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Research Article

Spatio-temporal analysis of fish and their habitat: a case study on a highly degraded Swiss river system prior to extensive rehabilitation

Christine Weber[1,*], Armin Peter[1] and Flavio Zanini[2]

[1] Swiss Federal Institute of Aquatic Science and Technology (Eawag), Seestrasse 79, CH-6047 Kastanienbaum, Switzerland
[2] Swiss Federal Institute of Technology Lausanne (EPFL), Geographical information Systems Laboratory (LaSIG), CH-1015 Lausanne, Switzerland

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Abstract. The failure of river rehabilitation projects is often reported in the literature. One possible reason for this failure is the insufficient consideration of factors degrading riverine ecosystems at large spatio-temporal scales. A precedent analysis of the evolution and significance of these factors at the watershed level is proposed as a prerequisite for a successful rehabilitation project. Based on a watershed-scale approach, we investigated the current and historical states of the fish assemblage and of relevant abiotic factors in the river Rhone, a seventh-order stream in Switzerland scheduled for large-scale rehabilitation. Recent field data gathered by electrofishing and habitat mapping were analysed by means of a mixed model approach and were qualitatively compared to historical information derived from topographic maps and documentary sources.

The length of the entire active channel has been reduced by 45% (102 km) since 1850, representing a significant diminution in lateral connectivity. Our recent fish survey revealed a depleted species set, with only two of 19 historically documented species found. The density of brown trout was generally low, but positively correlated with the presence of cover. Thus, morphological improvements, e.g. through local river widening, offer extensive potential for the restoration of native fish assemblages, but will probably only be successful in combination with a more natural hydrological regime.

Key words. Catchment; hydropeaking; rehabilitation; brown trout; historical analysis; river Rhone.

Introduction

River management philosophy has changed fundamentally in recent years (Gleick, 2001). Today, it no longer focuses exclusively on total control and exploitation. On the contrary, environmental and socio-economic concerns are equally highlighted in many countries' legislation (e.g. the European Water Framework Directive), and both the conservation of pristine sites and rehabilitation of lost ecological structures and functions are seen as a priority.

However, this change in management philosophy is often very difficult to implement in practice. Today, 59% of the world's large river systems are moderately to strongly affected by flow regulation, such as reservoir operation, irrigation or fragmentation by dams (Nilsson et al., 2005). In the United States only 2% of rivers and streams are categorised as relatively natural and more than one third is considered as heavily impaired or polluted (Benke, 1990). The majority of lowland rivers in Europe is canalised (Brookes and Shields, 1996). In

* Corresponding author phone: +41 41 349 21 84;
fax: +41 41 349 21 68; e-mail: christine.weber@eawag.ch
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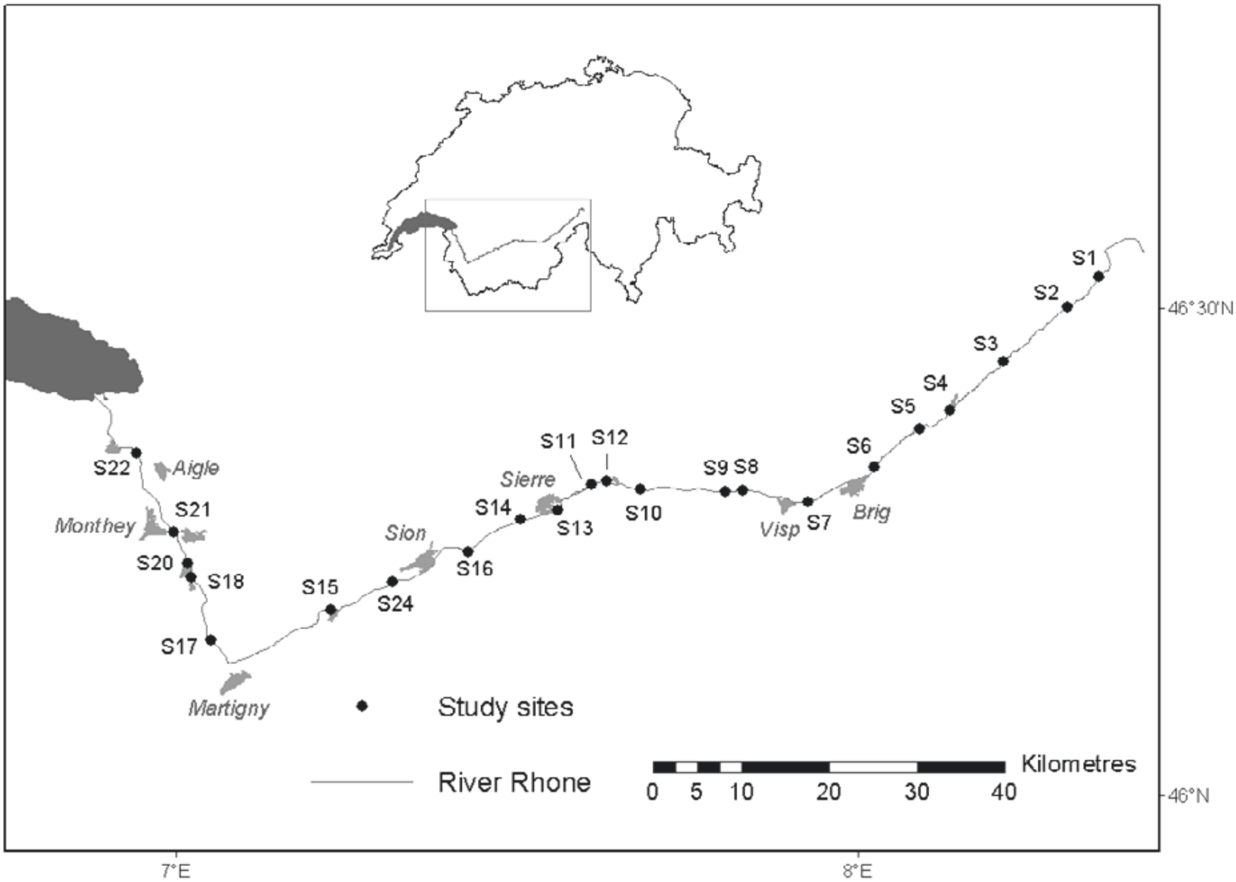

