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Floodplain restoration by reinforcing hydrological connectivity: expected effects on aquatic mollusc communities

WALTER RECKENDORFER,* CHRISTIAN BARANYI,† ANDREA FUNK* and FRITZ SCHIEMER*

**Department of Limnology and Hydrobotany and †Department of Microbial Ecology, Vienna Ecology Centre, Faculty of Life Sciences, University of Vienna, A-1090 Vienna, Austria*

Summary

1. One of the main targets of river–floodplain restoration is the reconnection of former side channels. While there is information about the overall impact of such measures, far less is known about specific species' response patterns to hydrological connectivity.

2. The present study examined the composition of aquatic mollusc communities based on the performance of individual species with respect to hydrological connectivity in the Donau-Auen National Park, Austria. Species' traits were used to make generalizations about community responses to hydrological changes.

3. We introduced a connectivity parameter (*Cd*, expressed in days year^{-1}) that could easily be derived from the river hydrograph and altitude of the inflow areas. This parameter integrated several key features of floodplain waterbodies and reflected the cause–effect chain of restoration schemes, thus allowing the outcome of restoration measures to be quantitatively predicted. Endangered rheophilic mollusc species reached higher frequencies as connectivity increased; for most eurytopic molluscs, however, increased connectivity reduced abundance.

4. With respect to species' traits, the proportion of large gastropods declined continuously with increasing *Cd*, whereas the percentage of gastropods with globolose shells and the relative number of strongly calcified (thick-shelled) individuals both increased. Species dominating in isolated sites were characterized by a higher resistance to desiccation, a food preference for higher plants and a preference for less shaded habitats. They matured later and typically had more offspring than rheophilic species.

5. Species number peaked at connectivity (*Cd*) values of about 1 month year^{-1}. Isolated and lotic habitats hosted significantly fewer mollusc species. Species turnover was highest when *Cd* was between 0 days and 2 months.

6. *Synthesis and applications*. Empirical models based on a connectivity parameter can be used to predict the consequences of restoration measures on the aquatic mollusc community in the Donau-Auen National Park. The analysis of species' traits also allows general prognoses for other river–floodplain systems. Furthermore, initial results based on other taxa indicate a broad applicability of the parameter. The methodology thus provides both an urgently needed and a practical tool for predicting the impact and success of restoration schemes.

Key-words: diversity, indicator species, river, river-engineering, species' trait, Unionidae, wetland

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Correspondence: Walter Reckendorfer, Department of Limnology and Hydrobotany, Althanstrasse 14, A-1090 Vienna, Austria (e-mail walter.reckendorfer@univie.ac.at).

Introduction

The loss of aquatic mollusc species, particularly mussels, is a global phenomenon that is mainly attributed to human activities (Layzer, Gordon & Anderson 1993; Strayer & Ralley 1993; Vaughn & Hakenkamp 2001). The most destructive impacts are alterations of stream hydrology as a result of damming and river regulation. River–floodplain habitats in particular have been strongly affected by these measures, which have initiated long-term trends towards terrestrialization and fragmentation of the river–floodplain systems (Dynesius & Nilson 1994; Ward, Tockner & Schiemer 1999).

In order to re-establish (semi)natural conditions within the human-altered river–floodplain systems, rehabilitation programmes have become increasingly important (Ormerod 2003; Giller 2005). Fluvial dynamics have proved to be important driving forces for the development of long-term self-sustaining alluvial river landscapes that exhibit a high degree of biodiversity (Amoros & Roux 1988; Ward & Stanford 1995; Tockner *et al*. 1999; Ward *et al*. 2002; Palmer *et al*. 2005). Thus the key step in river–floodplain restoration schemes is the enhancement of the lateral integration between the river and its floodplain (Schiemer 1999; Schiemer, Baumgartner & Tockner 1999; Buijse *et al*. 2005), which can be done by side-arm reconnections. This approach, which is described as passive and slow (Giller 2005; Gillilan *et al*. 2005), allows natural hydraulic forces to reshape waterbodies and reinstall the natural heterogeneity. Reconnecting old river branches may increase fine sediment removal, foster geomorphic processes and thereby increase the turnover rate between aquatic and terrestrial habitats. Other goals achievable via side-arm reconnection include compensation for structural shortfalls in the main channel and reduction of the bed scour in the main channel (Reckendorfer *et al*. 2005).

For ecologically orientated planning of side-arm reconnections, it is essential to gain an understanding of the relationship between hydrological connectivity and the requirements and performance of the biological components of the floodplain ecosystem. Such an understanding, together with knowledge of community assembly, interactions and functions, is crucial for quantitatively assessing the ecological outcome of restoration projects (Pywell *et al*. 2003). The importance of such conceptual models has recently been emphasized by Jansson *et al*. (2005). During this process of describing the ecological mechanisms prior to adopting particular restoration strategies, potentially conflicting processes may be identified and strategies may even be reconsidered (Jansson *et al*. 2005).

The hydrological connectivity between the main course of a river and various waterbodies lying in the alluvial floodplain strongly influences biogeochemical fluxes, biodiversity and the food-web structure of these waterbodies. Several of these aspects [e.g. the effect of water retention time on carbon fluxes, phytoplankton and bacterial productivity (Aspetsberger *et al*. 2002; Hein *et al*. 2003) but also on zooplankton biomass and community structure (Baranyi *et al*. 2002) and zooplankton grazing effects (Keckeis *et al*. 2003)] have been analysed in detail in the Danube Restoration Program, the first major restoration programme executed in the free-flowing section of the Austrian Danube east of Vienna in the Donau-Auen National Park (DANP). It has also been demonstrated that hydrological connectivity is significant for the diversity patterns of various vertebrate and invertebrate groups, including molluscs (Tockner *et al*. 1999), where diversity was highest in backwaters with intermediate connectivity.

