Naturwissenschaften (2008) 95:917–926
DOI 10.1007/s00114-008-0399-3

ORIGINAL PAPER

Nested patterns in hyporheic meta-communities: the role of body morphology and penetrability of sediment

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Received: 3 July 2007 / Revised: 28 April 2008 / Accepted: 30 April 2008 / Published online: 10 June 2008

Abstract Nestedness has been regarded as a common pattern of species distribution especially in terrestrial systems and vertebrate faunas. However, a significantly lower degree of nestedness has been reported for aquatic invertebrates. We analyzed the vertical distribution patterns of taxa in the upper 70 cm of the hyporheic zone. This biotope is abundantly inhabited by epigean fauna, which is morphologically pre-adapted to life within the limited space of sediment interstices. We tested the hypotheses that in the vertical profile of the hyporheic zone sediment acts as a physical barrier (filter), allowing only the morphologically pre-adapted and adapted (i.e., smaller, narrower, more flexible) taxa to penetrate to deeper layers. We demonstrated that this mechanism can promote a strongly nested and colonization-driven pattern at higher taxa levels. The sediment filter (1) constricted the body width: 0.50 mm appeared to be the upper limit for successful sediment colonization at the study site, and (2) favored elongated taxa against small sized taxa. We tested also the assumption that distribution of fine sediment affects the accessibility of hyporheic zone for fauna ("filter density") and thereby influences nestedness. However, we found that nestedness could be sufficiently explained by the depth itself. Our study offers a possible explanation of depth patterns in hyporeic meta-communities as a result of morphological characteristics promoting nestedness at higher taxa level.

Keywords Bed sediments · Body size · Colonization · Epigean fauna

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Introduction

During the last two decades, nested patterns of species composition (i.e., nestedness) have been addressed in a large number of empirical and theoretical studies. Nestedness has been shown to be a common pattern in nature since the seminal study of Patterson and Atmar (1986). Particular interest has been given to the mechanisms that promote nestedness, such as selective extinction (e.g., Patterson and Atmar 1986; Wright et al. 1998), selective colonization (e.g., Lomolino 1996), speciation (Cook and Quinn 1995), historical effects (Patterson 1990), habitat nestedness (e.g., Wright and Reeves 1992; Wright et al. 1998), nestedness of habitat quality (Hylander et al. 2005), different reproductive success (Blake 1991), and human disturbances (Fernández-Juricic 2002). However, nested patterns can also be produced as a sampling artefact (see Worthen 1996).

Even though nested distributions are common, at least when focusing on vertebrates or terrestrial assemblages, a considerably lower degree of nestedness has been observed among invertebrates, especially in aquatic environments (Boecklen 1997; Wright et al. 1998). A possible explanation is the high diversity of aquatic invertebrate assemblages that are often composed of many taxa with different origins and/or the scale on which invertebrates are usually sampled (Boecklen 1997; Wright et al. 1998). The apparent lack of nested pattern in freshwater systems was probably the reason why it has been only rarely tested in hydrobiological studies. Exceptions include the studies on distribution of aquatic insects in Sweden (Malmqvist and Eriksson 1995; Nilsson and Svensson 1995; Malmqvist et al. 1999; Malmqvist and Hoffsten 2000), Ostracoda in the Canary Islands (Malmqvist et al. 1997), larval odonates in a river basin in South Carolina, USA

(Worthen 2003), macroinvertebrates in fragmented Alpine streams (Monaghan et al. 2005), and moss-dwelling bdelloid rotifers in a NW Italian stream (Fontaneto et al. 2005). On a large scale, nested patterns have been found within some individual aquatic insect taxa, i.e., Dytiscidae and some Culicidae (Nilsson and Svensson 1995), Ephemeroptera, Plecoptera, Trichoptera, and Simuliidae (Malmqvist and Hoffsten 2000), and Odonata (Worthen 2003). Meta-communities of bdelloid rotifers displayed nested distribution only on an intermediate scale (Fontaneto et al. 2005). But regardless of a taxon being studied or a scale, probable nestedness-promoting factors are often difficult to reveal in freshwater systems because freshwater habitats represent highly variable environments in which suitable conditions result from combinations of a number of factors rather than from one underlying process (e.g., Malmqvist et al. 1999).

