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# HABITAT DIVERSITY AND FISH ASSEMBLAGE STRUCTURE IN LOCAL RIVER WIDENINGS: A CASE STUDY ON A SWISS RIVER

CHRISTINE WEBER,* EVA SCHAGER and ARMIN PETER

*Eawag, Swiss Federal Institute of Aquatic Science and Technology, 6047 Kastanienbaum, Switzerland*

## ABSTRACT

We investigated habitat availability and fish assemblage structure in three local river widenings, completed 3–14 years ago, and five adjacent canalized reaches on the river Thur, a seventh-order river in Switzerland. To account for seasonal variability, surveys were repeated in winter and summer 2005. Results were compared with historical pre-disturbance data to evaluate whether the current abiotic and biotic conditions in the study reaches have attained historic near-natural levels.

Hydro-physical habitat diversity (depth, flow velocity, cover availability) was considerably greater in the two longer widenings (>900 m length) than in the canalized reaches and in the shortest widening (300 m length), with higher proportions of shallow or deep areas of different flow velocities. However, the comparison of current and historical near-natural shoreline lengths indicated that the current geomorphological complexity is still considerably impaired in all reaches.

No overall significant relationship was found between the reach type (canalized or rehabilitated) and the number of species or the total fish abundance which were strongly correlated with the availability of suitable cover and moderate flow velocity. However, highest winter abundances were observed in deep, well-structured backwaters of the rehabilitated reaches, documenting their significance as wintering habitats. Assemblage structure and composition were similar in canalized and rehabilitated reaches. Compared to the historical data, however, fewer and different dominant species were found, and guild composition changed towards a higher representation of generalists and tolerant species. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS: river rehabilitation; canalization; fish assemblage; habitat; evaluation

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## INTRODUCTION

Riverine fish assemblages are structured by diverse habitats (Schlosser, 1991; Cunjak, 1996; Matthews, 1998). Therefore, most rehabilitation measures attempt to re-establish the structural complexity lost by anthropogenic impacts (Gore *et al*., 1995) such as canalization or stream clearing for log floating (Nilsson *et al*., 2005). In many rehabilitation projects habitat structures are actively created, for example, through the placement of boulders (Lepori *et al*., 2005), large woody debris (Hilderbrand *et al*., 1997) or spawning gravel (Iversen *et al*., 1993). Most of these measures emphasize one specific species, usually salmonids (Frissel and Ralph, 1998). Several studies have documented a limited durability of artificial habitat structures (Frissell and Nawa, 1992; Linlokken, 1997; Roni *et al*., 2002), particularly in streams with high peak flow or high sediment load. In recent years, rehabilitation has therefore increasingly focussed on the recreation or maintenance of ecosystem processes or functions (Angermeier and Karr, 1994; Frissel and Ralph, 1998; Muhar and Jungwirth, 1998). In functioning ecosystems, site-specific habitats are naturally formed and connected (Beechie and Bolton, 1999; Roni *et al*., 2002) over various spatial and temporal scales. Patches are continually destroyed and recreated by spatio-temporal variations in processes. In this way, a shifting mosaic of diverse habitats is formed, which fulfils the requirements of different fish species and age classes (Bormann and Likens, 1979), depending on temporal and spatial scales.

River widening is a common rehabilitation measure to re-establish natural riverine dynamics in canalized rivers of Austria, Germany and Switzerland. The riverbed is significantly widened along a particular stretch through the removal of the embankments and the setback of the flood levees (Rohde *et al*., 2005a). Channel migration and

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*Correspondence to: Christine Weber, Eawag, Swiss Federal Institute of Aquatic Science and Technology, 6047 Kastanienbaum, Switzerland. E-mail: christine.weber@eawag.ch braiding are enabled within the widened reach, leading to greater structural and hydraulic heterogeneity (Peter *et al*., 2005; Woolsey *et al*., 2007). Widenings are particularly appropriate for the rehabilitation of formerly braided rivers with intact or little impaired bed load. A technical aim of this measure is to halt riverbed erosion (Peter *et al*., 2005).

System-wide enhancement is not possible for most canalized rivers; therefore, widenings are often conducted as local measures. Their effect on the fish fauna has not been documented. It remains unclear whether a potential response is only restricted to the restructured area or is also observable in adjacent canalized reaches, for example by colonization from the rehabilitation sites.

Rehabilitation measures tend to improve ecosystem functions and structures towards more natural conditions (Bradshaw, 1996). Comparisons with a guiding image or *Leitbild* describing the near-natural reference state are important for the evaluation of the degree of this approximation and the presence of ongoing shortcomings. Historical information, such as maps or documentary sources, offers an alternative when natural rivers are lacking as current references (Kondolf and Larson, 1995; Jungwirth *et al*., 2002; Hohensinner *et al*., 2004).

We studied the habitat availability and fish assemblage structure in three local river widenings, completed 3–14 years ago, and five adjacent canalized reaches on the river Thur, a seventh-order river in northeastern Switzerland (Pfaundler, 2005). We addressed the following research questions: (i) Can the observed differences in habitat availability and fish assemblage structure be explained by the rehabilitation (rehabilitated vs. canalized) or are other factors more relevant (e.g. habitat composition, distance to the mouth)? (ii) Did the abiotic and biotic conditions of rehabilitated reaches attain near-natural levels, in other words are the current conditions comparable with historical pre-disturbance data? From our findings we derived practical implications for the design of local river widenings.

## MATERIAL AND METHODS

### *Study site*

The river Thur, a tributary of the river Rhine (High Rhine), is located in the northeastern part of Switzerland (Figure 1). Along its 127 km length it drains a catchment of 1750 km$^2$ and overcomes an altitude difference of 1150 m. Average annual discharge is 47 m$^3$ s$^{-1}$. The flow regime is flashy: strong rainfall in the catchment gives rise to a very rapidly increasing water level up to 723 m$^3$ s$^{-1}$ (HQ$_{5,}$ 5-year flood frequency) or 817 m$^3$ s$^{-1}$ (HQ$_{10}$).

As a result of a large-scale modification in the late 19th century, the formerly braided to meandering Thur is now mainly canalized and most of the floodplains are disconnected from the river. The longitudinal connectivity is disrupted by seven dams and numerous weirs (Schager and Peter, 2005). Only the lowest 36 km provide free passage for migratory fish.

After repeated severe flood events, it was decided to carry out a second large-scale river modification in the 1970s with the main focus on flood protection. However, Swiss law also requires the simultaneous enhancement of ecological conditions. As a result, three river widenings and several smaller-scale habitat enhancement measures have also been completed over the past 16 years. The widenings differ considerably in their spatial dimension and design: over the course of time longer and wider river widenings have been implemented and the structuring of the active channel has been increasingly left to the dynamic of the river itself.