While the significance of hydrology in determining the distribution of molluscs has been suggested by many authors (Foeckler 1990; Strayer 1993; Foeckler *et al*. 1994; Mouthon 1998), detailed information on the effects of hydrology are lacking and, until now, only qualitative statements on the outcome of river–floodplain rehabilitation schemes are possible.

Bivalves and gastropods have an important impact on riverine ecosystems through filter feeding, deposit feeding, bioturbation and nutrient excretion (Brown, Alexander & Thorp 1998; Vaughn & Hakenkamp 2001). Together with the well-known threat of extinction for these taxa, it is crucial to gain an improved understanding of the factors determining their distribution, for both ecosystem restoration and conservation efforts.

The present study analysed the composition of mollusc associations in a river–floodplain system based on the performance of individual species with respect to hydrological connectivity. We relate a quantitative measure of connectivity to species' traits such as body size, feeding habits and desiccation resistance, with the aim of generalizing on the mechanisms underlying community responses to hydrological change.

Specifically, we addressed the following questions. (i) What effect does varying hydrological connectivity have on different mollusc species? (ii) Can meaningful, quantitative predictions be based on an easily derived hydrological parameter? (iii) What implications do these predictions have for the planning of future restoration programmes?

Methods

STUDY AREA: THE DANP IN AUSTRIA

The Danube River, the second largest river in Europe, is 2900 km long and drains an area of 817 000 km^2. At Vienna the Danube is a ninth-order river with a mean annual discharge of about 1950 m^3 s^{-1} and a bank-full discharge (recurrence time of approximately 1 year) of 5800 m^3 s^{-1}. The average slope in this section is 0·45‰. In 1996 the river–floodplain system east of Vienna was given national park status (DANP). The size of the national park area is about 93 km^2 and comprises 65% floodplain forest, 20% water area and 15% meadows and fields.

Historically braided, the river–floodplain system has been constrained by the major regulation schemes that began in 1875 (Fig. 1). Restoration in this stretch

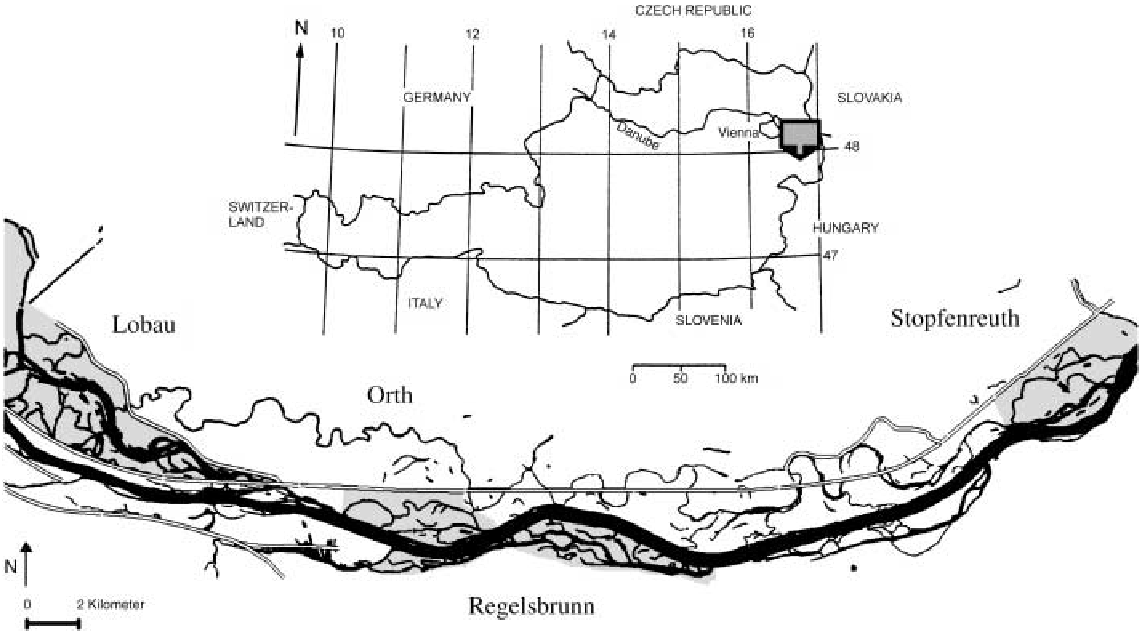

Fig. 1. The Austrian Danube and the study site in the Donau-Auen National Park (DANP). Black lines, water area; open lines, flood protection dyke; the grey areas mark the mentioned floodplain segments.

started in the mid-1990s. To improve the connectivity between the side arms and the main channel, abandoned side channels were reconnected to the Danube River by reactivation of former inflow channels. Existing check dams that crossed side arms and divided them into single sections were removed and additional outlets were created. Detailed descriptions of the restoration works can be found elsewhere (Tockner & Schiemer 1997; Schiemer, Baumgartner & Tockner 1999). Today the connectivity between the main channel and floodplain waterbodies is partially intact (Baranyi *et al.* 2002; Reckendorfer & Steel 2004) and the DANP contains sections of differing connectivity (Fig. 2). The dominant habitat type (40%) comprises disconnected habitats. Areas of intermediate and high connectivity (> 30 days) account for 11% and 18%, respectively (Fig. 2). Implementation of the Integrated River Engineering Project (IREP) of the Austrian Federal Waterway Agency (Reckendorfer *et al.* 2004) is expected to further increase connectivity. The planned river branch reconnections should raise the proportion of highly connected and lotic side channels to more than 60% of the total water surface area.