Figure 1. Location of the river Rhone upstream from Lake Geneva in southern Switzerland (© 2003 swisstopo). Points indicate the study sites.

North America and Europe, 90% of all floodplains have lost their ecological functioning due to cultivation (Tockner and Stanford, 2002).

Despite the completion of numerous rehabilitation projects, the positive effects of rehabilitation measures on riverine biota have rarely been documented, while the failure of several practical measures such as placement of log weirs (Frissell and Nawa, 1992), artificial riffles (Pretty et al., 2003), boulders (Lepori et al., 2005) or spawning gravel (Iversen et al., 1993) has been reported. The reasons for the biological failure could include failure to consider different spatio-temporal scales or confusion between them (Kondolf and Downs, 1996; Moerke and Lamberti, 2003). For financial or planning reasons, rehabilitation measures are often designed at a local level, neglecting processes and deficits operating at the watershed scale (Kondolf and Downs, 1996). Similarly, temporal aspects, such as pristine morphology, the natural flow regime (Poff et al., 1997; Richter et al., 1997) and the evolution of deficits over time, are often ignored in project planning (Jungwirth et al., 2002).

To improve rehabilitation practice, the factors that degrade a stream ecosystem need to be identified at an extensive spatio-temporal scale (Kauffmann et al., 1997; Lewis et al., 1996; Moerke and Lamberti, 2003), i.e. by carrying out an analysis of the current and historical state at the watershed level (Kondolf and Downs, 1996). Both of these aspects were addressed in the presented project. We studied the evolution, distribution and relative influence of physico-chemical deficits of relevance to fish along the river Rhone, a seventh-order stream in Switzerland. The river is scheduled to undergo large-scale rehabilitation as part of a flood protection project. Fish are highly suitable organisms for the detection of stream impairment and recovery due to their high mobility and longevity and the extensive knowledge available on their ecological role (Fausch et al., 1990; Jungwirth et al., 1995; Karr et al., 1986). Our watershed-scale approach is intended to achieve the following aims: 1) to demonstrate the importance of both spatially and temporally broader concepts that may be useful in rehabilitation practice and 2) to asses the potential to rehabilitate the fish assemblage of a hydrologically and morphologically impaired river system.

Materials and methods

Study sites

This study was conducted in the Swiss section of the river Rhone (Fig. 1) from its source at the Rhone Glacier (1,763 m a.s.l.) to its mouth at Lake Geneva (374 m a.s.l.). Along this 167.5 km stretch, the river Rhone drains a catchment of 5,220 km^2 consisting mainly of forest and pastures (46%), rocks (24%) and glaciers (14%), and agricultural land (16%) (Loizeau and Dominik, 2000; Spreafico et al., 1992).

The river Rhone has been considerably altered over the past two centuries, morphologically due to two corrections of the river corridor carried out in the late 19th and early 20th centuries (Département Fédéral de l'Intérieur, 1964) and also as a result of hydrological alterations arising from the exploitation of hydropower in the catchment (Loizeau and Dominik, 2000). Today, the Rhone is mainly channelized and river reaches with a near natural flow regime are rare. The mean natural annual discharge has been reduced by more than 20% along 22% (36 km) of the entire river course between the source and Lake Geneva. Hydropeaking prevails over a distance of 109 km (65% of the entire river course; data from Spreafico et al., 1992). In most reaches affected by hydropeaking, winter flows are significantly increased (Meile et al., 2005; Spreafico et al., 1992) due to the predominant release of water during the winter months.

It is planned to renovate and improve existing flood protection measures along a significant part of the river Rhone (69.9 km) over the next 25 years. A simultaneous improvement of ecological and socio-economic concerns is also planned. The aim is to re-create a diverse, more naturally functioning river that will also provide a popular recreation area for the local population and tourists.

