

An example of niche partitioning between *Dikerogammarus villosus* and other invasive and native gammarids: a field study

Axel KLEY and Gerhard MAIER*

Department of Experimental Ecology of Animals, Section Limnology, University of Ulm, Albert-Einstein-Allee 11, 89069 Ulm, Germany

*e-mail corresponding author: gerhard.maier@biologie.uni-ulm.de

ABSTRACT

The invasive gammarid *Dikerogammarus villosus* is known to be a strong predator preying voraciously on a wide array of prey organisms including other gammarids. Predation by *D. villosus* on other gammarids is regarded as a main reason which led to the elimination of native and invasive gammarids in many reaches of European streams. At several sites in the River Danube and in a Rhine tributary, *D. villosus* was found co-existing with other gammarids. We studied whether predatory *D. villosus* is spatially segregated from other gammarids which would reduce predatory interactions. Two sites were investigated, one in the Danube (site 1) where *D. villosus* co-existed with the invasives *Echinogammarus ischnus* and *Dikerogammarus bispinosus* and another site in a Rhine tributary (site 2) where *D. villosus* co-existed with the invasive gammarid *Echinogammarus berilloni* and two native gammarids, *Gammarus pulex* and *Gammarus roeseli*. At site 1, *D. villosus* was spatially segregated from *E. ischnus* but not from *D. bispinosus*; *E. ischnus* lived at the uppermost shoreline in boulder substrate while *Dikerogammarus* spp. lived in greater depth in stony to gravelly substrate. At site 2, *D. villosus* prevailed in greater depth and gravelly to stony substrate where *Corbicula molluscs* were present while the other species lived in near-shore areas in macrophytes. Our results suggest that co-existence of predatory *D. villosus* with gammarids is possible by niche partitioning and that high habitat complexity as at site 2 facilitates co-existence. The fact that at site 1 *D. bispinosus* occupied approximately the same spatial niche than *D. villosus* cannot be explained at present time.

Key words: Gammarids, invasive species, niche partitioning, Central Europe

1. INTRODUCTION

The Ponto-Caspian gammarid *Dikerogammarus villosus* SOVINSKIJ invaded Central European waters in the last two decades and has displaced invasive and native gammarids in many reaches (e.g. Dick & Platvoet 2000; Müller *et al.* 2002; Kley & Maier 2003). Intra-guild predation (IGP), i.e. predation between potential competitors which belong to the same guild, is widely accepted as a reason for species displacements (Dick 1992, 1996; MacNeil *et al.* 1997; Kinzler & Maier 2003). *Dikerogammarus villosus* is known to be a strong predator preying voraciously on other gammarids (e.g. Dick & Platvoet 2000; Kinzler & Maier 2003). Although *D. villosus* is the prevailing and often the only gammarid in some Central European streams, it can be found coexisting with other invasive and/or native gammarids in certain reaches. For example, in the Main River, in southern Germany, *D. villosus* frequently co-exists with another Ponto-Caspian gammarid, *Echinogammarus ischnus* STEBBING (Kley & Maier 2003). Coexistence of *D. villosus* with other, less predatory gammarids may be possible by niche partitioning.

In this paper we investigate two sites, one site in the River Danube and another in a tributary of the Rhine River, where *D. villosus* coexisted with invasive (*E. ischnus* and *Dikerogammarus bispinosus* MARTINOV) and invasive (*Echinogammarus berilloni* CATTÀ) plus

native gammarids (*Gammarus pulex* L. and *Gammarus roeseli* GERVAIS), respectively. We studied distribution of gammarids in different substrates and different depths. We expected that the predatory *D. villosus* is spatially segregated from the other gammarid species.