### *Study design*

We concentrated our study on the three widenings (W1–W3) and the five canalized reaches adjacent to them (C1–C5; Figure 1; Table I). The eight study reaches can be grouped into an upper (river km 28.0–32.2) and a lower river segment (river km 15.5–20.6). Both segments are located at the transition from barbel to grayling zone in a formerly braided stretch and are accessible for migratory fish from the river Rhine (Schager and Peter, 2005). Habitat was mapped with two different methods (mesohabitat vs. reach scale), and altogether 76 mesohabitat units were studied by means of electrofishing (Table I). Mesohabitat units were selected randomly using ArcMap 8.3 (ESRI). The different mesohabitat types were sampled proportionally and rare, underrepresented types were additionally included.

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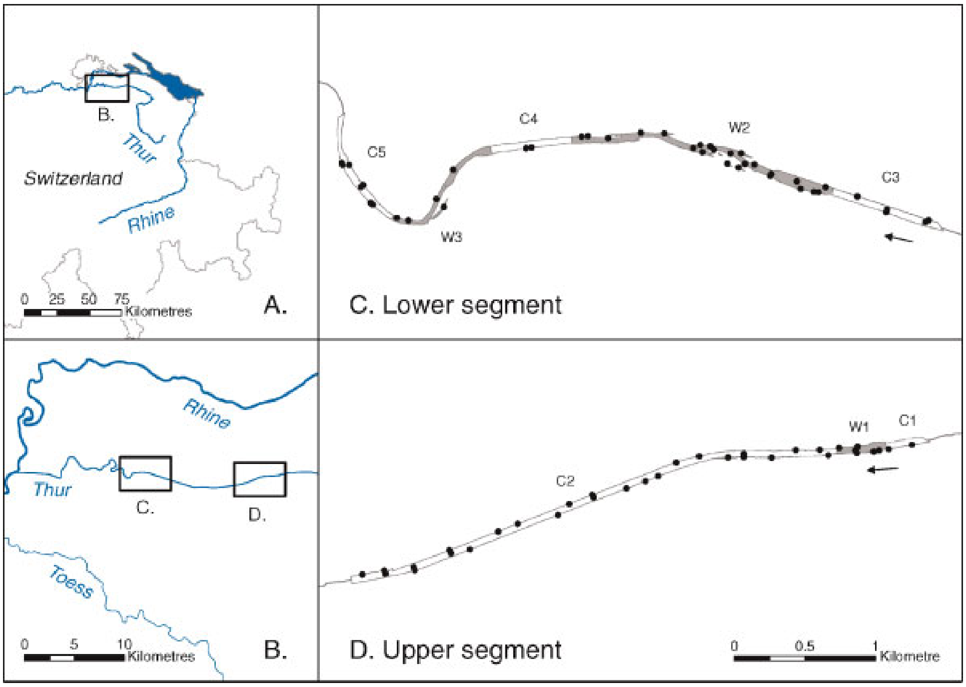

Figure 1. Location and dimension of the study segments and reaches. The wetted areas in inset B and C were determined in winter 2005 by means of a dGPS (TSC1; Trimble, Sunnyvale, CA, USA). Widenings (W) are shown in grey, canalized reaches (C) in white. Points indicate mesohabitat units sampled by electrofishing. This figure is available in colour online at www.interscience.wiley.com/journal/rra

Sampling and mapping took place in winter and summer 2005 (February and June and August, respectively) under comparable discharge conditions of about $19\,\mathrm{m}^3\,\mathrm{s}^{-1}$, corresponding approximately to a $Q_{274}$, that is a discharge that is reached or exceeded for 274 days on average per year. The results were compared with historical pre-disturbance data using two indicators that describe relevant ecosystem characteristics such as aquatic habitat diversity along the shoreline ecotone (indicator 'shoreline length'; Tockner and Stanford, 2002) and presence and strength of fish species and guilds (indicator 'fish assemblage structure'; Woolsey *et al*., 2005; Woolsey *et al*., 2007).

Table I. Characteristics of canalized and rehabilitated reaches of the river Thur

| Reach | Segment | Reach type (year of completion, dimension*) | Length (km) | Number of mesohabitat units for electrofishing |
|---|---|---|---|---|
| C1 | Upper | Canalized | 0.3 | 2 |
| W1 | Upper | Rehabilitated by widening (1991, 1.8) | 0.3 | 6 |
| C2 | Upper | Canalized | 3.6 | 26 |
| C3 | Lower | Canalized | 0.8 | 5 |
| W2 | Lower | Rehabilitated by widening (2002, 2.2) | 1.9 | 23 |
| C4 | Lower | Canalized | 0.5 | 2 |
| W3 | Lower | Rehabilitated by widening (1992, 1.7) | 0.9 | 5 |
| C5 | Lower | Canalized | 0.9 | 7 |

*Factor by which the canalized channel was widened (Hunzinger, 1998; Rohde *et al*., 2005b).

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### *Data collection*

*Habitat diversity in canalized and rehabilitated study reaches.* Mesohabitats were mapped in the field in all eight study reaches (total length: 9.1 km). A mesohabitat is defined as a quasi-discrete area which is homogenous with respect to the factors of water depth, current velocity and availability of fish cover (Kemp *et al*., 1999). We divided each factor into two or three categories which combined to form a total of 18 possible habitat types (Table II). Categories were visually estimated in the field. The mapping of all study reaches was conducted within 4 days. Whenever possible, mesohabitats were delineated by walking along them carrying the receiver of a differential Global Positioning System (TSC1; Trimble, Sunnyvale, CA, USA). Position was recorded automatically every 2 s. Non-wadeable instream areas were mapped from the shore by visually estimating mesohabitat dimension and recording geographical reference points. Field data were later corrected using records from a stationary reference receiver (Zurich, Switzerland) what resulted in a measurement precision of $\leq$0.3 m. Spatial data were converted into habitat maps using ArcMap 8.3 (ESRI). Visually estimated mesohabitats were added manually through digitization. The total and relative area of each habitat type were determined for each study reach and the habitat diversity (using Shannon's index of diversity; Krebs, 1989), the number of habitat types and the evenness (Shannon's evenness; Krebs, 1989) were calculated. Shoreline length [km/km], defined as the ratio of both shores' total length to river length (along the thalweg), was determined from the digitized data for each study reach (Tockner and Stanford, 2002; van der Nat *et al*., 2002).

Table II. Habitat factors and categories used for the qualitative habitat mapping (reach scale)

| Factor | | Factor categories | | |
|---|---|---|---|---|
| | | 1 | 2 | 3 |
| Depth | [cm] | $\leq 30$ | 30–110 | >110 |
| Flow velocity | [cm s$^{-1}$] | $\leq 10$ | 10–50 | >50 |
| Cover availability* | [%] | $\leq 5$ | >5 | |

*Cover was defined as the area providing shelter from predators and high current velocities. Both overhead cover and slow water areas behind submerged objects were considered in accordance with Peter (1992).