SAMPLING AND DATA ANALYSIS

Connectivity (*Cd*) is defined as the average annual duration (days per year, mean of 1961–90) of the upstream surface connection of floodplain waterbodies with the main stem of the Danube River. This parameter primarily depends on the flow pattern of the river and the position of these waterbodies relative to river height (Hillman & Quinn 2002). It was derived from data on: (i) the stage–discharge relationship of the river at the upstream end of each channel; (ii) the discharge frequency distribution of the river; and (iii) the stage at which water flows into the channel. The altitude of the inflow area and the water level data were provided by the Austrian Federal Waterway Agency (Austrian Federal Waterway Agency 1997). *Cd* was calculated for each waterbody within the study area. Waterbodies were delineated from aerial photographs (provided by the National Park Donau-Auen GmbH, Orth/D, Austria) based on inflow areas and transversal check dams using ArcView 3·1.

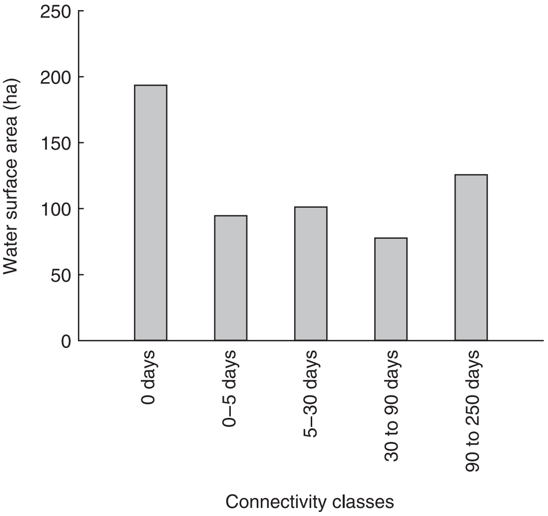

Fig. 2. Surface area of waterbodies of different connectivity (excluding the main channel) for the whole Donau-Auen National Park area.

A total of 735 quantitative samples, spanning a connectivity range from 0 to 235 days year^{-1}, was collected between May and October in the years 1995 and 1996 and 1999–2003. Sampling encompassed various

Table 1. Number of samples taken at different connectivity levels: disconnected waterbodies, isolated sites connected at bank-full discharge (0–5 days year^{-1}), 5–30 days year^{-1}, 30–90 days year^{-1} and 90–250 days year^{-1}

Group	Phrase used in text	Connectivity (days)	Number of samples	Samples with molluscs
1	Disconnected	0	82	45
2	Isolated	0–5	172	131
3	Short connectivity	5–30	215	179
4	Intermediate connectivity	30–90	92	66
5	High connectivity	90–250	174	120

waterbodies located in floodplain sections on the right (e.g. Regelsbrunn) and left (e.g. Lobau, Orth and Stopfenreuth) banks of the Danube River (Fig. 1). No samples were available from the main stem. Samples were grouped according to their degree of connectivity (Table 1).

Molluscs were collected using a sediment dredge with an average sediment sample volume of 7 L (0·5–16 L). When high macrophyte densities occurred at a sampling station, macrophytes where additionally sampled with the dredge and the total volume of sediment plus macrophytes in the dredge was estimated. Sampling was confined to the littoral zone with water depths between 0 and 140 cm.

The sediment was sieved through a 1-mm mesh net. All molluscs retained in the net were preserved in 96% ethanol for subsequent identification, except for the Unionidae which were identified directly in the field. Molluscs were identified to species level following Glöer & Meier-Brook (1994). Seventy-four per cent (541) of samples contained molluscs and were used for further analysis.

Biotic and abiotic variables estimated at each sampling point included density of macrophytes (% cover), sampling depth (cm), shading by trees (as angle to the horizon in four directions in degrees) and sediment characteristics [fine sediment layer (cm), proportion of fine sediment in the dredge (%) and diameter of the largest stone in the dredge (mm)].

A second environmental data set was gathered independently from the mollusc samples and restricted to restoration sites. Data included current velocity and shear stress (one-dimensional hydraulic model), sediment composition, water depth and macrophyte densities. These features are also commonly considered to be important determinants of mollusc distribution patterns (Strayer 1993).

Detrended correspondence analysis (DCA) of the sampling sites based on the mollusc abundance data was performed using the software package CANOCO for Windows (Version 4·5). DCA proved to be the most suitable analysis for these communities because the gradient length of the first canonical axis was greater than 7 SD. Species occurring in fewer than three samples were excluded from analysis because rare species (in terms of occurrence) can seriously bias the outcome of ordination analysis. If *Cd* affects mollusc distribution, then the DCA scores of the samples should be significantly correlated with *Cd*. Single species should then differ in their optimum and tolerance range with respect to *Cd*. Thus we calculated the median as well as the 5% and 95% percentiles of *Cd* for each species. The mean was interpreted as the species' optimum (with respect to connectivity) and the percentiles as the species' range.