Under current conditions, the river Rhone is categorized as a trout-grayling zone (Huet, 1959). Considerable stocking of brown trout with both young-of-the-year and adult trout exceeding the legal limit size of 240 mm is carried out along the entire river course. The annual stocking of the latter averages around 5 tons (R. Collaud, personal communication).

Study sites were selected by stratified random sampling (Krebs, 1989). This method allows for possible heterogeneity within the sampled population due to variation in environmental attributes (Jeffers, 1998). We divided the river Rhone into 18 segments or strata on the basis of topographical (slope), hydrological (influencing of the discharge volume by hydropower generation) and morphological (bank type) data. Sites accessible with field equipment were determined randomly within each stratum. Because of the difficult topography, 7 shorter strata with a total length of 10.7 km (6.4%) could not be sampled. Altogether, 22 sites located in 11 strata were included in the investigation (Fig. 1).

Fish parameters

Each randomly determined site was electrofished once using a semiquantitative approach (one pass, without stop nets). The survey took place in February and March 2003 under winter, low flow conditions. A stationary electroshocker was used in most cases (EFKO, 8 kW, 150–300/300–600 V). Stretches that were difficult to access were fished using backpack electrofishing equipment (EFKO, 1.5 kW, 150–300/300–600 V).

Fishing was conducted on strips of the riverbed of at least 100 m length. In the lower part of the river, sampling was restricted to the banks; a strip in the mid-channel was also included at sites with minor discharge. Bank and mid-channel strips were 3.2 m wide on average. Narrow reaches in the headwaters were fished over the entire width. A total of 36 strips were fished over the 22 sites, and the fished area was determined by multiplying strip length and width.

The fish were handled in accordance with a standardized procedure (controlled conditioning, anaesthesia with clove oil (Hänseler AG, Herisau, Switzerland; 0.5 mL diluted in 9.5 mL alcohol added to 20 L water)). Body length (±1 mm) and the presence and type of any anomalies were determined. All of the fish were released along the fished stretch after recovery.

The following biological parameters were determined from the catches: density of individuals in total and per species [individuals $\cdot$ m^{-2}], median length of brown trout [cm] and percentage of brown trout with anomalies and injuries.

Environmental variables

The strips were divided into 10 sectors of equal length for measuring environmental variables. Substratum composition was estimated in four randomly selected sectors (Bain et al., 1985) and assigned to one of nine classes using a modified Wentworth scale (Cummins, 1962).

Aquatic habitats (Hawkins et al., 1993) were mapped and their percentages visually estimated in each sector. Based on this mapping, habitat diversity was determined using Shannon's index of diversity and evenness (Arscott et al., 2001; Matthews, 1998). Presence and type of suitable fish cover were determined visually, i.e. the area providing shelter from predators and high current velocities was identified. Both overhead cover and slow water areas behind submerged objects were considered in accordance with Peter (1992). Shoreline composition regarding particle type and size was recorded.

Water samples were taken at each site directly after electrofishing (one sample per site) and immediately deep frozen in dry ice. In the lab, the samples were thawed and analysed for total phosphorous (Tot-P), NO_3-N, NO_2-N, NH_4-N, pH, alkalinity, dissolved organic carbon (DOC), total organic carbon (TOC) and suspended solids according to standard methods.

Table 1. Temporal evolution of four riverine features relevant to fish ecology and the fish-biological zonation for a section of the river Rhone (between Brig and Lake Geneva).

	Year			
	1850	**1900**	**1950**	**2003**
Length of the main channel (km)	123.6	119.3	119.3	119.0
Total length of the active channel (km)	228.8	133.4	132.4	126.6
Shoreline length (km)	414.4	264.4	257.1	250.6
(km shoreline length /km main channel length)	3.36	2.22	2.16	2.11
Median wetted width (m)	93	53	69	53
Fish zone	Trout – Grayling – Zone			

The impact of hydropower installations on each study site was expressed using selected hydrological parameters based on the hydrological atlas of Switzerland (Spreafico et al., 1992): the degree of water diversion was described by the percentage of the mean natural annual discharge remaining. The impact of hydropeaking on the seasonal discharge regime was quantified as a percentage increase in the natural winter flow.

Statistical analysis

Abiotic factors were analysed by means of principal components analysis (PCA) to identify environmental variables that varied most between the sites. This procedure involves the creation of uncorrelated groups of intercorrelated variables, which are referred to as principal components. In order to determine the relationship between environmental variables and biotic parameters, all principal components with an eigenvalue >1 were compared with the fish parameters using a linear mixed-effects model procedure (SPSS Inc., 2005). This method allows the inclusion of both random and fixed factors as well as the consideration of experimental units that are nested in a hierarchy (i.e. several strips per site). The analysis was conducted using the SPSS 11.0.1 for Windows software package. Prior to the analysis, all data were transformed using standard transformations (arcsin, log, square root).