The hyporheic zone in running waters is defined as an ecotone between surface water and groundwater. It can be colonized by fauna from both sources—hypogean and epigean (Gibert et al. 1990). Hyporheos (hyporheic fauna), although comprised of taxa with different origins, displays only a few typical morphological adaptations to life within the limited space of sediment interstices, such as miniaturization, shape elongation, higher flexibility, or protective exoskeleton (e.g., Williams and Hynes 1974; Giere 1993). In hard substrates, even primary superficial epigean fauna can take advantage of their body morphology and penetrate deep into the hyporheic zone (up to a depth of 70 cm, Williams and Hynes 1974; Bretschko 1991). We assume that at localities, where epigean fauna prevails and hypogean fauna is relatively rare or absent, the penetration ability of various taxa can be the main factor influencing the community composition of the whole hyporheos in vertical direction and can promote a nested pattern.

In this study, we examined the vertical distribution of invertebrate communities in the hyporheic zone of a gravel stream on the small scale (less than 1 m). We envision the riverbed sediments as a distance filter (Wright et al. 1998), which restricts some taxa from colonizing deeper hyporheic sediments. Thus, samples from deeper layers should be nested subsets of samples from the surface. Further, previously published studies described nestedness as a pattern originating rather from natural processes and ecological traits of species than their morphological characteristics. Here we bring evidence that body shape, which consequently favors penetration abilities of invertebrates, generates nested distributional patterns at the higher taxa level. Because the space limits within sediment interstices do not support shape diversity at any taxon levels (Giere 1993), treating higher and relatively morphologically homogeneous taxa was particularly desirable for testing our hypotheses.

Materials and methods

Study site

The study was carried out in the Loučka River, a fourth order gravel stream with a drainage basin of ca 400 km^2 located in the Hercynian subprovince in the Czech Republic (49°22′32″ N, 16°19′35″ E; 300 m a.s.l.). The riverbed is of gneissic origin and is composed of very poorly sorted gravel with median grain size of 39.5 mm. The discharge in the stream fluctuates highly. For example, during the study in years 2002–2004 the discharges ranged between 0.13 and 24.5 m^3/s, with an average of 1.30 m^3/s (as measured at the gauging station ca 3 km upstream from the sampling site).

Our previous research documented that the upper 70 cm of hyporheic zone at the study site is inhabited by epigean fauna with a ratio of permanent/temporal fauna about 3:1, and both invertebrate density and the number of taxa decrease with the increasing depth (Omesová and Helešic 2007). The gradual reduction of the number of taxa with increasing depth was a precondition for the existence of nested distribution within the vertical profile.

Field sampling and sample processing

To obtain undisturbed samples of the vertical profile in the hyporheic zone, we used the freeze-core sampling (with liquid nitrogen) which consist in freezing the sediment around a metal corer, suggested first for sampling sediment by Stocker and Williams (1972). This method has been shown to be reliable for studies on vertical distribution of hyporheic fauna in gravel streams by many authors (e.g., Williams and Hynes 1974; Bretschko and Klemens 1986; Olsen et al. 2002). The corers were inserted to a depth of 70 cm. A 1-week period was left between inserting and removing the cores in order to allow for settling. After removal, the cores were cut into 10 cm depth layers. Each 10 cm layer represented a sample, but the terminal 20 cm were merged together; thus, we obtained six samples per core. All stones >70 mm were removed from samples. That was because the distribution of large stones in the riverbed was proved to be random and of no special relevance for fauna (Omesová and Helešic 2004). Then the volume of each sample was measured and the material was preserved in 4% formaldehyde.

The cores were taken from two positions in the riverbed: the streamline and the downstream end of a gravel bar. These two positions substantially differed in hydrogeological conditions: the streamline is under the permanent influence of strong water flow and good oxygen supply, whereas the end of the bar shows slow water flow, bad oxygenation, and temporally superficial drying. By sampling the two sites, we thus recorded wide variability of conditions within the river site. The sampling was carried out on five occasions: October 2002, March 2003, July 2003, October 2003, and March 2004, always at discharges close to the annual mean or lower. Our dataset was thus a mixture of spatial and temporal variability, comprising 58 samples (i.e., 6 depth layers×2 sites×5 dates−2 samples that had lost).

Invertebrates were extracted from the samples by elutriation of the sediment through two nets of 250 and 100 μm mesh sizes. Detailed description of the separation method is given in Omesová and Helešic (2004). The elutriated material was divided into subsamples using a laboratory divider, and invertebrates were sorted under a dissecting microscope into main taxonomic groups. Invertebrate counts were standardized for $1\ \mathrm{dm}^3$ volume samples. After elutriation and sorting, the sediment was dried and used for grain size analysis. As a consequence of the used separation method, the study is limited for fraction >100 μm, which concerns both sediment and fauna. The loss of sediment accounts only for about 1.5% (max. 3.5%) of dry weight. The loss of fauna included micro and smaller meiofauna (see "Discussion").