Species' traits are used to make generalizations about the mechanisms underlying the community responses to hydrological changes. We derived the species' traits from Falkner *et al.* (2001) and considered traits that are presumably interpretable with regard to hydrological connectivity. These included finite body size, shell shape and shell thickness, oxygen and temperature tolerance, feeding habits and the ability to resist desiccation. We did not consider some morphological traits (e.g. number of whorls, ornamentation of the shell and periostracal structures) that are not easily interpretable and physiological traits with low variability in the sample (i.e. which are the same for all aquatic molluscs, such as humidity preference and inundation tolerance).

In the database (Falkner *et al.* 2001) the association between a species and categories of a trait is described using a fuzzy coding technique with values ranging from 0 (no association to a trait category) to 3 (strong association to a trait category) and a species can fall into several categories of a single trait. The disadvantage of this coding technique is that arithmetic operations cannot be performed. In order to allow calculation of the numbers of individuals in a specific trait category for a sampling site or to combine two trait categories into a single one, the data from the database (Falkner *et al.* 2001) were transformed into a frequency distribution according to Tachet *et al.* (2003). For example, in Falkner *et al.* (2001) *Valvata piscinalis* received 3 points for the category deep shade and 3 points for the category light shade in the trait light preference. We transformed these values to 0·5 and 0·5, respectively (the sum of the scores for a given trait equals 1). The total number of individuals in a trait category was calculated as $N_{tc} = \Sigma(N_i \times C)$, where N_i is the abundance of species *i* and *C* is the score of the respective category. This procedure refers to existing macro-invertebrate analyses, such as the assessment of biological water quality, the calculation of longitudinal stream zonation patterns and functional feeding groups and the calculation of the floodplain index (Zelinka & Marvan 1961; Moog 1995; Chovanec *et al.* 2005).

The mean percentage of individuals in each trait category was calculated for every trait and connectivity group (Table 1) and analysed by a chi-quadrat test.

Table 2. Characterization of waterbodies differing in connectivity, mean value (number of samples). POM, particulate organic matter; KI, Kohler index

			Connectivity (days)				
Scale	Parameter	Unit	0	0–5	5–30	30–90	90–250
Macrohabitat	Velocity at mean water	$m\ s^{-1}$	0·0	0·0	0·0	0·0	0·2 (280)
	Velocity at high water	$m\ s^{-1}$	0·0	No data	0·9 (236)	1·0 (122)	1·0 (413)
	Shear stress at mean water	$N\ m^{-2}$	0·0	0·0	0·0	0·0	2·0 (280)
	Shear stress at high water	$N\ m^{-2}$	0·0	No data	7·7 (158)	5·7 (122)	8·3 (280)
	Mean grain size	mm	0·6 (38)	0·3 (44)	3·4 (65)	9·9 (38)	8·3 (89)
	Proportion of fine sediment	%	82·1 (47)	98·0 (88)	88·7 (130)	72·7 (26)	69·9 (95)
	Layer of fine sediment	cm	43·5 (1414)	112·1 (168)	18·3 (2334)	8·8 (1221)	13·3 (2053)
	POM	%	9·0 (148)	5·3 (44)	2·2 (65)	1·8 (25)	1·7 (89)
	Macrophyte density	KI	4·1 (425)	2·4 (134)	1·6 (268)	2·0 (23)	1·8 (97)
	Maximum depth at mean water	m	0·2 (43)	0·4 (223)	2·4 (100)	3·7 (11)	2·8 (36)
Microhabitat	Depth	cm	34 (82)	36 (162)	42 (162)	43 (87)	49 (173)
	Macrophyte cover	%	29 (82)	28 (162)	5 (152)	4 (87)	2 (166)
	Shading	Angle to horizon	47 (82)	53 (136)	57 (132)	50 (86)	51 (174)
	Fine sediment layer	cm	51 (45)	117 (122)	81 (133)	45 (84)	69 (169)
	Fine sediment proportion	%	88 (80)	97 (149)	87 (153)	70 (87)	73 (172)
	Largest stone	mm	7 (78)	2 (149)	10 (153)	22 (87)	16 (173)

This analysis was restricted to gastropods because we were unable to find comparable data for bivalves in the literature. Species' ranges were used to calculate the theoretical species number at any point along the *Cd* gradient. A species was assumed to occur at a specific point of the *Cd* gradient when this *Cd* value fell within the species' range. The theoretical species turnover was estimated using the individual ranges. Turnover here refers to the number of theoretically appearing and disappearing species plotted against the *Cd* gradient. The shape of these two curves indicates where the major community changes take place and thus in which habitats restoration measures would cause the maximum impact.

Results

CHARACTERIZATION OF WATERBODIES DIFFERING IN HYDROLOGICAL CONNECTIVITY

The connectivity parameter (*Cd*) integrated several features of the different waterbodies, such as current velocity, sediment composition, shear stress and macrophyte densities. Sedimentation in disconnected and isolated waterbodies leads to a reduction in water depth. These effects could be seen at both the microhabitat and macrohabitat scales (Table 2).

Disconnected waterbodies thus corresponded to intermittent to permanent waterbodies with high macrophyte cover. Water velocity and shear stress were 0 so that autochthonous sediments were not removed. This led to accumulation of fine sediments with a high organic content. Isolated habitats were very similar to disconnected ones, but because of additional allochthonous sediments the fine sediment layer exceeded that of disconnected habitats.