Historical analysis

For quantification of the former morphological state of the river Rhone, historical maps from 4 different periods (1850, 1900, 1950 and 2003) were georeferenced and digitized by using ArcMap™ 8.3 (ESRI). With the exception of a small region on Lake Geneva in 1900 (1: 25,000) and all of the 1850 maps (1:100,000), most of these maps were at a scale of 1:50,000. Due to the limited availability of suitable maps, the historical analysis was restricted to the region between Brig and Lake Geneva. Four measures quantifying important riverine characteristics were calculated on the basis of the digitizing: 1) The total length of the main channel [km], and 2) the total length of the entire active channel [km] characterize the river type and structure; 3) the wetted width of the active channel [m] gives information about flow patterns; and 4) to identify the degree of lateral connectivity, the shoreline length was measured in kilometres of shoreline per river kilometre (van der Nat et al., 2002).

Due to limitations in data availability, it was not possible to carry out a more in-depth analysis of historical fish data. An estimate of the potential fish fauna was carried out from available historical sources (Fatio, 1882, 1890; Gattlen, 1955).

Results

Historical analysis

The main channel length of the river Rhone between Brig and Lake Geneva has been reduced by 4.6 km or 3.7% over the past 150 years (Table 1). This difference increases substantially (–102.2 km, –44.7%) when the length of the entire active channel (cumulative length of all branches) is considered. The most extensive decrease took place between 1850 and 1900. The length of the main channel and of the total active channel has been more or less stable since then.

The shoreline length of the river Rhone between Brig and Lake Geneva decreased by 39.5% (163.8 km) between 1850 and 2003, and the shoreline length per river kilometre was reduced from 3.4 to 2.1. The most significant change in shoreline length took place between 1850 and 1900, with a decrease of 150.0 km (36.2%), indicating a decline from 3.4 km $\cdot$ km^{-1} to 2.2 km $\cdot$ km^{-1}.

The median wetted width has been reduced by 40 m or 43% since 1850, with the most important reduction also occurring between 1850 and 1900. This decline was interrupted by a temporary increase in the median wetted width in 1950.

Based on the morphometric conditions retrieved from the historical maps, the river Rhone was categorized as a trout-grayling zone (Table 1). Eight fish species were

Table 2. Fish species in the river Rhone reported in historical sources (columns 1–2) and in selected recent literature (columns 3–5).

	1	2	3	4		5
				Tributaries	Canals	
Brown trout *(Salmo trutta fario)*	x[a)]	x	x	x	x	x
Lake resident trout *(Salmo trutta lacustris)*		x				
Whitefish *(Coregonus spp.)*		x				
Rainbow trout *(Oncorhynchus mykiss)*			x		x	
Brook Trout *(Salvelinus fontinalis)*			x			
Grayling *(Thymallus thymallus)*	x	x	x			
Bullhead *(Cottus gobio)*	x	x	x	x	x	x
Eurasian minnow *(Phoxinus phoxinus)*		x	x	x	x	x
Bleak *(Alburnus alburnus)*		x	x			
Threespine stickleback *(Gasterosteus aculeatus)*			x		x	
Northern pike *(Esox lucius)*	x	x			x	
European chub *(Leuciscus cephalus)*	x	x			x	
European Perch *(Perca fluviatilis)*		x				x
Gudgeon *(Gobio gobio)*	x[b)]	x				x
Goldfish *(Carassius auratus)*						x
Common carp *(Cyprinus carpio)*	x	x				
Stone loach *(Barbatula barbatula)*	x[b)]	x				
Tench *(Tinca tinca)*	x	x				
Roach *(Rutilus rutilus)*		x				
Rudd *(Scardinius erythrophthalmus)*		x				
Burbot *(Lota lota)*		x				
Spirlin *(Alburnoides bipunctatus)*		x				
European Eel *(Anguilla anguilla)*		x				
Total	**8**	**19**	**8**	**3**	**7**	**5**

1 Sebastian Münster's Kosmographie from 1544 (see Gattlen, 1955): a) inclusion of subspecies unclear. b) common name unclear, gudgeon or stone loach.
2 Fatio (1882) and Fatio (1890)
3 Etat du Valais (1999)
4 Küttel (2001): Electrofishing survey in selected tributaries and canals of the Rhone valley.
5 Peter (2004)

mentioned in the oldest available documentary source dating from 1544 (Table 2; see Gattlen, 1955). In the late 19th century, 19 fish species were documented in the river Rhone and its tributaries (Fatio, 1882; 1890).

Fish parameters

Our electrofishing surveys revealed a low diversity of fish species in the river Rhone. Only two species, brown trout (*Salmo trutta fario*) and bullhead (*Cottus gobio*), were found in the 36 strips sampled. The relative abundances showed a high dominance of brown trout, amounting to 99.6% (714 individuals) of the total catch (717 individuals). Generally, very low densities were found, ranging from 0 in 4 strips to 43 fish$\cdot$100 m^{-2}, with a mean of 5 fish$\cdot$100 m^{-2}.