Tested variables

Altogether, we distinguished 16 main taxonomic groups (Appendix 1) which showed only minimal within-group variability of the studied morphological features. Because plecopteran, ephemeropteran, and coleopteran larvae were not abundant and did not display notable morphologic variability at our study site, we treated them as orders. For more diverse insect taxa, namely Diptera, we singled out the families of Chironomidae, Ceratopogonidae, and Simuliidae. Cased Trichoptera did not occur in our samples, otherwise they should be discerned from caseless Trichoptera. Identification to a lower taxonomic level was not performed because (1) it is often unfeasible in hyporheic fauna, where the majority of community consists of small juvenile stages, and (2) it would introduce variability not related to the body morphology.

As the features describing morphological pre-adaptations of taxa to interstitial life, we consider body sizes (length, width, length/width ratio) and body flexibility. Because taxa are composed of individuals in different life stage, they display large variability of body sizes within each group. We were not, however, interested in describing the whole body size variability of taxa but in revealing how body size limits their penetration capability. Therefore, for each taxon we assessed its maximal size in the layer where the taxon reached the deepest occurrence in a core. We visually selected several largest specimens for measuring in order to obtain the highest value. Median of these values was used to characterize the body sizes of each taxon. To characterize body flexibility, we modified a scale created by Gayraud and Philippe (2001) to account for 4° of flexibility, where 4 represented the highest flexibility (>360°, i.e., body can spin around), 3 represented high–medium flexibility (360–130°, body is flexible, it can roll up but cannot spin around), 2 represented medium–low flexibility (130–10°, body is quite flexible but cannot roll up), and 1 represents the lowest flexibility (<10°, body flexibility is limited by shell or exoskeleton; Appendix 1).

As the variables describing accessibility of sediment for fauna, we considered depth and penetrability of layers. As a proxy of penetrability, we used content of grains <1 mm ($G_{<1\ \mathrm{mm}}$), which is easily measurable and negatively related to living space available for sediment-dwelling fauna (Bretschko 1991; Maridet and Philippe 1995). The vertical distribution of $G_{<1\ \mathrm{mm}}$ in the Loučka River is shown in Fig. 1. We also presumed that conditions in other parts of the core, especially above a given layer, may be relevant for penetrability. Therefore, we also calculated two additional variables: (1) max. $G_{<1\ \mathrm{mm}}$, which is the maximal value of $G_{<1\ \mathrm{mm}}$ attained from surface down to each layer, e.g., for a sample from 20 to 30 cm depth, it is the highest $G_{<1\ \mathrm{mm}}$ attained in the samples 0–10, 10–20, and 20–30 cm from the same core; and (2) mean $G_{<1\ \mathrm{mm}}$, which is the mean $G_{<1\ \mathrm{mm}}$ of the whole core.

Ranking of samples for correlation was performed using several different approaches. (1) We created a ranking order of samples using depth of layers alone. Thus, we assigned rank values 1–6 to the samples according to the depth layer

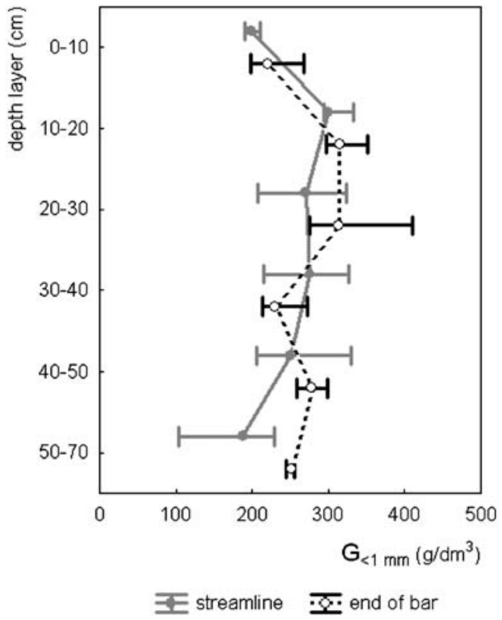

Fig. 1 Vertical distribution of grains <1 mm ($G_{<1\ \mathrm{mm}}$) at streamline and end of gravel bar in the Loučka River (N=5). Medians and quartiles are indicated

(1 for each 0–10 cm, … , 6 for each 50–70 cm). (2) Within the first ranking order we rearranged the samples from the same depth layer along max. $G_{<1\ \mathrm{mm}}$ (see above). (3) Within the first ranking order, we rearranged the samples from the same depth layer along mean $G_{<1\ \mathrm{mm}}$ (see above). (4) To put greater emphasis on the influence of sediment structure and less on the depth, we first arranged all samples according to max. $G_{<1\ \mathrm{mm}}$, and then rearranged the samples with the same max. $G_{<1\ \mathrm{mm}}$ along their depth. (5) We created a ranking order of samples by arranging all samples according to their mean $G_{<1\ \mathrm{mm}}$ and rearranging the samples within the same mean $G_{<1\ \mathrm{mm}}$ according to depth. We assumed that by comparing the strength of the correlations between the sample rank in the packed matrix and the ranking orders of samples described above (see Table 1 A), we would be able to assess the influence of depth and fine grain content on the accessibility of sediment for fauna.