The other groups were very similar and corresponded to permanent waterbodies with low macrophyte cover. The main difference was in their sediment grain size.

SPECIES COMPOSITION

A total of 59 aquatic mollusc species was found during this study (see Appendix S1 in the supplementary material), of which 71% were registered on the Red List of Austria (Frank & Reischütz 1994). Seventeen were classified as endangered, 17 as vulnerable and eight as rare. *Valvata piscinalis* had the widest distribution range and was represented in 33% of all samples. Most other species were represented in only 1–10% of samples, while 23 species were found in less than 1% of all samples. The 10 most frequently encountered species, *Valvata piscinalis*, *Lithoglyphus naticoides*, *Bithynia tentaculata*, *Sphaerium corneum*, *Dreissena polymorpha* and five species of the genus *Pisidium* (see Appendix S1 in the supplementary material), accounted for 76% of the total mollusc abundance. The mean abundance of these species ranged between 3·8 and 49·4 individuals 100 L^{-1}, while 35 species did not reach a mean density of 1 individual 100 L^{-1}.

SIGNIFICANCE OF HYDROLOGICAL CONNECTIVITY FOR MOLLUSC DISTRIBUTION

DCA (Fig. 3) and correlation analysis demonstrated a significant relationship between mollusc community structure and the hydrological conditions. The first canonical axis (DCA axis 1) was significantly correlated with the degree of connectivity (Spearman's correlation coefficient $R = 0{\cdot}52$, $P < 0{\cdot}01$). Samples along DCA axis 1 ranged from disconnected stagnant waterbodies (mean 1 on Fig. 3) to highly connected habitats

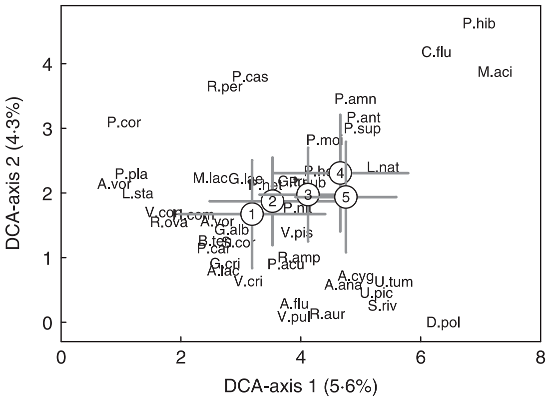

Fig. 3. Ordination of the sampling locations by detrended correspondence analysis (DCA) based on 541 mollusc samples. The mean (± SD) of each defined connectivity class (1–5; Table 1) is given in addition to the distribution of the species (for abbreviations see Appendix S1) on the first factorial plane.

(mean 5 on Fig. 3). This hydrological sequence of mollusc species along the connectivity gradient showed a clear taxonomic pattern (Fig. 4). Sites with high connectivity were dominated by bivalves such as *Corbicula fluminea*, *Unio tumidus* and *Unio pictorum*, whereas disconnected and isolated sites were typically dominated by pulmonates such as *Lymnea stagnalis* and *Planorbarius corneus*. Prosobranch species covered the widest hydrological range, from disconnected sites (*Viviparus contectus* and *Valvata naticina*) to highly dynamic waterbodies (*Lithoglyphus naticoides* and *Potamopyrgus antipodarum*).

The relationship between species' range and species' optima could be described with a quadratic relationship (Fig. 4, inset). Species for which isolated sites were optimal generally possessed a low connectivity tolerance. The mollusc community of such stagnant waterbodies included species such as *Viviparus contectus*, *Anisus vortex* and *Planorbarius corneus*. Species with

