

INITIAL IMPACT OF THE GABČÍKOVŔO HYDROELECTRIC SCHEME ON THE SPECIES RICHNESS AND COMPOSITION OF 0+ FISH ASSEMBLAGES IN THE SLOVAK FLOODPLAIN, RIVER DANUBE

J. ČERNÝ,^{a,*} G. H. COPP,^{b,1} V. KOVÁČ,^c R. GOZLAN^d and L. VILIZZI^e

^a *Institute of Zoology, Slovak Academy of Sciences, Dúbravská cesta 9, 842 06 Bratislava, Slovakia*

^b *University of Hertfordshire, Hatfield, UK, and Station d'Hydrobiologie lacustre-INRA, Thonon-les-Bains, France*

^c *Department of Ecology, Faculty of Natural Sciences, Comenius University, Mlynská dolina B-2, 842 15 Bratislava, Slovakia*

^d *Centre for Ecology and Hydrology—Dorset, Winfrith Technology Centre, Winfrith Newburgh, Dorchester, Dorset DT28ZD, UK*

^e *Via Giolitti 45, 10123 Torino, Italy*

ABSTRACT

Relatively little information exists on the effects of hydroelectric schemes on 0+ fish composition in large European rivers because few or no pre-impact data exist. We compared 0+ fish species richness and composition, relative density, fish size as well as available and used habitat using data from 12 floodplain sites sampled just prior to (1992) and four years after (1996) the start of operations of the Gabčíkovo hydropower station on the River Danube (Slovakia). We also used modelling techniques to assess the change in species richness and habitat use and to predict 1996 occurrences from the 1992 data set. The floodplain was greatly modified by the hydroscheme. Only 12 of 27 sites sampled in August 1992 were extant in August 1996. Therefore, all four channel types identified (flowing, abandoned, weir, wing-dam) were more lentic in 1996 than in 1992, with increased width, smaller-sized sediment (silt, clay) and greater amounts of macrophytes. After the operations of the hydro-scheme, the overall relative density of fishes (individuals per surface area) of all ages decreased, with the exception of 0+ fishes, despite a slight reduction in 0+ fish density in all channel types except weirs. Species number increased from 25 to 28, although in all channel types there was a change in the composition of the 0+ fish assemblages, with rheophiles generally replaced by limnophiles and migrants from the lower Danube. The two most important microhabitat variables were the proportion of macrophytes and gravel, the latter being the factor distinguishing 0+ fish microhabitat use in 1992 (preferences) and 1996 (indifference or avoidance). Species richness and 0+ fish density in 1996 could be predicted from the 1992 data using simple log-linear models (density, richness, sample number). Species-specific occurrence in 1996 could not be predicted using environmental/fish data from 1992 with multiple regression or generalized additive models (GAM). However, the overall GAM from 1992 could predict overall fish occurrence in 1996. Copyright © 2003 John Wiley & Sons, Ltd.

KEY WORDS: backwaters; 0+ fish; point abundance sampling; microhabitat; habitat selection; generalized additive models

INTRODUCTION

Most of the major rivers of the world have been regulated to exploit their hydroelectric potential, to attempt control variations in discharge, and/or to facilitate the redistribution of the water to other areas of the neighbouring landscape (Boucher, 1990). None of these schemes avoids impacts on the river ecosystem, with the various impacts being both universal and site-specific. One of more controversial river regulation projects in recent history is the Gabčíkovo hydroscheme on the River Danube (Balon and Holčík, 1999). Originally conceived as a joint Slovak-Hungarian project (which included a compensation dam at Nagymaros, Hungary), the scheme was eventually finished as a lone Slovak project after the Hungarian government decided to withdraw. This withdrawal resulted in the Slovak government implementing a revised plan, which diverted most of the Danube's discharge through the Gabčíkovo by-pass reservoir and hydropower station.

* Correspondence to: J. Černý, Institute of Zoology, Slovak Academy of Sciences, Dúbravská cesta 9, 842 06 Bratislava, Slovakia.
E-mail: uzaecern@savba.sk

¹ Current address: CEFAS, Pakefield Road, Lowestoft, Suffolk, NR33 0HT, UK.

