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Coexistence of species of two amphipod genera: *Niphargus timavi* (Niphargidae) and *Gammarus fossarum* (Gammaridae)

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Coexistence of species of two amphipod genera: *Niphargus timavi* (Niphargidae) and *Gammarus fossarum* (Gammaridae)

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Abstract

The co-occurrence of amphipods *Niphargus timavi* and *Gammarus fossarum* was studied. A small brook in SW Slovenia was sampled monthly for one year. Below the primary spring the brook sinks, flows for about 150 m below the surface and springs again. *Gammarus fossarum* never reached the stretch above the sink. Both species were found at all sampling sites below the secondary spring throughout the year, but the abundance of the two varied along the stream spatially and temporarily. Differences in life cycles between *G. fossarum* and *N. timavi* were not informative; however, the estimated reproductive potential of *G. fossarum* was much higher than of *N. timavi*. A result of the higher reproductive potential may be the dominance of gammarids in permanent waters, while *N. timavi* may invade a surrounding fissure system where it survives gammarid competition and summer desiccations when the gammarid population becomes extinct.

Keywords: *Amphipoda*, *co-existence*, *life cycles*, *Gammarus fossarum*, *Niphargus timavi*

Introduction

The genus *Niphargus* is the largest amphipod genus living in freshwaters (Väinölä et al. forthcoming) with twice as many species and subspecies as the second largest genus *Gammarus* (Pinkster 1978; Väinölä et al. forthcoming). The two genera occupy different types of freshwater. While most niphargids live in various types of subterranean waters (Karaman and Ruffo 1986) and only a minor part of the genus lives in surface waters (e.g. Karaman 1950; Rejic 1956, 1958; Sket 1958, 1981; Ginet and David 1963; Petrescu 1997a, 1997b; Fišer et al. 2006), the gammarids are predominantly found in surface waters (Pinkster 1978).

Several authors have reported syntopic co-occurrences of different niphargid species (e.g. Sket 1971, 1972, 2003; Fišer et al. 2006) and the coexistence of various *Gammarus* species (e.g. Stock et al. 1966; Pinkster et al. 1970; Goedmakers 1981a; Konopacka and

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Jazdzewski 1985). Also, a competitive exclusion of autochthonous gammarids by recent congeneric invaders is well documented (Dieleman and Pinkster 1977; Savage 1981, 1982; Hautus and Pinkster 1987). However, little is known about the coexistence of the species of *Gammarus* and *Niphargus*. Some authors (Karaman 1952; Sket 1970, 1981) emphasize the general absence of *Niphargus* spp. in the presence of *Gammarus* populations, while some others list localities where species of the two genera may co-exist (Motaş et al. 1962). No case of co-existence or competitive exclusion has been further investigated, thus the interpretation of the syntopic co-occurrence of members of the two genera remains unsolved.

This paper presents a study of the co-occurrence of two species, one niphargid and one gammarid, in a small brook in the Western Dinaric region. *Niphargus timavi* S. Karaman is a narrowly endemic species that can be found in the basins of rivers Reka-Timavo and Riječina (Fišer et al. 2006) in surface and subterranean waters. *Gammarus fossarum* Koch is generally considered a widely distributed surface species (e.g. Karaman and Pinkster 1977) although this name in fact encompasses a number of “cryptic” species (compare e.g. Müller 1998) that have not been morphologically recognized so far. A local co-occurrence of the two genera was noted on several occasions during recent studies of the distribution of niphargid species regularly living in the surface waters within the Western Dinaric region (Fišer et al. 2006). This study tested the hypothesis that the representatives of both genera may coexist in surface water. Samples were collected on an upper stretch of a brook over a period of one year in order to answer the following questions. Is *Niphargus timavi* present in all samples through the entire year, or can it be temporarily out-competed by *Gammarus fossarum*? Is the proportion of both species stable temporarily and/or spatially, e.g. does the proportion of both species depend on distance from the spring, and whether a particular site is predominantly occupied by one genus during the year? Finally, do life histories of the two species differ and do these differences contribute to the co-existence of the species or not?

Materials and methods

Study area

Studies were performed on about 1 km long upper stretch of the brook Kolaški potok, which drains to the river Reka, close to the village Zabiče near Ilirska Bistrica town in SW Slovenia (Figure 1). The geological foundation of the study area consists of silicate-clay rich sediments in marly-arenaceous layers in a facies of flysch (Šikić and Pleničar 1975; Mihevc 1994; Babić and Zupanič 1996).