*Fish assemblage structure in different mesohabitat and reach types.* At each randomly selected mesohabitat unit, a strip of at least 25 m in length and of an area of about 100 m$^2$ was electrofished semi-quantitatively (one pass, no block nets). Due to their usually smaller dimension, specific mesohabitat types, such as backwaters or isolated pools, were fished over the entire area. A stationary electroshocker was used in most cases (EFKO, 8 kW, 150–300/300–600 V). Two mesohabitat units which were difficult to access were fished using backpack equipment (EFKO, 3 kW, 150–300/300–600 V). Non-wadeable mesohabitat units, such as deep backwaters, were sampled from an inflatable boat tied ashore. Captured fish were handled in accordance with a standardized procedure including controlled conditioning and anaesthesia with clove oil (Hänseler AG, Herisau, Switzerland; 0.5 ml diluted in 9.5 ml alcohol added to 15 L water). Because of difficulties in catch and determination, young-of-the-year fish hatched in 2005 were excluded from the survey. Fish species, total length (±1 mm) and presence and type of any anomalies were determined. All fish were released along the fished stretch after recovery. The number of species and guilds, the strength of guilds, the proportion of exotic species and the fish abundance in total and per species [individuals/100 m$^2$] were determined for each mesohabitat unit and each reach type (canalized vs. rehabilitated). Guild assignment was based on Schmutz *et al*. (2000) and Woolsey *et al*. (2005).

*Abiotic characteristics of individual mesohabitat units.* In order to specifically quantify local conditions, habitat measurements were recorded at each mesohabitat unit after electrofishing. Mean water depth was calculated from 15 to 20 measurements made in regular intervals, and current velocity was visually estimated (Table II). The

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dominant substratum was assigned to one of nine classes using a modified Wentworth scale (Cummins, 1962). Presence and type of suitable fish cover were determined visually (%). In order to consider the proximity of potential sources of colonizers, the distance to the closest near-natural river reach upstream and downstream ('Dist up' and 'Dist down' variables, respectively) was determined for each mesohabitat unit using ArcMap 8.3 (ESRI). The position of each mesohabitat unit in the river Thur was described in terms of the distance from the mouth into river Rhine ('Dist mouth' variable). The reach membership of each mesohabitat unit was defined by the variable 'reach number'.

*Reconstructing the historic fish assemblage in the study region.* Species lists and qualitative information on the historic assemblage composition (dominance structure) were retrieved from a high-quality historic fish inventory of the lower Thur River (Wehrli, 1892). The descriptive inventory is based on the observations and fish trap catches in various habitats and on angler surveys. We assigned each species to one of four occurrence classes (very high, high, medium or low occurrence). Based on that, the number of species was determined and guild composition and strength were described qualitatively.

*Measuring the shoreline length of the historic near-natural Thur (reach scale).* A high-quality topographic map published in 1851 (Wild Map; 1:25′000) was georeferenced and digitized by using ArcMap 8.3 (ESRI). Shoreline length was calculated for each study reach according to the procedure described for current habitat data, assuming the centre line of the main channel as the thalweg.

### *Data analysis*

*Comparison of rehabilitated and canalized study reaches.* Habitat diversity measures (Shannon's diversity and evenness, number of habitat types) of the two reach types were compared graphically due to the small number of replicates (three rehabilitated reaches and five canalized reaches). Current shoreline lengths and Shannon's diversities were evaluated by Pearson correlation coefficient to prove the assumption of shoreline length being an indicator for habitat richness. For each reach type, the number of fish species was determined. As species numbers are influenced by the number of individuals captured per mesohabitat unit, they must be standardized to a common number of individuals. Using rarefaction functions (Estimate S software program; Colwell, 2005), the expected species number, given $n$ individuals, is calculated analytically and not by iterative re-sampling (Gotelli and Colwell, 2001).

*Identifying factors that structure the fish assemblage (mesohabitat scale).* Fish abundances and abiotic characteristics of the individual mesohabitat units were compared using a general linear model (GLM; SPSS 13.0 for Windows). All variables were introduced into the model as covariates, except for the reach number. As it represents a nominal measure, it was treated as a fixed factor, nested in the variable reach type. Prior to the analysis, all interval-scaled data were log-transformed [log10 $(1+x)$] to homogenize variances of residuals. Analysis was

Table III. Shoreline length in the canalized and rehabilitated reaches in river Thur

| | Canalized | | | | | Rehabilitated | | |
|---|---|---|---|---|---|---|---|---|
| | C1 | C2 | C3 | C4 | C5 | W1 | W2 | W3 |
| Shoreline length [km/km] | | | | | | | | |
| 1851 (reference) | 2.02 | 3.14 | 4.96 | 3.63 | 2.23 | 2.01 | 4.47 | 3.27 |
| 2005 (mean) | 2.01 | 2.02 | 2.07 | 2.00 | 2.02 | 2.15 | 2.80 | 2.42 |
| Percentage from reference [%]* | 83 | 2 | 2 | 0 | 8 | >200 | 32 | 32 |

For 2005, the mean from winter and summer mapping is shown.
*Ratio of current shoreline length to reference shoreline length. The minimum value of 2 (km/km) is subtracted from both values prior to the calculation.

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carried out separately for the two seasons. A standard Bonferroni correction was applied to compensate for the increased likelihood of finding a significant result when calculating multiple statistical models with the abundance data (total abundance, abundance of chub and abundance of spirlin). The common significance level $p < 0.05$ was divided by the number of tests performed, resulting in a significance level of $p < 0.017$.

*Comparison with historic pre-disturbance data (reach scale).* Historic data were used as reference values representing near-natural conditions in a certain study reach (shoreline length) or over the entire study region (fish assemblage structure). The degree of naturalness was either expressed as the percentage from the historic reference value (shoreline length) or in words (fish assemblage structure). The current high resolution shorelines recorded in the field by dGPS were simplified using the simplify line function in ArcMap 8.3 (bend simplify, 10 m) to render them comparable with the lower resolution historic maps. This led to minor reductions in shoreline lengths of between 1 and 4%.