Statistical analysis

Several methods have been developed to assess nestedness, each having different limitations (Atmar and Patterson 1995; Wright et al. 1998; Brualdi and Sanderson 1999; Fisher and Lindenmayer 2002; Higgins et al. 2006; Rodríguez-Gironés and Santamaría 2006). We used the BINMATNEST (Binary Matrix Nestedness temperature calculator)—a new and robust algorithm for calculating nestedness temperature of presence–absence matrices (Rodríguez-Gironés and Santamaría 2006; free version of this software is available at http://www.eeza.csic.es/eeza/personales/rgirones.aspx). This algorithm yields an index called the matrix temperature (T), which ranges between 0 for a perfectly nested matrix and 100 for a maximally "unnested" matrix (Atmar and Patterson 1993). As the matrix temperature is non-dimensional, Rodríguez-Gironés and Santamaría (2006) have proposed to avoid giving any unit to it. To test the significance of the nested pattern, the matrix temperature is compared with a mean temperature of randomly generated matrices. For this purpose, we chose the null-model proposed by Fisher and Lindenmayer (2002) as the biologically soundest null-model with low frequency of type I error (see Rodríguez-Gironés and Santamaría 2006; the null-model 2 in the BINMATNEST). This model accounts for the process known as passive sampling, i.e., ubiquitous species have a higher probability of being drawn at random than rare species (see Fischer and Lindenmayer 2002). Five hundred random matrices were performed using default settings (see above cited website).

To test the influence of proposed factors on nestedness we used Spearman rank correlations (r_{S}): the sample rank in the final nested matrix was correlated with the order of samples after rearranging the samples along the analyzed factors (samples with the same presences and absences were treated as an equal rank); the taxon rank in the final nested matrix was correlated with morphological characteristics of taxa. A significant correlation suggests that a community is packed in a predictive order explainable by a given factor (Patterson and Atmar 2000). We modified α level by sequential Bonferroni rule, i.e., divided α by the number of performed statistical tests (Holm 1979).

Results

We recorded 16 taxonomical groups in 58 samples (Appendix 2). The distribution of taxa was significantly nested: $T^{\circ}_{\mathrm{obs}} = 4.70$, $T^{\circ}_{\mathrm{rand}} = 22.93$, SD=7.21, $P<0.001$. If the two sampling sites were evaluated separately, they both displayed the same low temperature: streamline $T^{\circ}_{\mathrm{obs}} = 5.37$ ($T^{\circ}_{\mathrm{rand}} = 27.33$, SD=12.34, $P<0.001$) and end of the gravel bar $T^{\circ}_{\mathrm{obs}} = 4.17$ ($T^{\circ}_{\mathrm{rand}} = 16.39$, SD=12.28, $P<0.001$).

Table 1 Spearman rank correlations (r_{S}) between ranking orders of taxa/samples originated from the packed matrix and tested variables

	Ranking criteria	r_{S}	P
A: samples (N=58)	Depth	0.63	<0.0001
	Depth, max. $G_{<1\ \mathrm{mm}}$	0.60	<0.0001
	Depth, mean $G_{<1\ \mathrm{mm}}$	0.47	0.0002
	Max. $G_{<1\ \mathrm{mm}}$, depth	0.28	$0.03619^{n.s.}$
	Mean $G_{<1\ \mathrm{mm}}$, depth	−0.04	$0.7767^{n.s.}$
B: taxa (N=16)	Length	−0.17	$0.5276^{n.s.}$
	Width	0.82	<0.0001
	Length/width	0.65	0.0067
	Flexibility	0.66	0.0057