The brook never exceeds 1.5 m in width and consists of an array of pools of variable size, depth, and shape. The depth of the pools ranges from a few centimetres up to 50 cm. The bottom of the brook is patchily covered with a layer up to 2 cm thick of granulated substrate of clay, pieces of marl, larger (10–40 cm in length) flattened stones and a variously thick layer of organic litter. The brook is without vegetation. There is no gravel or sand, thus the brook has no vertical or lateral extension into the hyporheic. Velocity of the current largely varies with respect to the brook bed. Some 250 m below the primary spring the brook sinks (hereafter called “the sink”), flows for about 150 m below the surface and springs again (hereafter called “resurgence”; Figure 1).

The water level is influenced by rainfall that is more abundant between autumn and spring as well as by the melting of the snow on the mountain of Snežnik in the springtime

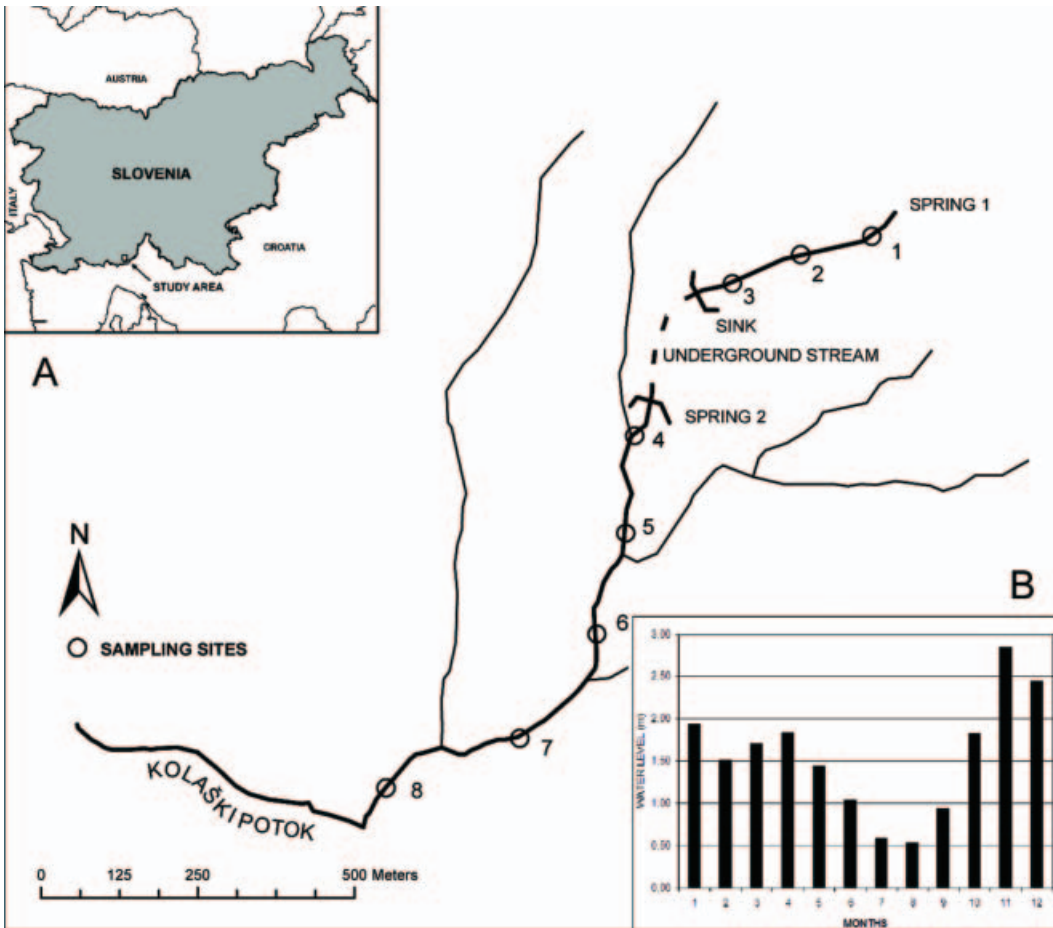


Figure 1. (A) The study area with numbers indicating the eight sampling sites; (B) average water level (m) of river Reka at Ilirska Bistrica, measured between 1958 and 2003.

(Figure 1; data from ARSO). In the summer, the part of the brook above the sink dried up and the resurgence moved about 20 m downhill.

The water is oligotrophic, populated with few taxa; apart from amphipods some leeches (Erpobdellidae) and trichopteran larvae were found. The isopod *Proasellus istrianus* (Stammer), which is regularly present in similar habitats in that area, was absent from the present samples.