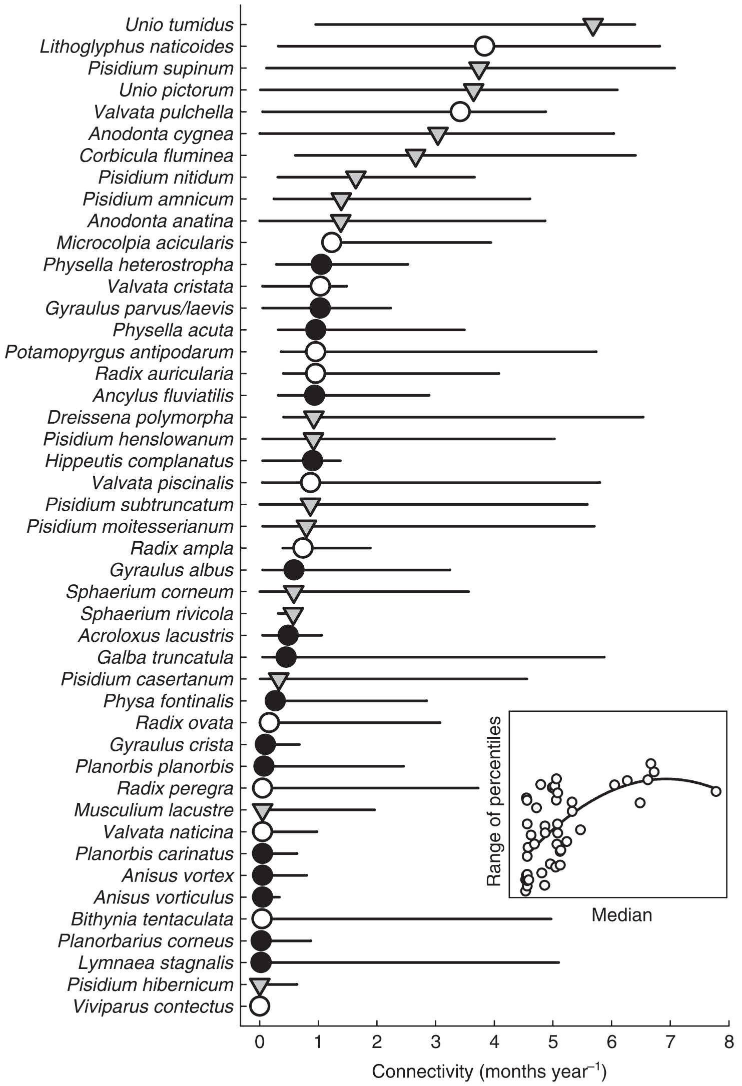

Fig. 4. Species' optima (median) and tolerance ranges (5% and 95% percentile) with respect to connectivity. Grey triangles, bivalves; white circles, prosobranchs; black circles, pulmonates. Inset, the relationship between species' optima and tolerance ranges (for details see text).

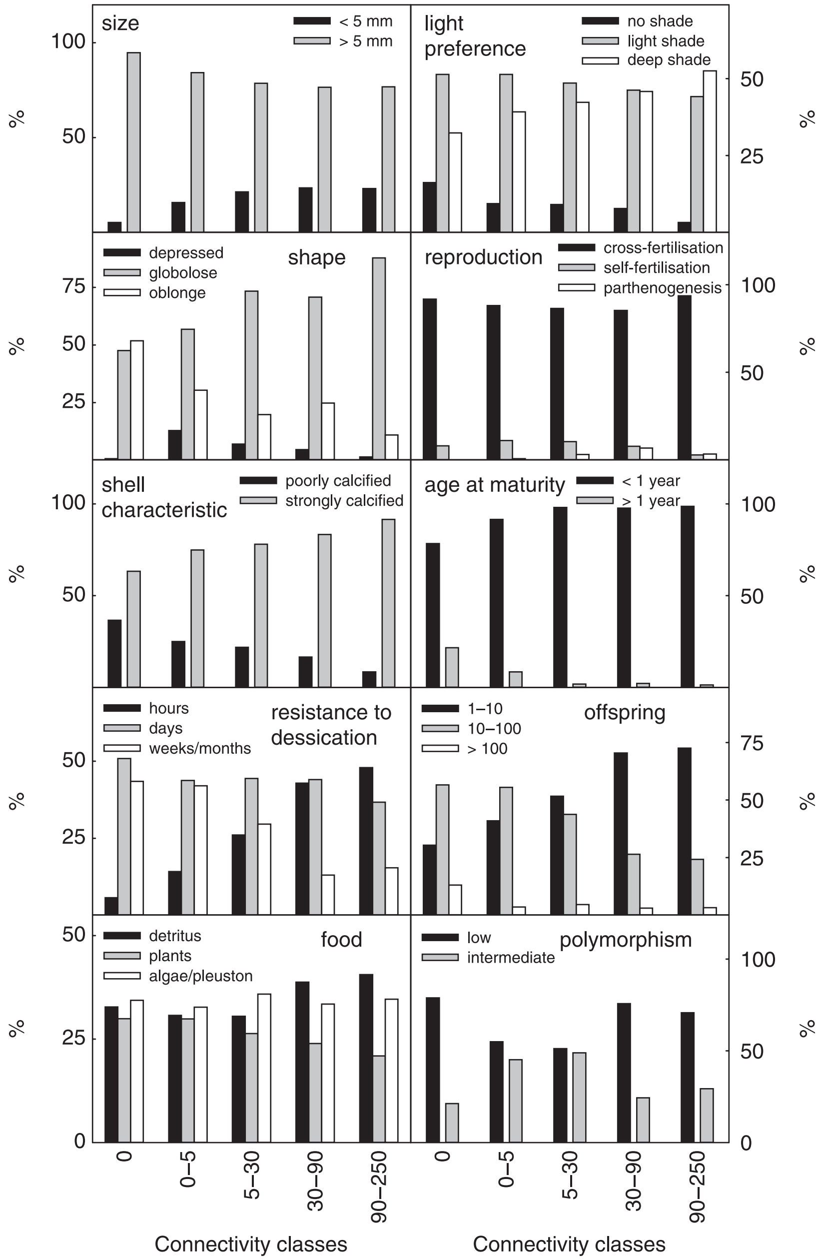

Fig. 5. Selected species' traits of gastropods along the connectivity gradient (percentage of individuals).

optima under more lotic conditions also had broader ranges (e.g. *Corbicula fluminea*, *Lithoglyphus naticoides*, *Unio tumidus*, *Unio pictorum* and *Pisidium supinum*).