## RESULTS

### *Comparison of rehabilitated and canalized study reaches*

*Habitat diversity.* The canalized reaches and the shortest widening W1 were dominated by medium flow velocities, whereas in the longer widenings W2 and W3, the relative amount of both slow and fast flowing habitats was higher (results not shown). Shallow water areas were generally underrepresented in canalized reaches and in W1, whereas they compose a higher proportion in the widenings W2 and W3. Regarding the different habitat diversity measures the ranges of values for canalized and rehabilitated reaches overlapped (Figure 2). The maximal values for all three variables, however, were for both seasons attained in rehabilitated reaches. Among the rehabilitated reaches, W1 performed worst, whereas W2 and W3 behaved similarly. For both seasons, there was a significant correlation between habitat diversity and current shoreline lengths (Pearson correlation coefficient $r_{\text{winter}} = 0.862$, $p_{\text{winter}} = 0.006$; $r_{\text{summer}} = 0.795$, $p_{\text{summer}} = 0.018$).

*Numbers of fish species and population structure.* A total of 4149 individuals belonging to 20 species were caught over both sampling campaigns (Table IV). The spirlin, *Alburnoides bipunctatus*, was the numerically dominant winter species in both reach types, followed by the European chub, *Leuciscus cephalus*. The European chub was the numerically most abundant species in the summer sampling in both canalized and rehabilitated reaches, followed by the spirlin. Young animals dominated in most species (Table IV), whereas adult fish were generally underrepresented compared to an intact population structure.

In both seasons, no difference was found in the standardized species numbers of the canalized and rehabilitated reaches, as demonstrated by the overlapping confidence intervals of the rarefaction curves (Figure 3).

*Fish abundances.* In winter, median total abundance was highest in C4 (Figure 4). Extreme winter values were reached in the widenings W2 and W1. At 25 mesohabitat units, no fish were caught in winter. Such mesohabitat units could be found in almost every reach; 12 of them were located in widening W2 leading to a winter median of 0. Fish abundances in summer were clearly below those observed in winter (Figure 4). Median total abundances were highest in the largest widening W2, whereas maximum total abundances were found in W2 and C2. At six mesohabitat units, we found no fish in summer, as was the case in winter.

### *Identifying factors that influence the fish assemblage structure*

In winter, only cover and velocity contributed significantly in the overall multiple regression model ($p < 0.008$, $R^2 = 0.740$; Table V): fish abundances increased with increasing available cover and with decreasing current velocities. A significant positive correlation between the total fish abundance and the cover availability was also found in summer (Table V), but the summer model explained less of the total variance ($R^2 = 0.341$). No other variables showed any significant relationship. Only two species, that is European chub and spirlin, were sufficiently abundant among the reaches to be studied separately. Both in winter and summer, the abundance of the European chub decreased significantly with increasing distance from the Rhine (Table VI). Similarly, significant differences between reaches were found in both seasons, indicating higher abundances in the reaches located in the lower part

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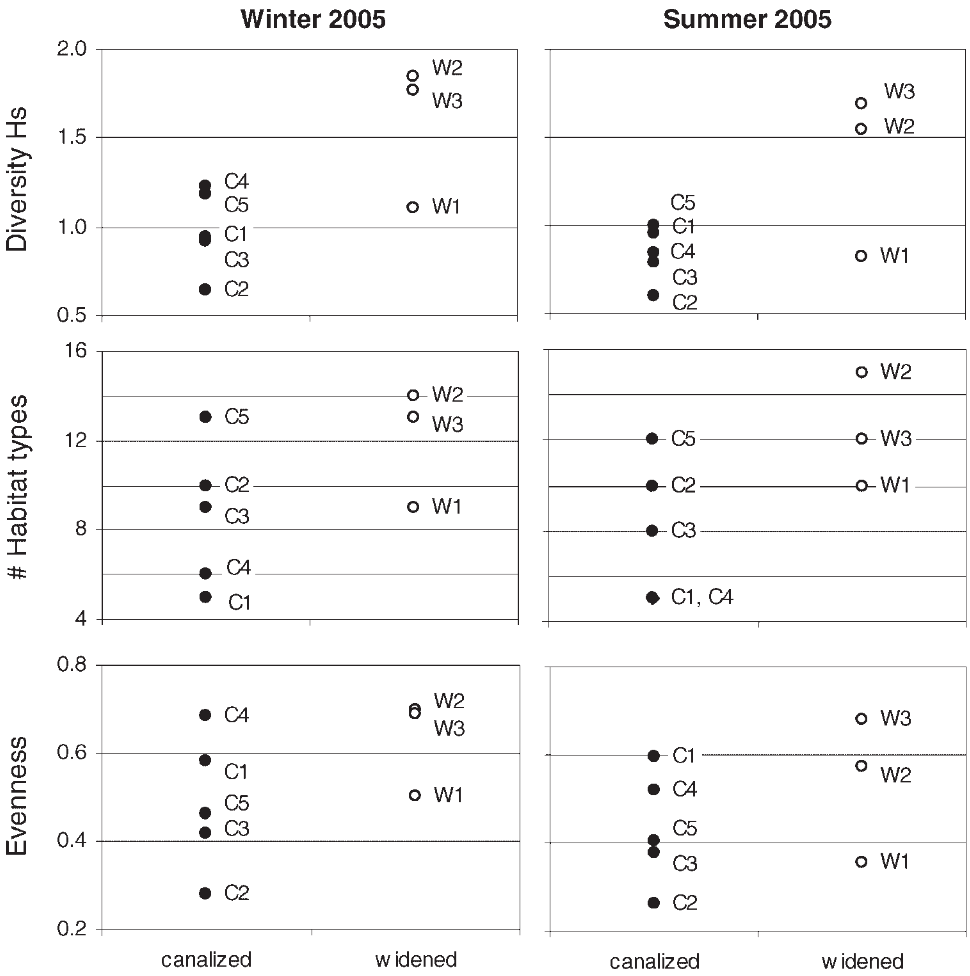

Figure 2. Habitat composition in canalized and widened reaches in the river Thur. Habitat diversity and evenness are calculated according to Shannon's formulas (Krebs, 1989)

of the study area. In winter, the abundance of the chub was significantly positively related to the substrate size, while in summer it increased with increasing availability of cover. Again, the summer model explained less variance than the winter one ($R^2 = 0.434$ and 0.657, respectively). A significant positive relationship between the availability of cover and the abundance of the spirlin was established in winter (Table VI). In summer, however, none of the variables used in the model showed a significant relationship.

### *Comparison with historic pre-disturbance data*

*Shoreline lengths.* The historic shoreline lengths varied considerably between the different reaches (Table III), but were in general longer than today. The current shoreline lengths in all the canalized reaches almost reached the minimum of 2 km/km. With the exception of C1, where both reference and current values were close to the absolute minimum of 2 km/km, this corresponds to a proportion of less than 10% of the historic reference value. The rehabilitated reaches showed consistently longer shorelines than the canalized reaches and thus achieved generally higher percentages (32–200%).