Eight sites were sampled every month between April 2005 and March 2006 (Figure 1). Data are lacking for February, when heavy snowfalls covered the brook and prevented access to the water.

Sampling, analysis of demographic structure

The samples were collected with a hand net (diameter 25 cm, mesh size 0.2 mm). Sampling that would be quantitatively comparable was not possible due to the heterogeneous brook morphology, which represents a problem also in larger and morphologically more homogeneous streams (Goedmakers 1981a); see also problems in

Gledhill (1977). The samples were preserved in 4% formaldehyde and sorted in the laboratory.

When analysing the samples, the following assumptions and simplifications were made. (1) Adult males (recognized by developed genital papillae), adult females (recognized by developed oostegites), which included ovigerous and non-ovigerous females, and juvenile specimens (specimens without genital papillae or oostegites) were treated separately. In contrast to similar studies (e.g. Gledhill and Ladle 1969; Hynes and Harper 1972; Alouf 1986; Konopacka 1988; Zielinski 1995, 1998), the latter were not further classified according to their sizes. Eggs were counted and treated as a separate category. (2) It was assumed that the differences in the population structure of a single species between the simultaneous samples along the stream (but see Goedmakers 1981b) are unimportant with respect to the differences between months. This simplification was necessary, as the number of specimens of *N. timavi* in most of the samples was insufficient to study the demographic structure. For this purpose, several samples were pooled and treated as a unique sample. However, the proportion of juveniles and adults in *N. timavi* above “the sink” and below “the resurgence” did not differ significantly (tested with paired *t* test, $P > 0.05$).

In order to study the distribution pattern of amphipods along the brook, the relative abundance of *G. fossarum* and *N. timavi* was calculated for every sample (see e.g. Goedmakers 1981a). Relative numbers were used to find out (1) whether the species ratios at sampling sites spatially differ from each other, and (2) whether the species composition at a single site changes during the year. The questions were tested with the Mann–Whitney *U* test. The samples missing due to the absence of water during summer drought were excluded from the calculations.

The demographic structure was based on selected monthly gathered sample(s). The minimal number of animals used for analysis was 50. It was expressed as a relative number of males, females (ovigerous and non-ovigerous), and juvenile specimens. Eggs, as undeveloped specimens, were excluded from these calculations. The reproductive potential of both species was estimated with respect to (1) clutch size, (2) the proportion of ovigerous and non-ovigerous females, and (3) the relative egg number (total egg number/total number of specimens including juveniles).

Results

Distribution of Niphargus timavi and Gammarus fossarum in the studied stretch of the brook

A file with raw data is available on the website http://www.bf.uni-lj.si/bi/zoologija/cene_fiser/niphargus/index.htm. In general, results suggest that the *G. fossarum* population is much denser than the *N. timavi* population, even though the samples cannot be evaluated with absolute numbers due to uneven sampling (e.g. Goedmakers 1981a). The number of *G. fossarum* specimens gathered often exceeded 100, while *N. timavi* (with three exceptions: sampling site 4 in May, sampling site 2 in September, and sampling site 3 in December) was never this abundant.

The distribution of both species varied along the stream and across the different times of the year (Table I). In the upper three sampling sites (above the sink) only *N. timavi* was collected, with the exception of a single specimen of *G. fossarum* collected at sampling site 2 in July. Below the resurgence, the samples included members of both genera. It is noteworthy that the proportion of each species varied at several sampling sites throughout

Table I. Pairwise comparison of the proportion of *Niphargus timavi* at the sampling sites over the year of study.

	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8
Site 2	—						
Site 3	0.875	—					
Site 4	0*	0.001*	—				
Site 5	0.005*	0.020*	0.005*	—			
Site 6	0*	0*	0.019*	0*	—		
Site 7	0*	0*	0.173	0*	0.223	—	
Site 8	0*	0.002*	0.282	0.003*	0.282	0.971	—

Mann–Whitney *U* test was used; numbers indicate *P* values. *Sites with significantly different fauna.

the season (see Figure 2), although both species were always present. On average, at sampling sites 4 (niphargid median=0.285), 6 (niphargid median=0.100), 7 (niphargid median=0.217), and 8 (niphargid median=0.209) *G. fossarum* prevailed. By contrast, *N. timavi* prevailed at sampling site 5 (median=0.912) throughout most of the year.

On a finer scale, no obvious differences were noted in microhabitat selection. Both species preferred organic litter as a shelter rather than stone or sand. To a lesser extent, members of both species were found crawling on bare ground and hidden below the stones.