All analysed traits showed clear variation between the defined connectivity groups (Fig. 5; chi-quadrat, *P* < 0·001). For example, the proportion of large (> 5 mm) gastropods declined continuously with increasing *Cd* (chi-quadrat 692, d.f. = 4) whereas the percentage of gastropods with globolose shells (chi-quadrat 4372, d.f. = 8) and the relative number of strongly calcified (thick-shelled) individuals (chi-quadrat 1614, d.f. = 4) increased with connectivity (Fig. 5). Species dominating in disconnected and isolated sites were characterized by a higher resistance to desiccation (chi-quadrat 5211, d.f. = 8), a food preference for higher plants (chi-quadrat 436, d.f. = 8) and a preference for less shaded habitats (chi-quadrat 979, d.f. = 8). They matured later (chi-quadrat 2819, d.f. = 4) and typically had more offspring than rheophilic species (chi-quadrat 3913, d.f. = 8). Intraspecific variation (polymorphism) was most pronounced in species inhabiting shortly connected habitats (chi-quadrat 2060, d.f. = 4).

Species number followed a hump-shaped relationship with *Cd*, peaking at a connectivity value of approximately 1 month (Fig. 6a). Species turnover along the hydrological gradient was high in the low connectivity range (Fig. 6b), where small shifts in *Cd* led to drastic changes. The whole local species pool was present at low connectivity (0 to *c*. 1 month; Fig. 6b). No new species appeared at more dynamic sites (> 1 month). Thus, the turnover was characterized by the appearance of many species at *Cd* values slightly higher than 0 and by a continuous disappearance of species at higher connectivity values.

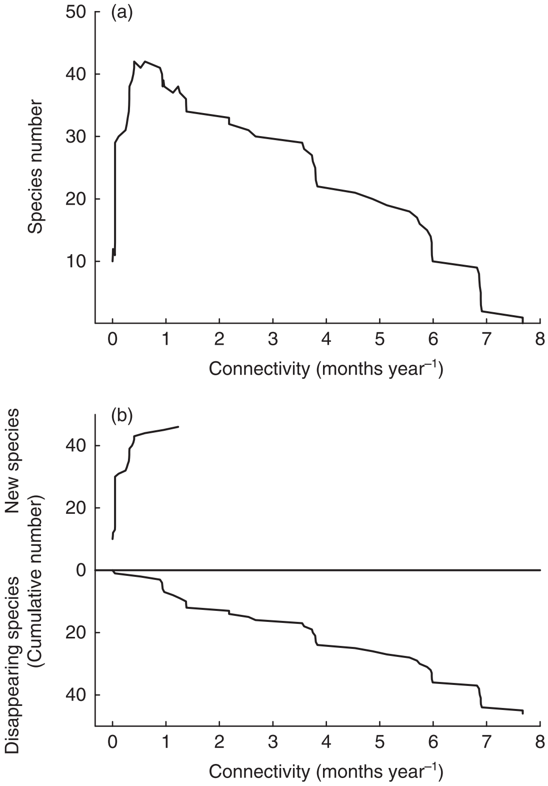

Fig. 6. Theoretical species number and species turnover along the connectivity gradient. For details see text.

Rare and endangered species were represented in all habitats, with numbers increasing with connectivity from 3% to 15%.

Discussion

THE SIGNIFICANCE OF HYDROLOGICAL CONNECTIVITY FOR SPECIES' ASSOCIATIONS AND UNDERLYING SPECIES' TRAITS

The 59 mollusc species identified (39 gastropods and 20 bivalves) represented approximately 80% of all mollusc species occurring in the Austrian Danube. Moreover, these species accounted for 35% of the gastropods and more than 60% of the bivalves registered in the species list of central Europe (Moog 1995; Moog, Humpesch & Konar 1995). Comparable species numbers (46 in total) and a similar species composition occurred in a floodplain system of the Danube River in Germany (Foeckler 1990; Foeckler *et al.* 1994).

Hydrological connectivity between the main stem of the river and the associated floodplain waterbodies has a major bearing on both diversity and distribution of species. The latter was indicated by the distinct connectivity optima and range of individual species, with species possessing the narrowest ranges (habitat specialists) found under completely lentic conditions. Traits favoured in these habitats were oxygen and temperature tolerance, large body size and the ability to resist desiccation. Typical species included pulmonates such as *Lymnaea stagnalis*, *Anisus vortex* and *Planorbarius corneus*. Their pulmonary respiration allows survival under low oxygen conditions (Brown, Alexander & Thorp 1998), a situation favoured by a high particular organic matter (POM) content and often encountered in small lentic waterbodies. They have a wider temperature tolerance than prosobranchs (Aldridge 1983; McMahon 1983), which is in accordance with the much greater temperature variation in isolated waterbodies. Pulmonates are also better adapted to resist desiccation because of their ability to store excretory products as urea and their ability to aestivate by forming an epiphragm to minimize water loss (Brown, Alexander & Thorp 1998). The larger size of pulmonate and prosobranch species such as *Lymnaea stagnalis*, *Viviparus contectus* and *Planorbarius corneus* found under lentic conditions enables them to consume tougher material such as living or dead macrophytes (Dillon 2000), which reached their highest densities in disconnected and isolated habitats (Table 2). On the other hand, the large body size associated with depressed or oblong shells leads to a low ability to resist water current and restricts the ability of theses species to colonize connected habitats (Dussart 1987).