Most brown trout were of medium body size. The average length per strip (median) ranged between 87 mm and 261 mm with a mean of 157 mm. Larger and young individuals were largely missing. A considerable number of brown trout (28%) showed anomalies such as deformed fins and shortened opercula, as can often be found in hatchery-reared animals.

Environmental variables

Table 3 summarizes the distribution of the untransformed original environmental variables. The values of all the chemical parameters were within the tolerable range for brown trout (Alabaster and Lloyd, 1980).

In the principal components analysis (PCA), the 28 original variables were reduced to 9 principal components, accounting for 85.6% of the total variation (Table 4). Every original variable displayed high loading (>0.5) in a single principal component only, thereby enabling clear interpretation. The variables "(abundance of) riffles" and "(concentration of) suspended solids" did not show any loadings >0.5 (Table 4).

The extracted components can be labelled in accordance with the grouping of the original variables. Component 6, for instance, can be referred to as presence of cover, with variables like availability of cover, larger substratum and pools being the most important (see the high positive loadings in Table 4). In addition, the percentage of glides is negatively correlated with component 6.

Component 4 summarizes the organic content of the water sample while component 7 includes the availability of middle-sized substratum (positive loading for particles between 8 and 64 mm, negative loading for larger particles).

Comparison between abiotic and biotic variables

The linear mixed-effects model procedure revealed a significant positive relationship between component 6 (cover availability) and two biotic variables (Table 5). Thus, large numbers of brown trout were found in stretches with a considerable amount of cover, substra-

Table 3. General statistics for environmental variables used for the Principal Component Analysis (PCA). The values are calculated on the basis of the individual fishing strips (N = 36).

Environmental variable	Unit	Median	Minimum	Maximum	Interquartile Range
Substratum <8 mm	%	0.00	0.00	100.00	31.25
Substratum 8–64 mm	%	5.00	0.00	100.00	50.00
Substratum 64–256 mm	%	50.00	0.00	100.00	41.67
Substratum >256 mm	%	0.00	0.00	50.00	25.00
Cover availability	%	2.40	0.00	36.57	6.16
Riffles	%	22.80	0.00	91.70	46.63
Glides	%	11.00	0.00	87.50	29.08
Runs	%	12.74	0.00	100.00	49.63
Edgewaters shallow	%	7.50	0.00	41.50	17.62
Pools and deep edgewaters	%	11.35	0.00	100.00	23.82
Number of habitat types	count	5.00	1.00	11.00	3.00
Evenness	nondimensional	0.75	0.00	0.99	0.20
Shanon index of diversity	nondimensional	1.71	0.00	2.89	0.68
Shoreline fine	%	0.00	0.00	77.00	0.00
Shoreline mixed	%	0.00	0.00	54.50	0.00
Shoreline organic	%	0.00	0.00	52.75	0.00
Shoreline coarse or rock	%	100.00	0.00	100.00	70.25
Residual flow	nondimensional	9.00	1.00	10.00	5.00
Increased winter flow	nondimensional	1.00	0.00	3.00	2.00
[Tot-P]	$\mu g \cdot L^{-1}$	20.60	5.10	85.60	21.65
[NO_3-N]	$mg \cdot L^{-1}$	0.68	0.34	1.10	0.47
[NO_2–N]	$\mu g \cdot L^{-1}$	8.55	1.00	25.80	9.55
[NH_4–N]	$\mu g \cdot L^{-1}$	109.35	5.00	519.00	160.70
pH	nondimensional	7.34	7.06	7.70	0.27
Alkalinity	$mmol \cdot L^{-1}$	1.46	0.68	2.65	0.87
Suspended solids	$mg \cdot L^{-1}$	15.71	3.67	65.30	8.03
DOC	$mg \cdot L^{-1}$	0.67	0.43	1.12	0.24
TOC	$mg \cdot L^{-1}$	0.79	0.54	2.11	0.69

tum larger than 25 cm in diameter, a high percentage of pools and a small percentage of glides.

It was not possible to establish any relationship between the environmental variables and the percentage of anomalies and injuries found on the brown trout.

Discussion

Morphological and hydrological deficits

In the mid-19th century, the Rhone system was still in a near-natural state with isolated human modifications of limited spatial scope. Despite this low degree of structural impairment in 1850, morphological characteristics such as the shoreline length clearly differ from contemporary values obtained in the Tagliamento, NE Italy, i.e. the only large morphologically intact Alpine river remaining in Europe (Ward et al., 1999). There, the shoreline length measured in the field averaged 14.4 km $\cdot$ km^{-1} (van der Nat et al., 2002). Our values are substantially lower. This discrepancy is most probably due to differences in data collection and spatial resolution (high resolution dGPS vs. on-screen digitization of historical maps).