Life cycles

This population of *Gammarus fossarum* mates and breeds during most of the year (Figure 3A, C) with the peak of ovigerous females (and eggs) between March and June (Figure 3A), followed by the peak of juveniles between June and October (Figure 3A, C). No ovigerous females were found in October and December. A single ovigerous female collected in November was damaged. She had a partially opened marsupium and possibly therefore an incomplete number of eggs.

Niphargus timavi does not show such a distinct life cycle (Figure 3B, D). The ovigerous females were found in spring (May to June) and, to a lesser extent, in the autumn

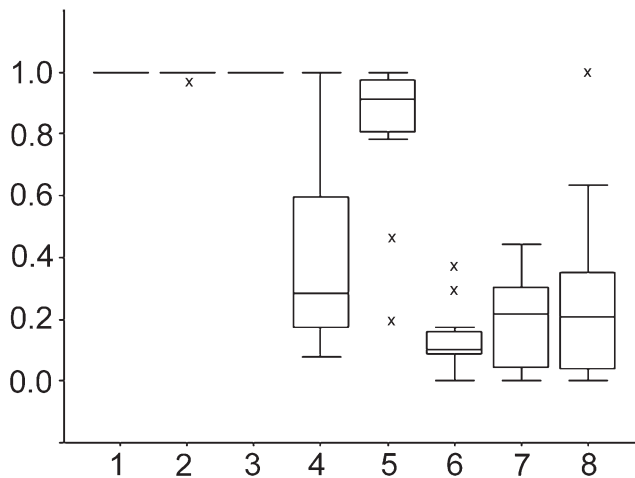


Figure 2. Relative abundance of *Niphargus timavi* at sampling sites 1–8 as box-whiskers plots with the median, lower and upper quartiles, and outliers (x) indicated.

