W. 1999. Contribution of *Gammarus lacustris* to phosphorus recycling in a fishless alpine lake. Canadian Journal of Fisheries and Aquatic Sciences 56: 1679–1686.
- Willer, A. 1922. Nahrungsuntersuchungen bei niederen Wassertieren. Zeitschrift für Fischerei und deren Hilfswissenschaften N.F. 5: 66–123.
- Yemelyanova, A. Y., Temerova, T. A. & Degermendzhy, A. G. 2002. Distribution of *Gammarus lacustris* in Lake Shira (Khakasia, Siberia) and laboratory study of its growth characteristics. Aquatic Ecology 36: 245–256.