A: sample rank correlated with depth and depth combined with values of fine grains content (max. $G_{<1\ \mathrm{mm}}$, mean $G_{<1\ \mathrm{mm}}$, for explanation see "Materials and methods"), B: taxon rank correlated with body morphology features. α corrected by sequential Bonferroni rule as (A) $P<0.01$, (B) $P<0.0125$

n.s. Not significant

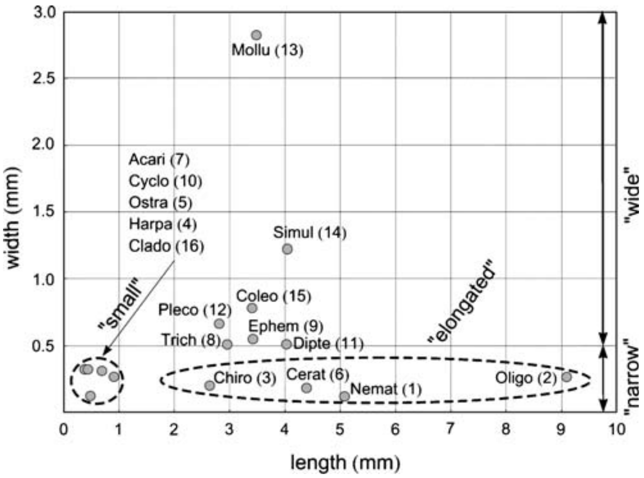

Fig. 2 Median body sizes of studied taxa measured on the largest individuals with the deepest occurrence in cores. *Numbers in parentheses* indicate taxon ranks in the packed matrix. Morphological types (narrow, wide, small, elongated) are marked. For full taxon names see Fig. 3

We found that the depth significantly correlated with the nested pattern (Table 1 A). Taxa recorded in deeper layers were subsets of those found in the upper layers. After rearranging the samples within the same layer along max. $G_{<1\ \mathrm{mm}}$ or mean $G_{<1\ \mathrm{mm}}$, we obtained weaker but still significant correlations. No significant correlation was found when the samples were arranged first along max. $G_{<1\ \mathrm{mm}}$ or mean $G_{<1\ \mathrm{mm}}$ and then along their depth (Table 1 A).

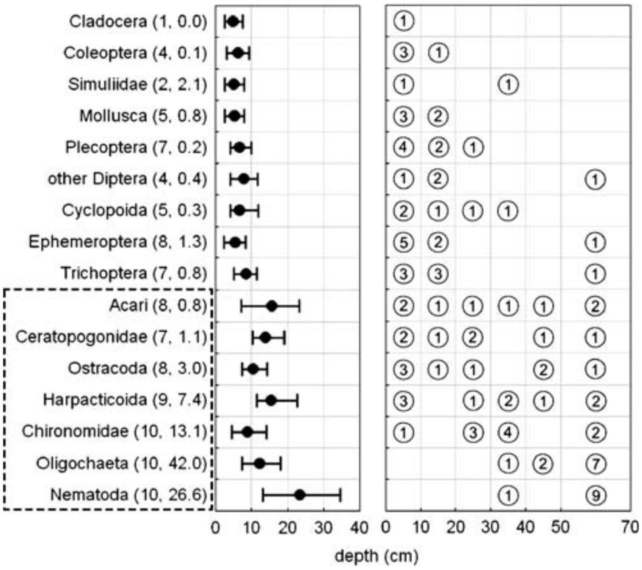

Fig. 3 Mean depth distribution (25%, median, 75%) of the hyporheic taxa in the Loučka River based on abundance data. Taxa are arranged according to their ranking order in the packed matrix. *Numbers in parentheses* (*1*) indicate the number of cores with the taxon presence and (*2*) taxon mean relative abundance (N=10). *Right*: *numbers in circles* represent the number of deepest occurrences of taxa. The first seven taxa in the packed matrix (*dashed box*) showed deeper distribution based on abundances than other taxa

When analyzing correlations of the taxon rank in the packed matrix we found that the body width was the best predictor (Table 1 B). Significant correlations were also observed between the taxon rank in the final nested matrix and length–width ratio and flexibility, whereas no correlation was found with the body length (Table 1 B).

The scatter plot of the body sizes (Fig. 2) shows that several morphological types can be distinguished among taxa: "wide" and "narrow", the latter comprising "small" (i.e., small sized on the whole) and "elongated" type (i.e., small only in one direction). The "narrow" taxa displayed lower ranks in the packed matrix, with the exception of Cyclopoida and Cladocera. The first seven taxa in the packed matrix differed from the rest also by the deeper vertical distribution based on abundance (Fig. 3). These seven most deeply distributed taxa constituted 94% of the total community abundance and "elongated" taxa alone ca 83%.

Discussion

Sediment-dwelling invertebrates usually show a decrease in both abundance and diversity with increasing depth (e.g., Williams and Hynes 1974; Gibert et al. 1990). This decrease is supposed to be related to a general decline in oxygen and food supply (e.g., Williams and Hynes 1974). Here, we found that the decrease of higher taxonomical groups within the vertical profile of a hyporheic zone had the character of a strong nested pattern, in which the number of taxa gradually attenuated and the taxa did not replace each other. This pattern can be explained well by the morphological characteristics characteristics which mechanically enable the penetration of taxa into sediment.