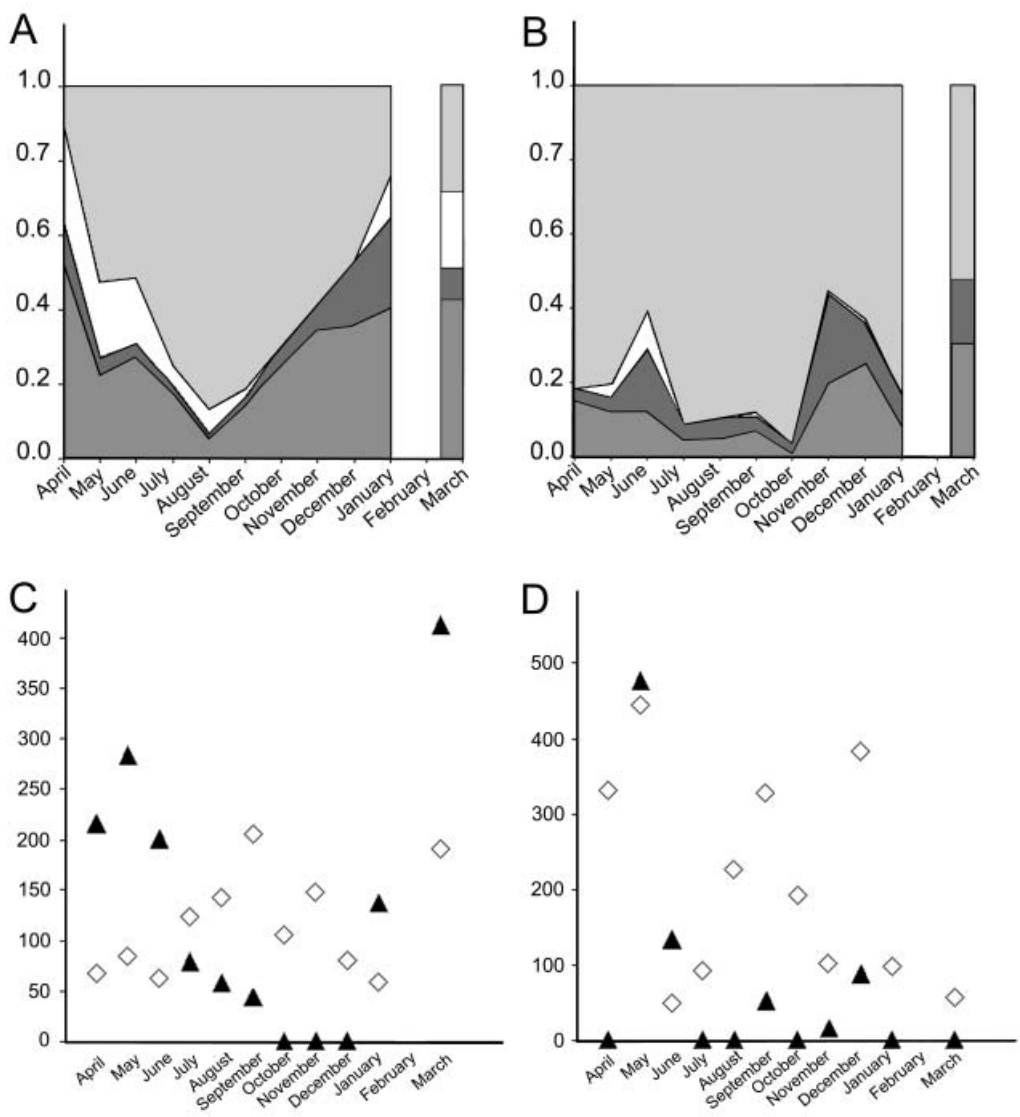


Figure 3. Life cycles of *Gammarus fossarum* (A, C) and *Niphargus timavi* (B, D). (A, B) Relative proportions of males (mid-grey), non-ovigerous females (dark grey), ovigerous females (white), and juveniles (light grey); (C, D) total number of specimens (◇) and total number of eggs (▲); note that several samples have been pooled for *Niphargus*.

(September to December) (Figure 3B, D). In contrast to the gammarids, the peak of juveniles in the niphargid population does not follow the two peaks of the ovigerous females. Instead, the proportion of juveniles fluctuates more or less irregularly throughout the entire year (Figure 3D).

The relative reproductive potential seems to be higher for *G. fossarum* than for *N. timavi*. In *G. fossarum* from 33% (in January) up to 85% of the females (during the high breeding season in June) carried eggs (Figure 4). By contrast, only a minor part (4–50%) of

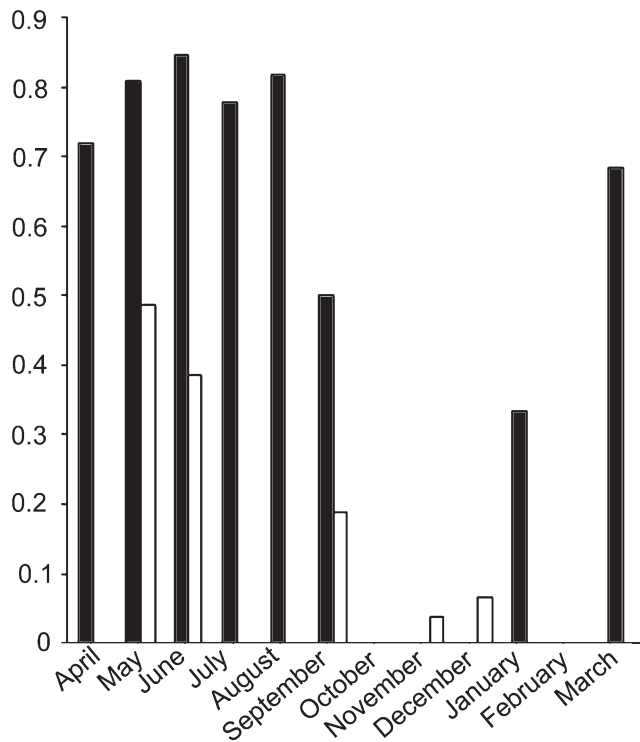


Figure 4. Percentage of ovigerous females for *Gammarus fossarum* (black bars) and *Niphargus timavi* (white bars).

niphargid females carried eggs (Figure 4). Also, the relative number of eggs collected over the year was much higher in the *G. fossarum* population (1.13 per hatched specimen) than in the *N. timavi* population (0.33 per hatched specimen), even though the clutch size of *N. timavi* (7–47 eggs per female) significantly exceeded the clutch size of *G. fossarum* (3–33 eggs per female; Mann–Whitney *U* test: $z = -4.266$, $P < 0.001$). However, the difference in clutch sizes may be a result of body size, which was on average larger in *N. timavi* than in *G. fossarum*.