2. DESCRIPTION OF SITES AND METHODS

Both sites can be characterized as summer warm (maximum temperature >24 °C in August) with a low current velocity (<0.05 m s⁻¹) and a hard (total hardness 3.3-4.5 mval l⁻¹, conductivity 400-520 µS cm⁻¹), nutrient and oxygen rich water (concentration of dissolved PO₄-P = 40-70 µg l⁻¹; O₂ saturation >75%). Substrate at site 1 (Danube, Deggendorf) was composed of large boulders (40 × 40 × 20 cm) at the shoreline (0-20 cm depth) and gravelly substrate (grain size 1.0 to 5 cm) in depths of 0.2-1.5 m; no aquatic vegetation was present. At site 2 (Rhine tributary) depths from 0.2 to 1 m were overgrown with aquatic plants (*Fontinalis antipyretica* L., *Callitriche* sp. and *Elodea canadensis* MICHX). Substrate of near-shore areas (to a depth of approximately 0.2 m) was also composed of large boulders (40 × 40 × 20 cm) followed by a mixture of gravel and larger stones (grain sizes between 1.0 to 15.0 cm) in greater depth. The stony and gravelly substrate was covered by *Corbicula* molluscs at the greatest depth (1.5 m). At site 1 *D. villosus* was the dominant amphipod in late spring and summer whereas at site 2 *E. berilloni* outnumbered

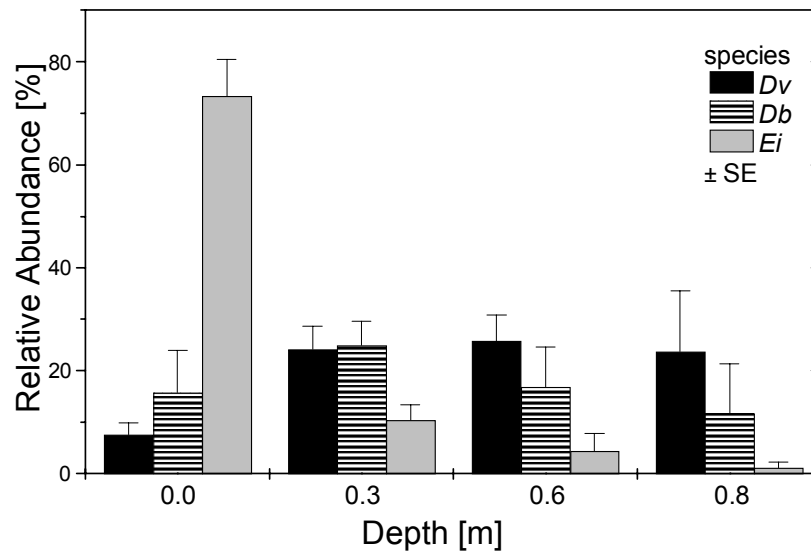


Fig. 1. Relative abundance of *Dikerogammarus villosus* (Dv), *Dikerogammarus bispinosus* (Db) and *Echinogammarus ischnus* (Ei) in different depths at site 1 (Danube, near Deggendorf, Germany).

D. villosus and the native species. Maximum abundance of *D. villosus*, *E. ischnus* and *D. bispinosus* at site 1 was 300, 160 and 130 ind. m⁻². At site 2 maximum abundance of *E. berilloni* was 200 ind. m⁻² while maximum abundance of *D. villosus* and native species was ≤100 ind. m⁻². *Dikerogammarus villosus* was first recorded in the German Danube (near site 1) in the early 1990s (Tittizer *et al.* 1994); it has replaced native species which prevailed there until the late 1980s. The first appearance of *D. villosus* at site 2 is not known. However, as *D. villosus* was recorded in the Rhine since 1995 (Schöll *et al.* 1995; Bj De Vaate & Klink 1995) it may be present at site 2 (Rhine tributary) since approximately the same time. *Dikerogammarus villosus* is the largest and heaviest gammarid species tested with an average fresh weight of 80 mg in the male and 47 mg in the female sex. *Dikerogammarus bispinosus*, *E. ischnus* and the native species *G. roeseli* were intermediate with 42 to 43 mg in the male and 25 to 37 mg in the female sex, respectively. *Echinogammarus berilloni* and *G. pulex* were smallest (25-30 mg in the male and 22-24 mg in the female sex).