To our knowledge, shoreline length has never previously been measured from historical maps. A critical problem in the comparison of various temporal states is that potential differences may indicate variations in discharge rather than changes in river morphology. Unfortunately, no information is available on the discharge conditions at the time of the cartographers' work. This must be considered in the interpretation of the data. However, from the inundation pattern in the last remaining braided section in the Rhone (see below), it can be assumed that none of the four states displays extreme discharge conditions, i.e. neither extremely low nor extremely high flows and that conditions are more or less comparable.

The geomorphological characteristics of the river Rhone have changed fundamentally over the past 150

Table 4. Loadings of environmental variables on principal components (PC) from PCA. Principal components with eigenvalues >1 were extracted. Loadings >0.5 are shown in bold print.

Environmental variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
[NO_3-N]	**–0.86**	–0.09	0.31	–0.03	–0.11	–0.09	–0.05	0.13	0.14
Residual flow	**0.85**	–0.01	0.29	–0.08	0.11	0.03	–0.21	–0.02	0.01
Runs	**0.82**	–0.30	0.02	0.10	0.03	–0.04	–0.24	0.04	–0.15
[Tot-P]	**0.77**	0.01	0.38	–0.15	0.27	–0.03	0.29	0.19	0.02
Increased winter flow	**0.72**	–0.10	0.47	–0.19	0.01	0.16	–0.24	0.00	0.09
pH	**–0.51**	0.21	0.05	–0.23	0.16	–0.33	0.15	0.35	–0.23
Alkalinity	**–0.73**	–0.29	–0.05	–0.24	–0.23	–0.03	–0.10	0.19	0.15
Shanon index of diversity	0.01	**0.94**	–0.03	0.02	0.14	0.04	0.03	–0.03	0.22
Evenness	–0.10	**0.80**	0.35	–0.14	–0.07	–0.07	–0.26	0.01	0.09
Number of habitat types	0.08	**0.75**	–0.41	0.23	0.22	0.03	0.23	–0.08	0.06
[NO_2-N]	0.01	0.03	**0.95**	–0.08	0.09	–0.04	0.05	0.02	0.02
[NH_4-N]	0.42	–0.02	**0.84**	–0.12	0.07	–0.09	0.11	0.14	–0.01
DOC	0.02	0.00	–0.01	**0.93**	–0.08	0.09	0.09	0.09	0.02
TOC	0.06	0.02	–0.21	**0.86**	–0.01	0.04	0.12	0.06	0.03
Substratum <8 mm	0.15	0.14	0.02	0.13	**0.89**	–0.04	–0.25	–0.12	0.09
Shoreline fine	0.21	0.08	0.13	–0.32	**0.87**	–0.09	0.07	0.01	–0.07
Pools and deep edgewaters	0.00	–0.33	0.09	–0.15	0.24	**0.78**	0.05	–0.22	0.10
Substratum >256 mm	–0.03	0.19	–0.27	0.21	–0.21	**0.71**	0.00	0.09	0.00
Cover availability	0.21	0.25	0.40	–0.02	–0.06	**0.66**	0.02	0.03	–0.39
Glides	–0.41	0.26	0.22	–0.19	0.09	**–0.53**	–0.05	–0.24	0.11
Substratum 8–64 mm	–0.20	–0.07	0.09	0.08	–0.27	–0.06	**0.88**	–0.12	0.04
Substratum 64–256 mm	0.03	–0.15	–0.06	–0.22	–0.50	–0.26	**–0.67**	0.16	–0.04
Shoreline mixed	0.02	0.04	–0.09	–0.35	0.13	0.01	0.34	**–0.74**	–0.08
Shoreline organic	0.17	0.09	–0.43	0.44	0.01	–0.19	–0.05	**–0.55**	–0.13
Edgewaters shallow	–0.22	0.43	0.06	–0.03	0.12	–0.14	0.09	0.04	**0.76**
Shoreline coarse or rock	–0.03	0.30	0.04	0.25	–0.32	0.49	–0.05	0.25	**0.54**
Riffles	–0.28	0.47	–0.38	0.20	–0.21	–0.02	0.35	0.33	–0.25
Suspended solids	0.35	–0.25	0.07	–0.49	0.46	–0.15	0.30	0.15	0.04
Eigenvalue	4.80	3.22	3.17	2.84	2.64	2.42	2.07	1.48	1.33
% total variation	17.14	11.49	11.30	10.13	9.42	8.64	7.38	5.29	4.76

years. This development is reflected in a slight decrease in main channel length and a dramatic reduction in shoreline length, total active channel length and, partly, median wetted width. The most significant changes between 1850 and 1900 coincide with the systematic straightening of the river Rhone in the 1860s and 70s (Département Fédéral de l'Intérieur, 1964).

Lateral connectivity was most strongly affected by channelization. Characteristic aquatic habitats, such as backwaters, side arms, oxbow lakes and marshes, completely disappeared or are now permanently uncoupled from the main channel, even during severe floods. With the loss of the natural riparian zone, a fundamental component of the river was reduced and impaired, affecting a variety of physical and ecological functions such as habitat structure, organic matter supply, etc. (Naiman and Décamps, 1997; Schiemer and Zalewski, 1992). The negative effects of reduced lateral connectivity on fish stocks are well known (Welcomme, 1979).