Discussion

From our results it is obvious that both species co-exist at sampling sites 4–8 through the entire year. It seems they share some aspects of their biology and that their niches most probably overlap to a certain degree. Both species preferentially search for shelter in the decaying organic litter (sharing microhabitat) and possibly compete for food in the oligotrophic stream (see Materials and methods section). However, the remarkable spatial and temporal variability of the populations of the two species (Figure 2) observed in the lower stretch of the brook suggests that interspecific competition influences local abundance of both *G. fossarum* and *N. timavi*. It is noteworthy that preliminary observations in the field and laboratory indicate cannibalistic and predatory behaviour between the two. Cannibalism is well documented in *Gammarus* species (Dick 1995) and predicted in *Niphargus* (Sket 1958; Mathieu and Turquin 1992), while predation has scarcely been studied so far (Dick et al. 1990). The latter probably plays merely a minor

role in the diet of both species, but it could be an important extreme mechanism of competitive exclusion (Dick et al. 1990; Grabowski et al. 2007). Apart from predation, at least two factors could be postulated to play a role in the spatio-temporal-dependent proportions of both species. (1) The hatching of *G. fossarum* could lead to the temporary increase in the gammarid abundance, which consequently decreases the proportion of the more permanent quantity of niphargids. (2) Local and seasonal environmental conditions may favour one of the two species out-competing the other. The absence of *G. fossarum* in the upper three sampling sites points towards its inability to invade the flysch fissure system and its lack of capacity to persist anywhere but in surface waters. The summer dehydration may cause temporary extinctions of the gammarids in the upper parts of the brook, which are followed by re-invasions from the lower stretch of the brook, where water appears to be more permanent (compare the variability of site 4 and sites 6–8, note higher reproductive potential of *G. fossarum*). Conversely, the presence of *N. timavi* in the upper stretch suggests that they might survive the dry period in the ground (similar to French species *N. rhenorhodanensis* Schellenberg (Dhomp-Avenas and Mathieu 1983; Mathieu and Turquin 1992)) or, alternatively, that they actively search or follow the water draining into the subsurface fissure system in the flysch during the dry period (Mathieu et al. 1987). On a spatial scale, the locally enhanced connections with the subterranean water, the kind of “springs” within the brook-bed, could be of special importance for niphargids (e.g. sampling site 5). Considering the similar ecology of *N. rhenorhodanensis* and *N. timavi* it is noteworthy to mention that *N. rhenorhodanensis* has lower metabolism and higher resistance to hypoxia than *Gammarus* species (Hervant and Mathieu 1995; Hervant 1996; Hervant et al. 1997, 1999a, 1999b). Higher tolerance to unfavourable environmental conditions may play a crucial role in the survival of *N. timavi*.

The differences in life cycles are ambiguous and contribute little evidence for the understanding of the co-existence of the two species. The life cycle of *Gammarus fossarum* is clear and it is similar to the life cycles of several other *Gammarus* species (e.g. Hynes and Harper 1972; Zielinski 1995). It is harder to interpret the life cycle of *Niphargus timavi*; the absence of a distinct peak of juveniles and high proportion of juvenile specimens could be explained as a consequence of the assumed longevity and slow development of *Niphargus* species (Ginet 1960). Alternatively, a significant part of the niphargid population could be restricted to the flysch fissures. Ovigerous females collected in the springtime could be washed out from the flysch as a result of the heavier rainfall during that period. The high proportion of juveniles could be a result of dispersion that follows hatching and the cannibalistic pressure of their adult conspecifics, which force them to search for other prospective environments (Mathieu and Turquin 1992). However, it seems reasonable to infer that the reproductive periods of both species are at least in weak agreement and that the reproductive potential of *G. fossarum* exceeds the reproductive potential of *N. timavi*.

The above assumptions can be formalized as a hypothesis on the dynamic relationship between *N. timavi* and *G. fossarum*, which needs to be further tested both in the field and in the laboratory.

Gammarus fossarum can thrive only in the permanent and well-aerated surface water. During the summer dehydration the gammarids become extinct if they fail to move to more permanent water bodies. Its high reproductive potential enables *G. fossarum* to re-invade the brook relatively quickly, and they can function as a serious competitor (and also predator) to *N. timavi*. *Niphargus timavi* can persist due to its ability to occupy the surrounding flysch fissure system and its higher tolerance to stagnant water. This immediate surrounding of the brook-bed acts as a retreat (thus enabling spatial separation),

and enables the survival of the species during the dry period. The presumed resistance of niphargids to starvation and hypoxia plays a crucial role in their survival during the harsher part of the year. Consequently, the dominance of a certain member of the amphipod fauna in such an unstable environment occurs only temporally and is locally limited. It depends on the present (and previous) environmental conditions, and cannot be inferred from a single sampling.

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