Gammarids were collected from May 2nd until March 4th (Danube) and from May 2nd to March 3rd (tributary of Rhine River) in approximately monthly intervals at 4 (Danube) to 5 (Rhine tributary) different depths (Danube: near shore, 0.3, 0.6, 0.8 m; Rhine tributary: near shore, 0.3, 0.6, 0.8, 1.0 m) and at 2 different substrates (site 1: boulders vs gravel and stones; site 2: stony substrate vs macrophytes). Sampling was not possible during some time in autumn/winter of 2002 because of the high water level. Different sampling techniques and equipments (kick and pond net samples, turning over rocks, dislodging gammarids and rinsing them into a net), dependent on the substrate and depths, were employed to get representative numbers of gam-

marids. Surber samplers were not used because the boulder substrate in near-shore areas made its use impossible. At each of the 12 (Danube) and 7 (Rhine tributary) sampling dates 1 to 3 areas of 0.5 × 0.5 m per depth and substrate were carefully searched for gammarids. Sampling procedures were repeated until no more gammarids were obtained from the areas.

Since absolute abundances varied with time of the year, the relative abundance of each gammarid per depth and per substrate was calculated (total abundance in all depths/substrates = 100%). A series of ANOVAs followed by Tukey's *post hoc* test served to test whether distribution of gammarids varied with the depth and the substrate.

3. RESULTS

Although there was a slight trend that gammarids were more evenly distributed during the cold than in the warm season, no significant difference in distribution of gammarids between different months could be observed (ANOVAs: *P*s = ns); therefore, we pooled the data for different months.

At site 1, the relative abundance of *E. ischnus* varied with depth (ANOVA: *F* = 52(3/55), *P* < 0.0001); the highest densities were observed at the uppermost shoreline in boulder substrate (Fig. 1). No difference could be observed between different depths in relative abundance of *D. villosus* and *D. bispinosus* (ANOVAs: *P*s = ns). Both species were more evenly distributed than *E. ischnus* with a prevalence in gravelly substrate. There is a trend that *D. villosus* preferred greater depths than *D. bispinosus*.

At the second site, both substratum and depth affected the relative abundance of *D. villosus* (two-way ANOVA: Factor substratum: *F* = 5.7(1/40), *P* < 0.02;

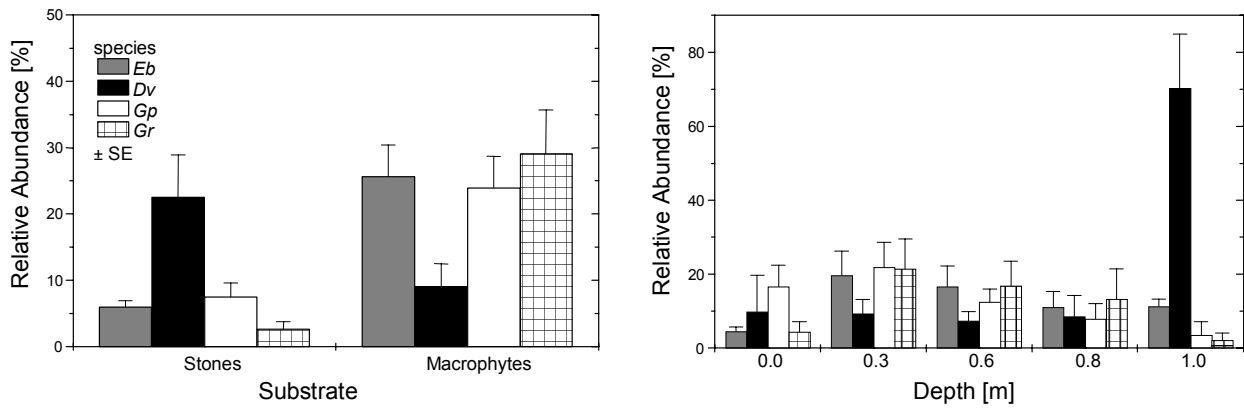


Fig. 2. Relative abundance of *Dikerogammarus villosus* (Dv), *Echinogammarus ischnus* (Ei), *Gammarus pulex* (Gp) and *Gammarus roeseli* (Gr) in different substrates and different depth at site 2 (Rhine tributary).