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The Gabčíkovo hydroscheme began operation in the winter of 1992, and just prior to that we carried out an intensive survey of 0+ fishes (Copp *et al.*, 1994) to aid assessment of the scheme's impact on the adjacent floodplain. The aim of the present study, undertaken four years later, was to assess the initial impact of the scheme on 0+ fish recruitment in terms of available and exploited habitat as well as with regard to changes in the structure of the 0+ fish assemblages, which reflect the fish reproductive potential of aquatic ecosystems (Copp, 1989b; Gozlan *et al.*, 1998). Our specific objectives were to: (1) compare species richness, relative densities and size-structure of 0+ fish assemblages in 1996 with those in 1992 (Copp *et al.*, 1994), both for the floodplain as a whole and for its various channel types; (2) compare channel character and 0+ fish assemblage structure; (3) assess 0+ fish micro-habitat use; and (4) evaluate the differences in the actual structure of 0+ assemblages in 1996 compared to that predicted using the model from the pre-impact survey (Copp *et al.*, 1994).

STUDY AREA, MATERIAL AND METHODS

The hydrology and geomorphology of the Hungarian/Slovak floodplain (Figure 1) have been described in detail elsewhere (Holčík and Bastl, 1976; Holčík *et al.*, 1981; Bethemont and Bravard, 1986; Boucher, 1990) and are reviewed by Copp *et al.* (1994). During the two study periods, the mean river discharge (station Devín, Bratislava) was low: $1280 \text{ m}^2 \text{ s}^{-1}$ in August 1992, and $1811 \text{ m}^2 \text{ s}^{-1}$ in August 1996. Twelve of the 26 study sites in Slovakia from the pre-operations study (Copp *et al.*, 1994) were extant in 1996 (Figure 1; sites 50, 51 and 52 in Copp *et al.* (1994) joined to one gravel pit, and therefore are considered as one site in the present study); these consisted of four types: (i) lotic, i.e. 'flowing' channels (fc), which had at least some flow of water; (ii) abandoned channels (ac), which were isolated from the river except during periods of elevated discharge; (iii) just below weirs (we), which were constructed to maintain water levels within the floodplain; and (iv) behind wing-dams (wd), which were perpendicular to the bank and extended out into the main channel.

As in 1992, large lotic side-channels could not be sampled in their entirety, so a 'representative' reach was selected; this consisted of a concave/convex stretch, with the shallow aggrading bank opposite a deeper eroding bank. Abandoned channels were generally sampled in their entirety, though in some cases their surface area was