*Fish assemblage structure.* Six fish and lamprey species are mentioned in the historic sources from the period prior to the systematic river modification which are not present in our current samples (*Cottus gobio*, *Lampetra*

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Table IV. Species represented in the seasonal catches (relative abundances) and their historical occurrence in the river Thur

| Species | Actual occurrence (%) | | | | Historical occurrence |
|---|---|---|---|---|---|
| | Winter | | Summer | | |
| | Can | Reh | Can | Reh | |
| *Alburnoides bipunctatus* | $70.9^{Y}$ | $39.5^{S}$ | $22.4^{Y}$ | $9.6^{Y}$ | Very high |
| *Alburnus alburnus* | | | | $0.1^{Y}$ | Low |
| *Anguilla anguilla* | $3.6^{A}$ | $1.0^{A}$ | $17.1^{A}$ | $3.5^{A}$ | Medium |
| *Barbatula barbatula* | $2.1^{Y}$ | $0.5^{Y}$ | $1.9^{Y}$ | $6.9^{Y}$ | High |
| *Barbus barbus* | $4.0^{Y}$ | $0.5^{S}$ | $20.8^{Y}$ | $0.8^{Y}$ | Very high |
| *Carassius* spp. | | | $0.1^{A}$ | | [b] |
| *Chondrostoma nasus* | $0.1^{A}$ | $0.3^{Y}$ | | $0.6^{S}$ | Very high |
| *Esox lucius* | | $0.1^{A}$ | | | High |
| *Gasterosteus auculeatus* | | $0.1^{Y}$ | | $0.1^{Y}$ | [a] |
| *Gobio gobio* | $1.3^{Y}$ | $1.8^{Y}$ | $4.6^{Y}$ | $3.2^{Y}$ | High |
| *Leuciscus cephalus* | $8.2^{Y}$ | $33.5^{S}$ | $27.1^{S}$ | $61.0^{S}$ | High |
| *Leuciscus leuciscus* | $0.1^{Y}$ | $0.7^{Y}$ | $1.9^{S}$ | $2.8^{Y}$ | Low |
| *Leuciscus souffia souffia* | $2.7^{Y}$ | $12.4^{Y}$ | $0.7^{Y}$ | $2.3^{Y}$ | Very high |
| *Oncorhynchus mykiss* | $0.1^{A}$ | | | | [b] |
| *Phoxinus phoxinus* | $4.3^{Y}$ | $6.1^{Y}$ | $1.9^{Y}$ | $5.3^{Y}$ | High |
| *Pseudorasbora parva* | | | $0.6^{Y}$ | $3.2^{Y}$ | [b] |
| *Rutilus rutilus* | | | $0.1^{Y}$ | | Low |
| *Salmo trutta fario* | $0.9^{S}$ | $0.7^{S}$ | $0.1^{A}$ | $0.1^{A}$ | Medium |
| *Scardinius erythrophthalmus* | | | $0.1^{Y}$ | $0.1^{Y}$ | Low |
| *Tinca tinca* | | | | $0.3^{S}$ | Restricted to lakes |
| *Cyp. spp.*[*] | $1.7^{Y}$ | $2.8^{Y}$ | $0.4^{Y}$ | $0.1^{Y}$ | |
| *Thymallus thymallus* | | | | | Low |
| *Lampetra fluviatilis* | | | | | Low (seasonal occurrence) |
| *Lampetra planeri* | | | | | Medium |
| *Perca fluviatilis* | | | | | Low |
| *Cottus gobio* | | | | | High |
| *Salmo salar* | | | | | Low (seasonal occurrence) |
| Total number of individuals | 920 | 1656 | 689 | 884 | |

A distinction is made between canalized (can) and rehabilitated (reh) reaches. Actual occurrence: population structure is indicated as follows: Y, predominantly young fish ($0^{+}$, $1^{+}$); A, predominantly adult fish ($>1^{+}$); S, individuals from several age classes. Historical occurrence: based on a detailed description (Wehrli, 1892), we classified each species' occurrence as very high, high, medium or low. Species that are not mentioned in the historical source are indicated as follows: a, native species in Switzerland; b, allochtonous species. [*] Indeterminable cyprinids.

*fluviatilis*, *Lampetra planeri*, *Perca fluviatilis*, *Salmo salar*, *Thymallus thymallus*; Table IV), whereas four recent species were not recorded in the historic source (*Carassius* spp., *Gasterosteus auculeatus*, *Oncorhynchus mykiss*, *Pseudorasbora parva*). With the exception of *P. parva*, of which 32 individuals were caught in summer, all of the new species were represented by single individuals. Of the four historically most abundant species, only the sprilin was numerously represented in our samplings. Barbel (*Barbus barbus*) and vairone (*Leuciscus souffia*) showed generally small abundances with marked seasonal differences. Only a few individuals of the nase (*Chondrostoma nasus*) were found.

The number and proportion of ecological guilds have also changed as compared with the historical reference (see Table AI in the Appendix). Today's assemblage is highly dominated by individuals of meso-eurythermal species in both reach types, but particularly in the canalized reaches. Oligo-stenothermal species are numerically underrepresented. Piscivorous species such as *Esox lucius* are virtually lacking today, whereas the proportion of omnivorous species is higher in both reach types. Species that are tolerant to various anthropogenic impacts are generally more abundant than they were around 1850, particularly in the rehabilitated reaches.

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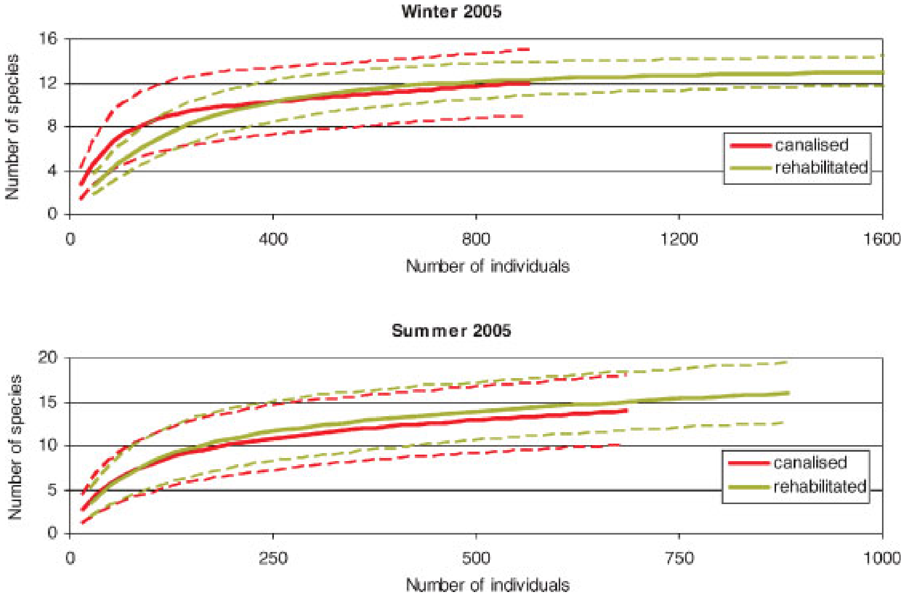