factor depth: $F = 13.0(4/40)$, $P < 0.0001$). This species prevailed in stony substrate and in greater depths (Fig. 2). Relative abundance of *E. berilloni*, and of native species (*G. pulex* and *G. roeseli*) were not affected by depth but significantly by substrate (two-way ANOVAs: Factor depth: $P_s = ns$; factor substrate: $F(1/40) = 14.2, 9.5$ and 19.4 , $P_s = 0.004$ to 0.0001). The three species were more evenly distributed in all depths and prevailed in macrophytes.

5. DISCUSSION

Overlap of spatial niches can lead to biotic interactions, such as predation and/or competition. Predation by *D. villosus* on other gammarids (Dick & Platvoet 2000; Kinzler & Maier 2003) and on an array of other macroinvertebrates (Dick *et al.* 2002; Kelly *et al.* 2002; Krisp 2004) is regarded to pose a threat to the fauna of invaded ecosystems. Indeed, extinction of native gammarids and declines in the whole macroinvertebrate community have been observed in European streams coincidental with the arrival of *D. villosus* (van der Velde *et al.* 2000; Devin *et al.* 2001). However, recently MacNeil & Platvoet (in prep.) have shown coexistence of *D. villosus* with other gammarids when habitat structures are complex. They further showed that IGP and cannibalism was reduced under complex habitat conditions.

The results of our study should be interpreted cautiously because of the shortcoming of our sampling procedures. Substrates varied with depths making sampling difficult (see Methods). In spite of these shortcomings, our results suggest niche partitioning between *D. villosus* and other gammarid species. At both sites *D. villosus* lived in places which were avoided by other gammarids. The only exception was *D. bispinosus* which lived in the same microhabitat as *D. villosus* at site 1. We cannot interpret this at present time. However, the fact that abundance of *D. bispinosus* decreased to zero or almost zero when *D. villosus* reached its maximum abundance in May to July (Fig. 3) suggests that the lat-

ter preyed heavily on the former. We cannot say why *D. villosus* lived in *Corbicula* banks at site 2. Possibly, the gammarid benefited by feeding on *Corbicula* faeces and prey organisms associated with the mussel (cf. Köhn & Waterstraat 1990; van Overdijk *et al.* 2003).

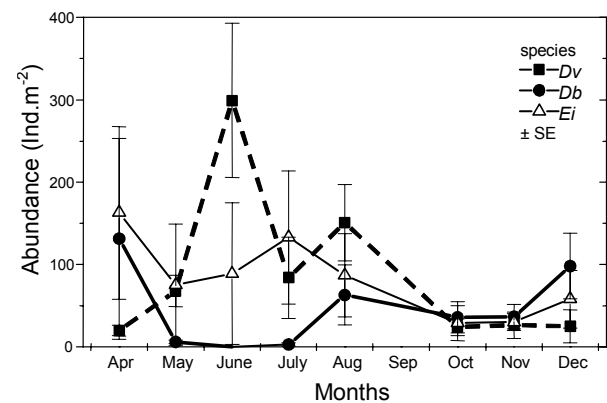


Fig. 3. Absolute abundance of *Dikerogammarus villosus* (Dv), *Dikerogammarus bispinosus* (Db) and *Echinogammarus ischnus* (Ei) at site 1.

It is also worthy to note that *G. pulex* which, like *D. villosus*, preferred stony substrate over macrophytes in laboratory experiments (Krisp 2004) was more numerous in macrophytes than in stones at site 2. Possibly *G. pulex* shifted from stony substrate to macrophytes to avoid contact with predatory *D. villosus*. Krisp (2004) showed in laboratory experiments that *G. pulex* shifted from stony substrate to macrophytes in the presence of *D. villosus*.

That no differences could be found in microhabitat use between native species and between *E. berilloni* and native species at site 2 can be an artefact. Possible differences may have been overlooked because quantitative sampling was difficult due to heterogeneous substrates.

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Received: July 2004

Accepted: February 2005