Today, only one 6 km reach of the river Rhone between Brig and Lake Geneva still shows a nearly natural braided structure (Pfynwald, upstream from Sierre, Fig. 1). However, despite this physical connection with the floodplain, the natural flow dynamics cannot develop to the maximum extent as an upstream water diversion causes residual flow throughout the year. Longer near-natural braided river reaches with extensive floodplains can still be found below Lake Geneva, in the French section of the river Rhone (Copp, 1989).

Instream structure has also been drastically reduced: prior to the first correction, a high variability in stream width – and with it probably in depth – resulted in a diverse physical habitat, an effect that was probably amplified by the large woody debris deriving from the vast

Table 5. Relationship between environmental and fish-biology variables (results from the linear mixed-effects model procedure).

Fish-biology variable	**Principal component**								
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Mean length of brown trout (median)	NS	NS	NS	NS	NS	NS	NS	NS	NS
Percentage of brown trout with anomalies	NS	NS	NS	NS	NS	NS	NS	NS	NS
Percentage of brown trout with injuries	NS	NS	NS	NS	NS	NS	NS	NS	NS
Number of fish $\cdot$ m^{-2}	NS	NS	NS	NS	NS	**p = 0.000 F = 24.34**	NS	NS	NS
Number of brown trout $\cdot$ m^{-2}	NS	NS	NS	NS	NS	**p = 0.001 F = 24.24**	NS	NS	NS

riparian forests indicated on the topographic maps. The systematic straightening of the river Rhone resulted in the development of a barely structured, uniform bed profile. Furthermore, due to the changes in land use and the removal of snags at the weirs, the structuring effect of large woody debris is now almost completely lacking. As a result, habitats with high current velocities and uniform depths prevail today. Habitats with slow flowing or even standing-water like pools are strongly underrepresented. Such a shift from lentic to lotic conditions represents a typical development in channelized rivers (Welcomme, 1979).

Changes in channel morphology can also be assumed to alter water temperature (Hawkins et al., 1997). In a naturally structured system, temperature variation in the cross-section can exceed that occurring in the main channel along the entire river course (Arscott et al., 2001). Standing water bodies of various connectivity with interstitial waters (phreatic or hyporheic) are responsible for much of this lateral temperature heterogeneity (Arscott et al., 2001). In a channelized river like the river Rhone, however, almost no lateral heterogeneity in water temperature exists. Temperature is known to be a key environmental factor structuring fish communities (Welcomme, 1979). In particular, the requirements of meso-eurythermal species like the European chub (*Leuciscus cephalus*) or the gudgeon (*Gobio gobio*) are not fulfilled under the present homogeneous temperature conditions prevailing in the river Rhone.

Deficits in the fish fauna

Assemblage level. Historical cartographical and documentary sources show a diverse habitat occupied by a relatively rich fish assemblage. Against this background, our recent survey revealed an extremely low species richness in the river Rhone, with only two species present. Moreover, the fish fauna is almost completely composed of brown trout, with a few bullheads accounting for <0.5% of the total catch. Previous local studies, partly conducted at confluences of tributaries, revealed a higher diversity, i.e. 6 and 8 species, respectively, but most species were represented by single individuals (Etat du Valais, 1999; Peter and Weber, 2004). Similar results were reported for the tributaries (3 species, low densities), whereas a slightly larger species pool of 6 species and higher fish densities were found in the channels of the Rhone Plain (Küttel, 2001). A richer species set is reported from the French section of the river Rhone, below Lake Geneva (see e.g. Copp, 1989; Persat et al., 1994), where near-natural floodplains exist that are still large and have a rich habitat supply.

The low species diversity and unnatural assemblage composition in the main river constitutes a serious biotic deficit. In our search for possible reasons, we confined ourselves to a qualitative interpretation. Because of the dominance of the brown trout, the statistical analysis had to be restricted to the population level of this species (see the following section). As described in the preceding chapter, the diversity of aquatic habitats in the river Rhone has suffered massive impairment. This morphological degradation is further compounded by hydrological alterations related to hydropower generation. Five dams on the main river and a large number of weirs in the tributaries interrupt longitudinal connectivity and inhibit the passage of migratory species such as the lake resident trout (*Salmo trutta lacustris*). The effects on the flow regime are also considerable. Extensive variability in width and depth can often be observed in stretches under residual flow. Because of the reduced discharge volume, however, the water column is very small, preventing larger fish from colonizing these sites. Furthermore, reservoir management has completely changed the daily and seasonal discharge patterns. The natural winter flow has increased substantially, and daily flow fluctuations lead to a general increase in current velocities and a lateral displacement or even disappearance of rare lentic zones (Bain et al., 1988). Species or age classes limited to this habitat are forced to relocate, and some individuals, especially smaller fish, may suffer from stranding (Saltveit et al., 2001).