Figure 3. Individual-based rarefaction curves demonstrating the taxonomic richness in canalized and rehabilitated river reaches in winter and summer. Dashed lines indicate 95% confidence intervals. This figure is available in colour online at www.interscience.wiley.com/journal/rra

## DISCUSSION

### *Habitat diversity in canalized and rehabilitated reaches*

Habitat diversity measures for canalized and rehabilitated reaches overlap as there is a considerable variation within both reach types. W1, the oldest and shortest widening, is comparable with the canalized reaches, whereas the two longer widenings, W2 and W3, display higher habitat diversities. This is not only due to their elevated number of habitat types, but also to their more balanced distribution as demonstrated by the higher evenness. Shallow slow-flowing water areas, for instance, compose higher proportions in the rehabilitated reaches W2 and W3, while they were underrepresented in canalized reaches and in W1. These results coincide with the conclusion of Grift *et al*. (2001) that shallow slow-flowing areas offering suitable spawning and rearing conditions for rheophilic fish are severely degraded or even absent in regulated rivers.

There is evidence that the spatial dimension of the widening influences habitat diversity. With a length of about 0.3 km, the widening with the lowest diversity, W1, is considerably shorter than the more diverse reaches W2 and W3 (1.9 and 0.9 km). However, more replicates of widenings of different lengths would be required to test this hypothesis. Based on laboratory experiments, Hunzinger (1998) suggests a minimal widening length of 420 m in order to initiate channel braiding at the river Thur. This is consistent with the recent strategy of the local river managers to build longer and larger widenings. W1 is shorter than the minimal requirements for braiding, and this leads to the development of alternating gravel banks instead. This morphology is further stabilized by the bed load deficit in this part of the Thur (Schälchli, 2005) and the location of W1 in a slight bend.

### *Factors influencing fish assemblage structure*

Total fish abundances and species numbers in all canalized and rehabilitated reaches in this study were comparable, even in W2 and W3 which displayed a more diverse habitat supply. Reach type was therefore an unsuitable variable to explain the observed differences between mesohabitat units.

A strong positive relationship was observed between the total abundance of fish and the availability of cover in both seasons. Due to the riprap bank reinforcement, cover availability is slightly elevated in the canalized reaches as compared with the three widenings. Woody debris is largely lacking as a naturally structuring element in the Thur

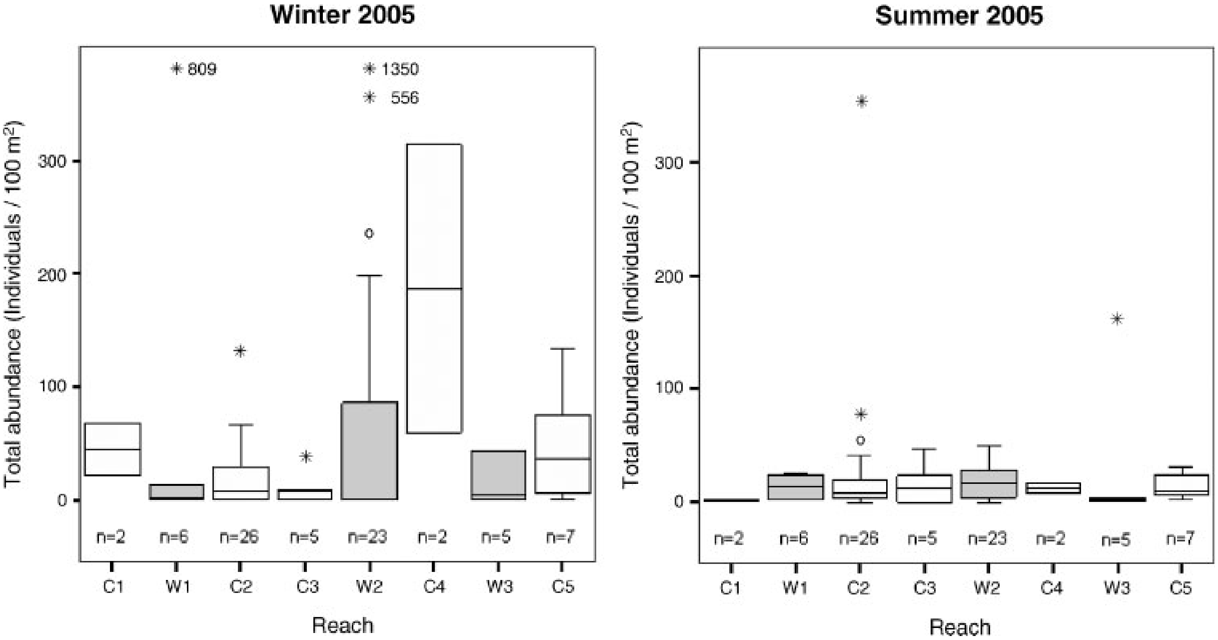

Figure 4. Total fish abundances in winter and summer in the different reaches. Rehabilitated reaches are shown in grey, canalized reaches in white. Circles and stars indicate outliers and extremes, respectively. *n*, number of mesohabitat units within each reach

system, because of a reduced input at the mostly fixed shores and removal at the small hydropower dams. The relative importance of cover in relation to the total fish abundance varied seasonally. The highly clustered distribution of fish in winter can be explained satisfactorily by the abiotic variables we used. Most species, including those classified as moderately structure dependent such as the nase or the barbel, retreat to well structured slow flowing or standing water habitats which provide shelter from hydraulic stress (Jungwirth *et al*., 1995) and other adverse physicochemical conditions (Cunjak, 1996). In particular, structure-rich backwaters and isolated pools of medium to high depth constitute winter hot spots (Cunjak, 1996; Lusk *et al*., 2001) where we found total fish densities >500 individuals/100 m$^2$. Furthermore, backwaters may serve as flood refugia throughout the year increasing the assemblage's resilience to flood events (Sedell *et al*., 1990; Townsend *et al*., 1997; Lusk *et al*., 2001;

Table V. GLM tables for the effects of different abiotic variables on the total fish abundance, separated by season

| Variable | Winter | | Summer | |
|---|---|---|---|---|
| | *F* | *p* | *F* | *p* |
| Reach type | 0.18 | 0.677 | 2.56 | 0.115 |
| Reach number (Reach type) | 1.30 | 0.273 | 1.46 | 0.208 |
| Dom substrate | 4.41 | 0.040 | 0.53 | 0.470 |
| Flow velocity | 7.55 | **0.008** | 0.55 | 0.459 |
| Dist to mouth | 4.57 | 0.037 | 3.67 | 0.060 |
| Dist up | 3.83 | 0.055 | 5.04 | 0.028 |
| Dist down | 1.02 | 0.316 | 0.34 | 0.563 |
| Mean depth | 1.26 | 0.267 | 0.76 | 0.386 |
| Cover | 40.27 | **0.000** | 9.23 | **0.003** |
| $R^2$ | 0.740 | | 0.341 | |

Significant *p*-values are shown in bold. The variable 'Reach number' is nested in the variable 'Reach type'. The variables 'Dist up' and 'Dist down' describe the closest distance to a near-natural river reach upstream and downstream, respectively. The distance to the mouth into river Rhine is considered using the variable 'Dist mouth'.