Such a conclusive nested pattern with very low matrix temperature ($T^{\circ}_{\mathrm{obs}} = 4.7$) is exceptional in assemblages of aquatic invertebrates, which have been generally considered to show low degree of nestedness in contrast to terrestrial systems and vertebrates (Boecklen 1997; Wright et al. 1998). The main reason for low nestedness has been seen in a too diverse composition of invertebrate assemblages (Boecklen 1997). Higher nestedness can be thus expected when testing either homogeneous groups of organisms (Malmqvist and Hoffsten 2000) or higher taxonomic levels than species (Wright et al. 1998). By testing higher taxa in our study, it was therefore more likely to detect a significant nested pattern than if testing species. On the species level, we can expect a higher turnover which would result in a warmer packed matrix and less significant nestedness. Further, a possible effect of the exclusion of fauna $<100\ \mu\mathrm{m}$ needs to be considered. This fraction usually includes microfauna (e.g., Rotifera, Tardigrada) and young stages of meiofauna (e.g., Nematoda, Harpacticoida, Acari). However, the meiofaunal taxa have been already recorded in the >100-µm fraction with such high frequencies that only few new occurrences could be added in the matrix if the fraction <100 µm is included. Similarly, including several new microfaunal taxa into the dataset would probably only slightly warm the matrix but not totally impair the overall pattern.

Colonization process in the hyporheic zone

Nestedness in the vertical profile of a hyporheic zone emerges when deeper (hyporheic) layers are colonized by fauna from the stream bottom surface. The dispersion of primary superficially living fauna to deeper sediment can be understood as a favorable strategy of enlarging the living space, just in accordance with the general principle of dispersion as an evolutionary stable strategy (Parker 1984). Extending deeper in the vertical profile can help a taxon to reduce both intra- and inter-taxon competition. In addition, the taxa with extended vertical distributions can use deeper layers as refuges in case of disturbances by flood or drought events (e.g., Schwoerbel 1961; Williams and Hynes 1974; Palmer et al. 1992).

In natural isolated archipelagos, significant nested patterns are attributed to extinction rather than colonization processes (Patterson and Atmar 1986; Wright et al. 1998). Colonization-driven assemblages can produce strongly nested patterns only over short periods of the early succession because even poor dispersers can reach the distant sites given sufficient time (Taylor and Warren 2001; Loo et al. 2002). In the vertical profile of the Loučka River, however, the colonization process through the connected interstitial space generated nestedness over a long period. We assume it to be a stable pattern because the sediment puts up constant resistance against the free spreading of fauna.

The formation of nestedness by colonization along the vertical profile of the hyporheic zone assumes that the only center of faunal dispersion is the surface layer. In this case, the nestedness would be restricted to the topmost layer of the hyporheic zone, the one that was termed “bed sediments” by Bretschko (1991) and was characterized only by the presence of epigean fauna. In the Loučka River, we proved nestedness in bed sediments up to 70 cm depth. Because of sampling limits, we have no information on the lower boundary of the hyporheic zone. The requirement of one colonization center is in apparent contradiction to interpreting the hyporheic zone as an ecotone between surface and groundwater system, where both epigean and hypogean forms are blended (Gibert et al. 1990). In the zones of upwelling groundwater, hypogean fauna can dominate hyporheic community (Dole-Olivier and Marmonier 1992a). We did not find any hypogean forms in our study but potential occurrence of a hypogean form belonging to a taxon already included in our dataset, such as Harpacticoida and Ostracoda, would not disturb the nested pattern because they were frequent also in deep layers. However, occurrence of a new idiosyncratic taxon (e.g., Amphipoda) would elevate the temperature of the packed matrix.

Morphological pre-adaptations

The penetration to deep sediment layers proved to be generally favorable for epigean fauna, even for its temporal component (insect larvae), which need to reach the sediment surface to accomplish the life cycle. For successful passing through the sediment filter, constrictions of body size play the main role in hard substrates (Ward et al. 1998). It is necessary to be small in at least one dimension (Williams and Hynes 1974; Giere 1993). This was also evident in our study, where the body width alone sufficiently explained the nested distribution of taxa within the vertical profile (r_S=0.82, P<0.0001). The narrower a body, the deeper hyporheic layer it was found in. Since the body length was of no importance, we can consider the significant correlation between the taxon rank in the packed matrix and the length–width ratio (r_S=0.65, P<0.01) to be mediated by the body width. Flexibility is naturally connected with the length–width ratio and therefore provided a similar correlation with the taxon rank (r_S=0.66, P<0.01).