Population level: brown trout. The observed densities of brown trout are very low for a river of the trout-grayling zone. Moreover, the age structure represented in the catches differs clearly from that of a natural population. Young trout (0+, 1+) are highly underrepresented in all sampled stretches. This observation is reinforced by former surveys that specifically documented the occurrence of brown trout fry shortly after emergence (Peter and Weber, 2004). Natural 0+ brown trout could only be found at isolated sites. There are several reasons for these small cohort sizes. Firstly, adult, reproductive animals are only found in very low densities. Secondly, our habitat surveys indicate that both spawning and rearing conditions are unsuitable. As mentioned above, the habitat preferred by young trout, i.e. shallow riffles with cobble substrata (Heggenes, 1988), is generally sparsely available in the river Rhone and, because of the flow fluctuations induced by hydropeaking, often of reduced persistence. The effects of these unstable habitat conditions, in particular on fry and juvenile trout (e.g. stranding, increased drift), are widely reported in the literature (Freeman et al., 2001; Hunter, 1992; Liebig et al., 1999; Saltveit et al., 2001).

The reproductive contribution of individuals inhabiting the tributaries is also of minor importance. Tributaries often lack a connectivity to the main river, and the impaired quality of spawning grounds and low densities of young fish (0+) have been documented (Küttel, 2001).

Although the brown trout densities observed in our study are low, variations could be observed between the different strips and sites. Some general relationships were observed in relation to the environmental variables. In general, more brown trout were caught where cover was available. This fact was particularly noticeable at sites where several strips with different cover availabilities were fished.

Cover in the river Rhone is mostly provided by artificial structures, in particular embankments. The dominant embankment type is riprap, followed by groins dating mainly from the first correction. Natural cover structures like woody debris, macrophytes or instream structures are largely missing. Cover is strictly reduced to the shoreline zone and is almost absent in the middle of the river. Accordingly, stretches fixed with riprap performed best in respect of cover availability. Both the highest brown trout densities and the highest biomasses were found in these stretches (Fette and Weber, 2007). Contrary to this, brown trout were absent from or only represented by single individuals along sparsely structured sandy shores secured by groins and in the monotonous median strips.

The large number of brown trout showing anomalies prompts the assumption that a significant proportion of the stock is hatchery-reared fish. Negative consequences for reproduction, the state of health and genetic composition of wild populations may be expected as a result (White et al., 1995).

Ecological potential and rehabilitation measures

Flood protection and river rehabilitation are no longer regarded as controversial in many countries (Nienhuis and Leuven, 2001). On the contrary, synergies have been identified that give rise to benefits for both. This is also true of the river Rhone. The third correction will change the face of the river considerably over the next 25 years. What priorities can be identified based on this study?

The most obvious structural deficits are the low quality of shoreline zones and the lack of instream structures such as pool-riffle-glide patterns. Under present conditions, linear banks fixed with riprap perform best in the promotion of brown trout density. They offer cover, but are not as diverse as well-structured near-natural shorelines (Schiemer and Spindler, 1989; Schmetterling et al., 2001). Many ecological functions would benefit from an improvement of the shoreline zone, and socio-economic services would increase (Hostmann et al., 2005; Naiman and Décamps, 1997; Tockner et al., 2008).

One measure that would enhance both the shoreline and the low instream habitat diversity and quality in formerly braided rivers is local river widening (Rohde et al., 2005). This would involve a significant widening of the river bed (Habersack et al., 2000), possibly by a factor >2 of the existing channel width, in order to re-create a braided river morphology. Apart from river-engineering advantages – stabilization of the bottom by decreasing the transport capacity of the widened channel (Hunzinger, 1998) – local river widening offers many ecological improvements through morphodynamical processes such as braiding and gravel erosion and deposition, thus leading to increased structural and hydrological heterogeneity. Up to now, local river widening has mainly been carried out in Switzerland, Germany and Austria (Habersack and Nachtnebel, 1995; Rohde et al., 2005; Völkl et al., 2002).

Few studies are available on the ecological success of local river widening, however their findings are generally positive. Habersack (2000) describes the enhancement of aquatic habitat conditions and the increased stock of juvenile grayling in local widenings of the river Drau, Austria. A comparison of the riparian vegetation in 5 river widenings in Switzerland revealed an increased degree of naturalness at both habitat and species level in most of the cases studied (Rohde et al., 2004; Rohde et al., 2005).

Local river widening under impaired hydrological conditions as found in the river Rhone is particularly delicate and challenging (Unfer et al., 2004). In most cases, purely morphological measures will probably not compensate for hydrological deficits. Hydrological actions such as the mitigation of hydropeaking using technical measures are also necessary, e.g. slower ramping rates of the turbines (Halleraker et al., 2003) or storage of the turbinated water in retention basins (Moog, 1993).

This combination of structural and hydrological measures alone can bring the anticipated success in degraded rivers with appropriate water quality and existing bedload dynamics (Fette and Weber, 2007).

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