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Table VI. GLM tables for the effects of different abiotic variables on the abundance of the European chub and the spirlin, separated by season

| Variable | *Leuciscus cephalus* | | | | *Alburnoides bipunctatus* | | | |
|---|---|---|---|---|---|---|---|---|
| | Winter | | Summer | | Winter | | Summer | |
| | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* |
| Reach type | 0.1 | 0.758 | 0.90 | 0.348 | 0.12 | 0.736 | 1.46 | 0.231 |
| Reach number (Reach type) | 4.52 | **0.001** | 3.18 | **0.009** | 0.91 | 0.497 | 2.33 | 0.043 |
| Dom substrate | 12.18 | **0.001** | 2.04 | 0.159 | 0.74 | 0.392 | 4.31 | 0.042 |
| Flow velocity | 6.44 | **0.014** | 1.01 | 0.320 | 5.98 | **0.017** | 0.07 | 0.792 |
| Dist to mouth | 18.70 | **0.000** | 9.71 | **0.003** | 3.54 | 0.065 | 0.20 | 0.656 |
| Dist up | 6.84 | **0.011** | 4.72 | 0.034 | 4.11 | 0.047 | 6.17 | **0.016** |
| Dist down | 2.89 | 0.094 | 0.04 | 0.850 | 1.51 | 0.224 | 0.02 | 0.898 |
| Mean depth | 3.62 | 0.062 | 1.19 | 0.279 | 1.27 | 0.265 | 0.10 | 0.759 |
| Cover | 2.93 | 0.092 | 10.96 | **0.002** | 27.59 | **0.000** | 0.16 | 0.694 |
| $R^2$ | 0.657 | | 0.434 | | 0.682 | | 0.318 | |

Significant *p*-values are shown in bold. The variable 'Reach number' is nested in the variable 'Reach type'. The variables 'Dist up' and 'Dist down' describe the closest distance to a near-natural river reach upstream and downstream, respectively. The distance to the mouth into river Rhine is considered using the variable 'Dist mouth'.

Schwartz and Herricks, 2005). As these parapotamal habitats suffered considerably from canalization works (Aarts *et al*., 2004), we only found them in the three widened reaches, underlying the local and maybe even regional significance of the rehabilitated river reaches (Cunjak, 1996; Lusk *et al*., 2001).

As indicated by the low level of explained variance, however, our model lacks important factors that influence the abundance of fish in summer. Due to their higher activity levels, it is possible that the summer distribution of fish was far more significantly driven by biotic interactions, such as intra- and inter-specific competition, than by abiotic factors. However, the abundances observed at most mesohabitat units were so low as to possibly render competition unimportant (Jackson *et al*., 2001).

Additional unconsidered abiotic variables, such as thermal heterogeneity, could therefore contribute to the observed patterns and to the generally lower abundances in summer. Based on the historical maps, we assume that a higher and larger-scale hyporheic exchange existed prior to canalization creating thermal refugia in both cold (Craig and Poulin, 1975; Cunjak and Power, 1986) and hot seasons (Gibson, 1966; Nielson *et al*., 1994). This assumption is strongly supported by the reduced relative (summer) abundance of oligo-stenothermal species, such as the vairone, the brown trout and the minnow, observable today and by the absence of the formerly abundant sculpin. Today, the river Thur displays a relatively homogeneous temperature pattern (Frey *et al*., 2003), in contrast to natural braided systems where lateral temperature differences of up to 15°C may be observed in summer (Arscott *et al*., 2001), Considerable temperature changes only occur at the few confluences of groundwater-fed drainage canals or in shallow, slow-flowing waters along gravel banks (Frey *et al*., 2003). Summer temperatures regularly exceed 21°C and reach >24°C on very warm summer days, an effect that has even increased over the past two decades (BUWAL *et al*., 2004).

## *Degree of naturalness attained by rehabilitation*

*Habitat diversity.* Expressed by the shoreline length, the rehabilitated reaches attained a generally higher degree of naturalness than the canalized reaches. Despite this improved lateral connectivity, rehabilitated reaches are still far from achieving near-natural conditions, as the low percentages from the reference values demonstrate. Shorter current shorelines are due to the virtual lack of multiple channels, groundwater channels and side arms and to the low number of backwaters or isolated floodplain water bodies. Habitat recovery requires space and may take several years. In the current case, no relationship can be observed between habitat diversity and time span since rehabilitation: W1 and W3 are about the same age, but their diversities differ clearly, whereas W2 and W3 differ in age but their diversities are comparable. We assume that the habitat set in the youngest widening W2 (completed in

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2002) will further diversify with every major flood event, in particular at the natural river banks (erosion, establishment of riparian vegetation), whereas in the two older widenings, the habitat potential was probably achieved during the 13–14 years of development.

In general, shoreline length appears to be a good indicator for overall habitat diversity, $H_s$. However, the extremely high percentages of C1 and W1 within their reach types must be treated with care. Due to their short length (300 m), the reference reaches were not representative of the historically braided reach. Compared with a larger-scale reference (historical reaches 1–3 combined), ratios of 1 and 15% result for C1 and W1, respectively, confirming the general trend of a slightly higher naturalness in rehabilitated reaches. The relatively small reference value in the lowest reach C5, however, is not biased by reach length but due to the reach's position at the transition from the braided to the meandering channel type which is naturally characterized by shorter shorelines.

*Composition of the fish assemblage.* Considerable changes in the assemblage's dominance structure and hence in its guild composition were documented for all study reaches. The observed increase in generalists and tolerant species, which is mainly due to the high relative abundance of the omnivorous tolerant European chub, and the lower representation of specialists such as piscivorous or insectivorous taxa, is very familiar from numerous rivers suffering from various human impacts (Shields *et al*., 1997; Paller *et al*., 2000). Apart from the thermal changes discussed above, migration barriers and degraded habitat conditions in the impounded High Rhine may also be responsible for the underrepresentation of formerly abundant migratory species such as the barbel and the nase which exists today (Gerster, 1998).