The body width showed a bimodal distribution with a lack of taxa between 0.35 and 0.50 mm. This enables to distinguish two well-defined groups of epigean fauna: “narrow” (width up to 0.35 mm) and “wide” (width more than 0.50 mm). Coincidently, there was no gradual change in the vertical distribution of fauna: the “narrow” taxa showed distinctly deeper vertical distribution than the “wide” taxa (Fig. 3). The only exception was Cladocera and Cyclopoida, which were represented by planktonic forms, washed from upstream and only persisted in the sediment. The restricting effect of body width was clearly supported also by the fact that the “wide” taxa (Mollusca and all insect taxa except Chironomidae and Ceratopogonidae) comprised together only ca 5% of the total community abundance. Thus, we conclude that the width of less than 0.50 mm was required for successful colonization of the bed sediments.

Among the “narrow” (well pre-adapted and adapted) fauna, two common morphological types—“small” and “elongated” (Williams and Hynes 1974; Giere 1993)—were clearly distinguishable in our study (Fig. 2). Concluded from their abundance, these morphological groups showed different success in sediment colonization: the “elongated” taxa (Nematoda, Oligochaeta, Ceratopogonidae, and Chironomidae) constituted together nearly 83% of the total community abundance, whereas the small sized taxa (Cladocera, Harpacticoida, Cyclopoida, Ostracoda, and Acari) were less abundant (11.5%). Moreover, elongated taxa showed deeper vertical distribution compared to small sized taxa (Fig. 3). Thus, the elongated shape seemed to be the most favorable morphological pre-adaptation for life within the sediments of the studied river. This is known especially in marine systems where the length–width ratio of typical interstitial animals can be prolonged up to 100:1 (Giere 1993).

Accessibility of sediment

Despite the unquestionable role of body size limits, sometimes even relatively big organisms and exclusive inhabitants of surface water can show surprisingly deep penetration in gravel riverbeds, for example fish (Adamicka 1987; Jurajda and Rulík 2001). Although such records are only exceptional, they indicate that in hard substrates the deep penetration can be both possible and favorable for a wide array of fauna if allowed by the sediment structure.

If we follow further the idea of the filtering sediment, we can easily imagine two possible effects leading to the reduction of taxon number in the vertical profile: (1) with increasing depth the filter is thickened, and (2) with decreasing extent of interstices it becomes denser. However, the nestedness in our study was explained best by the depth itself. Inclusion of the fine sediment characteristics did not improve the correlation and when their importance was given precedence to depth the correlation disappeared completely (Table 1 A). This provides the evidence that individual cores did not differ significantly in their accessibility and that penetrability decreased with increasing depth similarly in all cores. Values of $G_{<1\ \mathrm{mm}}$ were relatively low in the uppermost layers and were maximal in the depth interval of 10–50 cm. The increase of $G_{<1\ \mathrm{mm}}$, which occurred below the 0–10-cm layer, reduced particularly the penetration of "wide" epigean taxa. The finding that arranging the samples from the same depths along max. $G_{<1\mathrm{mm}}$ did not upset the correlation (unlike when arranged along mean $G_{<1\ \mathrm{mm}}$, Table 1 A) suggested that the penetration of epigean taxa to any depth layer is indeed controlled by $G_{<1\ \mathrm{mm}}$ in all the layers above. However, in cases where variability in penetrability among cores is high, the ranking order of samples along mean $G_{<1\ \mathrm{mm}}$ could still be useful.

Living conditions in sediment

Apart from the sediment structure, distribution of invertebrates in the hyporheic zone is driven by other important living conditions, especially oxygen and organic matter contents (Strayer et al. 1997). Gradients in these key factors are induced by hydrogeological patterns, which thus mediate also the depth gradients of hyporheos (e.g., Dole-Olivier and Marmonier 1992b). Therefore, a question arises if the habitat conditions could be the primary promoters of nestedness whereas depth was only their surrogate. When dissolved oxygen and organic matter are delivered to the system mainly by the surface water flow, the sediment acts as their filter as it does for epigean invertebrates, i.e., if the sediment is permeable enough for fauna, it had to be firstly permeable also for oxygen and organic matter. In accordance to that, the organic carbon content in the Loučka River declines with increasing depth (Omesová and Helešic 2007). However, there is some evidence that in less permeable hyporheic sediments vertical distribution of invertebrates can maintain constant in spite of the changes in hydrologic and physicochemical gradients (Storey and Williams 2004). In the Loučka River, we carried out our samplings always at similar discharge close to annual mean. Checking the presence of nestedness at different hydrologic conditions during the season was beyond this study. Nevertheless, the spatial differences in hydrological conditions seemed to have no impact on nestedness in our study—the packed matrices of the two sampling sites both displayed the same low temperature. We think that changes in living conditions are much more sensitively reflected in abundances of invertebrates but do not affect as much nestedness which is based only on presence/absence data. That is because the conditions have to come near to their limit values for a taxon to be completely eliminated or too rare to be sampled. This assumption was supported by the fact that although at the end of a bar there was the same high nestedness as in the streamline, the abundances here were very low which indicates unfavorable conditions for fauna (Omesová and Helešic 2007).