A distinct change in the species community was apparent between disconnected and intermediately connected habitats, with prosobranchs and bivalves dominating in the latter. Species of these groups typically occurred over a wide range of connectivity (i.e. habitat generalists), from shortly connected habitats to highly connected ones. Gastropod species' traits favoured under these conditions included a small body size accompanied by less flow resistance and thick shells. Smaller species depend upon softer food such as epiphytal, epipsammal and filamentous algae and detritus (Dillon 2000). In dense macrophyte vegetation larger species may thus be favoured as macrophytes provide a direct food resource and the epiphyton is expected to have an inverse relationship with the standing crop of the host plants (Cattaneo *et al.* 1998). Inhabiting permanent waterbodies may necessitate defence mechanisms to reduce predation pressure by fish: a small size together with a thick shell makes gastropods less attractive as prey (Brown, Alexander & Thorp 1998; Dillon 2000). Large, thin-shelled species require highly structured habitats and/or an amphibious lifestyle.

Bivalve species reached maximum densities at intermediate and high connectivity, possibly because of their feeding habits: larger bivalves such as *Dreissena polymorpha*, *Corbicula fluminea* and the unionids feed on suspended material at least as adults (Starmühlner 1953; Vaughn & Hakenkamp 2001). Habitats of intermediate connectivity have previously been shown to contain the highest chlorophyll *a* concentrations and the highest numbers of rotifers (Baranyi *et al.* 2002), a potential food source for unionids (Thorp & Casper 2002). Bivalves are also favoured in flowing water because of reduced pumping costs (Englund & Heino

1996). Small bivalves of the genera *Pisidium*, *Musculium* and *Sphaerium* feed primarily on organic detritus and bacteria in the sediments, either by filtering interstitial water or by pedal feeding. Thus their occurrence primarily depends on sediment composition (Vaughn & Hakenkamp 2001). Thick fine sediment layers were present in isolated waterbodies as well as in the inshore zones of frequently connected habitats. Isolated habitats may be unsuitable because of oxygen depletion in the sediments. Among the bivalves, the number of thick-shelled species, such as *Corbicula fluminea*, *Unio tumidus zelebori* and *Pisidium supinum*, increased with increasing *Cd*. It is known from other pisid species such as *Pisidium casertanum*, *Pisidium henslowanum* and *Pisidium nitidum* that individuals in riverine habitats tend to develop thicker shells (Glöer & Meier-Brook 1994), which is considered an adaptation to coarse sediments and mechanical stress in lotic systems (Starmühlner 1953; Glöer & Meier-Brook 1994).

Species number peaked at connectivity values of about 1 month, with isolated and lotic habitats hosting significantly fewer mollusc species. In a previous study mollusc species diversity also peaked at sites with intermediate connectivity to the main channel (Tockner *et al*. 2000). Characteristic features of such intermediately connected habitats include low flow velocities and a rare occurrence of oxygen depletion and desiccation.

Species turnover (appearance/disappearance of species) along the *Cd* gradient was highest between 0 days and 2 months. We propose that the observed patterns are caused by the concurrence of three environmental gradients: oxygen concentration in the sediment surface, predator density and flow velocity. A temporarily harsh environment with low oxygen excludes most of the mollusc species except the pulmonates. With increasing connectivity, oxygen depletion becomes less significant and other mollusc species, as well as predatory fish occur, which disadvantages large snails. In highly dynamic sites flow resistance becomes increasingly important and only burrowing forms, which can tolerate the high flow velocities, occur.

IMPLICATIONS FOR RESTORATION

The basic alteration caused by the restoration measures is the position of the side-arm inlet relative to the river height, and thus our connectivity parameter. When planning restoration projects environmental policy makers (politicians and, more importantly, scientists) have to set restoration objectives and they have to make decisions about the extent of reconnection. They thus need prognostic tools. By showing a clear relationship between our connectivity parameter and important environmental variables on the one hand, and mollusc community composition and species trait composition on the other, we provide both an urgently needed and practical tool for predicting the impact and success of restoration schemes (reconnecting former channels). Connectivity (expressed as *Cd*) reflects the cause–effect chain of restoration measures and thus allows for improved planning of future restoration programmes. For example, in the DANP a further increase in waterbodies with high connectivity should lead to an enhancement of endangered rheophilic species such as *Unio tumidus*, *Lithoglyphus naticoides* and *Pisidium supinum*. In contrast, a loss of surface areas with *Cd* values between 5 days and 1 month will lead to a decline in areas with high diversity. Some other species (e.g. *Bithynia tentaculata*, *Pisidium amnicum* and *Radix peregra*) have their optima in habitats of short-term connectivity but also tolerate a broad range of connectivities. For these species we predict lower abundances and a restriction to small retention areas within more dynamic sites.

Isolated and short-term connected habitats with stagnophilic species such as *Anisus vortex*, *Lymnaea stagnalis* and *Viviparus contectus* are not affected by restoration measures. Nevertheless, long-term trends towards terrestrialization will ultimately lead to a decline in these habitats. Therefore, restoration strategies sustaining the diversity of the entire habitat are urgently needed.

Initial results based on other indicators (Reckendorfer & Steel 2004; Reckendorfer 2004; Reckendorfer *et al*. 2004) are also promising and indicate a broad applicability of the connectivity parameter for floodplain management. Similar approaches have been proposed previously for macrophytes (Bornette, Amoros & Lamouroux 1998) and sediments (Tockner & Bretschko 1996).

The parameter connectivity, as defined and used in this paper, is a surrogate integrating several features of floodplain waterbodies that influence mollusc distribution, including current velocity, water level fluctuations, sediment composition and macrophyte density. In order to address these issues specifically, future studies have to focus on the autecological requirements of target species.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from http://w.w.w.blackwell-synergy.com.

Appendix S1. List of mollusc species ranked according to their frequency of occurrence.