Most of the historical species that are missing in our catches were of low historical abundance (Table IV). As the occurrence of rare species varies greatly over time (Jackson *et al*., 2001), their absence should not be weighted too negatively. Furthermore, single individuals of grayling (Peter, unpublished data), brook lamprey, perch and sculpin were observed recently in the river Thur (Schager and Peter, 2005). Although absent in our extensive sampling, these species are still present in the system, representing an important recolonization source for a future assemblage recovery (Niemi *et al*., 1990). The two anadromous species, Atlantic salmon and European river lamprey, however, became extinct on a nationwide scale. Re-colonization may only take place by large-scale, transboundary rehabilitation measures (Nienhuis *et al*., 2002). Despite the absence of several taxa, the species richness in the river Thur is still surprisingly high for a river that has been almost completely canalized for many decades.

## CONCLUSIONS

This study demonstrated that aquatic habitat diversity may be improved by local river widening provided that a minimal river-specific length is exceeded. The response of the river Thur fish assemblage was weak indicating that there could be ongoing deficits such as reduced thermal heterogeneity, or the failure of the faunal recovery process to be completed. Furthermore, the habitat condition of the entire river Thur must be considered: 65% of the lower 90 km of the river still display degraded morphological conditions and/or are impaired by fragmentation or residual flow. Therefore, we assume that a strong reaction of the total fish fauna could only be achieved by large-scale habitat rehabilitation. For future rehabilitation work, we recommend an extension to the main deficits in the river catchment. Reference comparison was proved to be an important prerequisite for the evaluation of the degree of naturalness, that is the success of rehabilitation.

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## APPENDIX

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Table AI. Guilds of fish and lamprey species in the river Thur and their change in occurrence from 1890 to present

| | Historical occurrence | Temperature | Habitat | Reprod. | Feeding | Migration | Tolerance | Structure | Longevity | Change in occurrence | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | can | reh |
| *Cottus gobio* | High | OLIGO | RHEO | SPEL | BENT-INS | SHO | INT | DEP | L-SHO | ↓ | ↓ |
| *Leuciscus souffia souffia* | Very high | OLIGO | RHEO | LITH | BENT-INS | SHO | INT | M-DEP | L-MED | ↓ | ↓ |
| *Oncorhynchus mykiss* | Non-native | OLIGO | RHEO | LITH | BENT-INS | MED | INT | M-DEP | L-MED | ↑ | — |
| *Phoxinus phoxinus* | High | OLIGO | RHEO | LITH | BENT-INS | SHO | TOL | M-DEP | L-SH | — | — |
| *Salmo trutta fario* | Medium | OLIGO | RHEO | LITH | BENT-INS | SHO | INT | DEP. | L-MED | ↓ | ↓ |
| *Salmo salar* | Low (seasonal) | OLIGO | RHEO | LITH | BENT-INS | LONG | INT | DEP | L-MED | ↓ | ↓ |
| *Thymallus thymallus* | Low | OLIGO | RHEO | LITH | BENT-INS | MED | INT | M-DEP | L-MED | ↓ | ↓ |
| *Alburnoides bipunctatus* | Very high | MESO | RHEO | LITH | BENT-INS | SHO | INT | M-DEP | L-SH | — | — |
| *Alburnus alburnus* | Low | MESO | EURY | PHYT | OMNI | SHO | TOL | IND | L-SH | — | — |
| *Anguilla anguilla* | Medium | MESO | EURY | PEL | OMNI | LONG | TOL | DEP | L-MED | — | — |
| *Barbatula barbatula* | High | MESO | RHEO | LITH | BENT-INS | SHO | TOL | M-DEP | L-MED | ↓ | ↓ |
| *Barbus barbus* | Very high | MESO | RHEO | LITH | BENT-INS | MED | INT | M-DEP | L-LO | ↓ | ↓ |
| *Carassius* spp. | Non-native | MESO | LIM | PHYT | OMNI | SHO | TOL | M-DEP | L-MED | ↑ | — |
| *Chondrostoma nasus* | Very high | MESO | RHEO | LITH | HERB | MED | INT | M-DEP | L-MED | ↓ | ↓ |
| *Esox lucius* | High | MESO | EURY | PHYT | PISC | SHO | TOL | DEP | L-LO | ↓ | ↓ |
| *Gasterosteus auculeatus* | Unmentioned | MESO | EURY | PHYT | OMNI | SHO | TOL | IND | L-SH | ↑ | ↑ |
| *Gobio gobio* | High | MESO | RHEO | PSAM | BENT-INS | SHO | TOL | M-DEP | L-SH | ↓ | ↓ |
| *Lampetra fluviatilis* | Low (seasonal) | MESO | RHEO | LITH | PISC | LONG | INT | IND | L-MED | ↓ | ↓ |
| *Lampetra planeri* | Medium | MESO | RHEO | LITH | DETR | MED | INT | IND | L-MED | ↓ | ↓ |
| *Leuciscus cephalus* | High | MESO | RHEO | LITH | OMNI | MED | TOL | DEP | L-MED | ↑ | ↑ |
| *Leuciscus leuciscus* | Low | MESO | RHEO | LITH | OMNI | SHO | INT | M-DEP | L-MED | — | — |
| *Perca fluviatilis* | Low | MESO | EURY | PHYT | BENT-INS | SHO | TOL | IND | L-MED | — | — |
| *Pseudorasbora parva* | Non-native | MESO | LIM | POLY | OMNI | SHO | TOL | IND | L-SH | ↑ | ↑ |
| *Rutilus rutilus* | Low | MESO | EURY | PHYT | OMNI | SHO | TOL | IND | L-MED | — | — |
| *Scardinius erythrophthalmus* | Low | MESO | LIM | PHYT | OMNI | SHO | TOL | M-DEP | L-MED | — | — |
| *Tinca tinca* | Restricted to lakes | MESO | LIM | PHYT | OMNI | SHO | TOL | DEP | L-LO | — | — |

Guild assignment according to Schmutz *et al*. (2000) and Woolsey *et al*. (2005). Historical occurrences derived from Wehrli (1892); Table IV; ↑, increase; ↓, decrease; —, no change. OLIGO, oligo-stenotherme; MESO, meso-eurytherme; RHEO, rheophilic; EURY, eurytopic; LIM, limnophilic; SPEL, speleophilic; LITH, lithophilic; PHYT, phytophilic; PSAM, psammophilic; PEL, pelagophilic; POLY, polyphilic; BENT-INS, benthic-insectivorous; OMNI, omnivorous; HERB, herbivorous; PISC, piscivorous; DETR, detritivorous; SHO, short distance; MED, medium distance; LONG, long distance; INT, intolerant; TOL, tolerant; DEP, structure dependent; M-DEP, moderately structure dependent; IND, structure independent; L-SH, short lived; L-MED, intermediate livetime; L-LO, long lived.

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