Of course, morphological adaptations for life within sediments are naturally accompanied by physiological adaptations which enable surviving in deeper layers, such as more effective uptake and diffusion of dissolved organic substances and gasses (Giere 1993). Thus, not only the body shape itself but also the physiological features can contribute to different depth distribution of taxa, and thus co-create nestedness. From this point of view, we can speculate about to which measure an extinction process, that excludes less physiologically pre-adapted and adapted taxa from less saturated (deeper) layers, can also participate on maintaining nested pattern in the hyporheic zone.

Acknowledgments We are obliged to many co-workers in the field and to Marcela Růžičková for helping in the laboratory. We thank Adam Petrusek and Stano Pekar for the critical reading of the previous version and Nicole Cernohorsky for language corrections. The project was supported by grants from the Ministry of Education of the Czech Republic (MSM 0021622416) and from the Czech Grant Agency (No. GA 206/02/0902).

Appendix 1

Table 2 Median body size and flexibility of studied taxa. Body sizes were measured on the largest individuals with the deepest occurrence in cores; taxa flexibility was expressed using a 4° scale from the lowest to highest flexibility (for a detailed explanation see “Materials and methods”)

	Length (mm)	Width (mm)	Length/width ratio	Flexibility
Nematoda	5.09	0.11	49.8	4
Oligochaeta	9.10	0.26	34.6	4
Mollusca	3.49	2.82	1.2	1
Cladocera	0.39	0.32	1.2	1
Cyclopoida	0.91	0.27	4.1	2
Harpacticoida	0.50	0.12	4.0	3
Ostracoda	0.69	0.31	2.0	1
Acari	0.44	0.32	1.4	1
Ephemeroptera	3.43	0.55	5.0	2
Plecoptera	2.82	0.66	4.9	2
Trichoptera	2.96	0.51	7.4	3
Chironomidae	2.65	0.20	13.5	3
Ceratopogonidae	4.40	0.18	24.4	3
Simuliidae	4.06	1.22	3.5	2
Diptera—other	4.05	0.51	6.6	2
Coleoptera	3.41	0.78	3.8	2

Appendix 2

Table 3 Packed matrix of 16 taxa×58 samples. Numbers in the heading represent depth layers of samples: 1—0–10 cm, 2—10–20 cm, 3—20–30 cm, 4—30–40 cm, 5—40–50 cm, 6—50–70 cm

	1	1	1	1	1	2	1	2	2	2	6	3	4	3	1	1	5	2	3	1	2	4	2	2	3	5	4	3	1
Nematoda	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Oligochaeta	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Chironomidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	0	1
Harpacticoida	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	0	0	1	0	0	1	1	0	1	0
Acari	1	1	1	0	1	1	1	1	0	1	0	1	1	1	0	0	1	0	1	1	0	1	0	0	0	1	0	0	0
Ceratopogonidae	1	1	1	1	0	1	0	1	1	1	0	1	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1
Ostracoda	1	1	1	1	1	1	1	1	1	0	1	1	0	0	1	0	1	0	1	0	0	1	1	1	1	1	1	0	0
Trichoptera	1	1	1	1	0	1	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0
Ephemeroptera	1	1	1	1	0	0	1	0	0	0	1	1	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0	0	0
Cyclopoida	1	1	1	1	0	0	0	1	1	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Plecoptera	1	1	1	1	0	1	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Diptera-other	1	0	1	1	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Simuliidae	1	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mollusca	1	1	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coleoptera	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cladocera	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 3 (continued)

	4	6	6	5	5	2	6	3	4	4	3	6	4	2	4	6	3	5	4	5	4	5	3	5	6	5	6	6	3
Nematoda	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Oligochaeta	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0
Chironomidae	0	0	0	0	0	1	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Harpacticoida	0	1	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acari	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratopogonidae	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostracoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trichoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ephemeroptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyclopoida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plecoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diptera-other	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Simuliidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mollusca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coleoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cladocera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

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