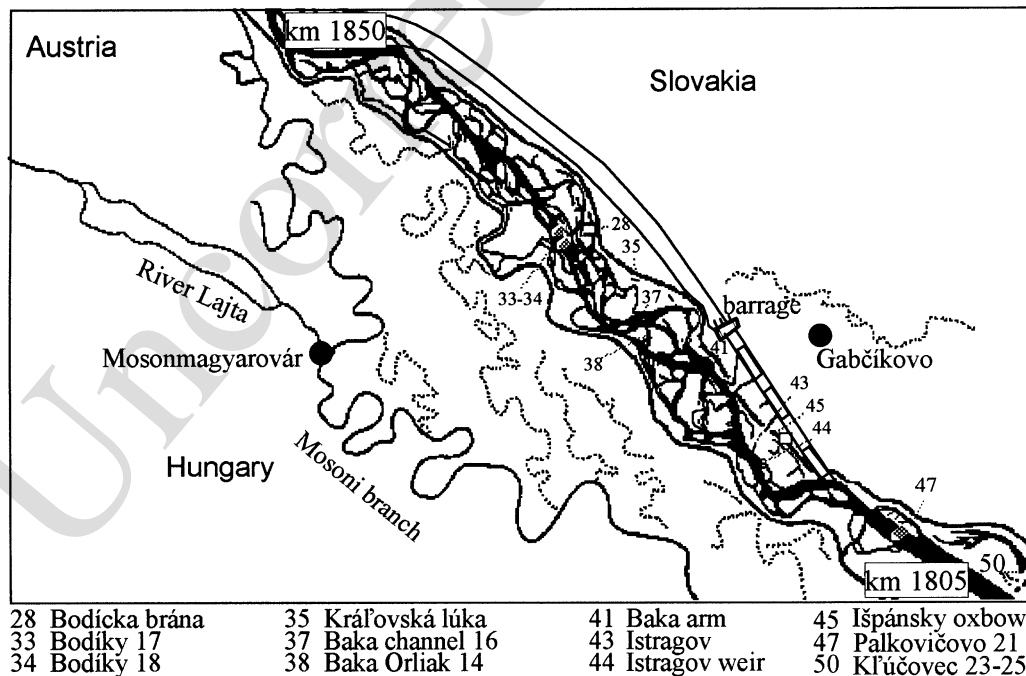


Figure 1. Map of the River Danube near Gabčíkovo, Slovakia, with the 12 study sites of 1992 (Copp *et al.*, 1994) still extant and studied in 1996

1 too great and so a representative area was selected as above; these locations were mostly former channels isolated
2 from other channels of the floodplain except during periods of elevated discharge, when they may be reconnected
3 to other channels by either or both of their extremities (upstream and downstream). The downstream vicinity of
4 weirs, with seepage through and between the boulder weirs providing localized flow, has been identified as a refuge
5 for the progeny of rheophilous fishes (Copp *et al.*, 1994); we sampled along the downstream side of the weir as well
6 as a further distance of 50–100 m downstream thereof. In both 1992 and 1996, sampling in the main channel of the
7 Danube was restricted to the area downstream of wing-dams, which are a probable refuge of any 0+ fish occurring
8 in the main channel (Copp *et al.*, 1994).

9 At each of the 12 sites (Figure 1), fish and environmental variables were sampled with the density of samples
10 approximately equal at each site (about one point per 10 m²). In total, 270 point samples were collected in 1992 and
11 504 samples in 1996. In extremely large channels, this intensity of sampling effort was not always possible due to
12 time and manpower constraints. Sampling was undertaken by two teams in late August using point abundance
13 sampling by electrofishing (Persat and Copp, 1989), with portable DEKA units modified for small fishes (anode
14 of 10 cm diameter; see Copp and Peñáz, 1988; Copp, 1989a). The same equipment was used in both years, and the
15 anode's effective field at each point sample was assumed to be *c.* 0.071 m² (Copp, 1989a), though this area will
16 vary according to water conductivity (Cuinat, 1967). Sampling points were selected randomly within each site via
17 a point of the finger with eyes closed. Sampling was generally undertaken from a dinghy, with the exception of
18 some wing-dams sites where the water was shallow enough to be sampled by wading. The sampling technique is
19 described in detail in Copp *et al.* (1994).

20 At each point sample, the fishes were either preserved in 4% formaldehyde immediately after capture for anal-
21 ysis in the laboratory (identified to species following Koblickaya (1981)), or measured for standard length (SL)
22 and returned to the water (i.e. fishes $\geq 1+$). Habitat characteristics were then evaluated using six quantitative and
23 seven semi-quantitative environmental variables: width (m); distance from bank (m); depth (cm); bank slope; per-
24 centages of clay (particle diameter <0.06 cm), silt (<0.06 cm), sand (0.06–0.2 cm), pebbles (0.2–2.0 cm), gravel
25 (>2.0 cm) and cobbles (>6.0 cm); ligneous structures and macrophytes; water velocity; and water temperature.
26 Bank slope was calculated from the depth divided by the distance from bank. Bottom substratum (clay, silt, sand,
27 pebbles, gravel) was evaluated as a percentage of the sample area (i.e. 0.071 m²), with clay and silt distinguished by
28 the greater between-particle adhesion in clay than silt. Ligneous structures (branches, logs, trunks, roots) within
29 each point were counted in a manner similar to that described by Kinsolving and Bain (1990) but on a scale of one
30 to ten. Submerged, floating and emergent macrophytes were estimated visually as a percentage of the area sampled
31 at each point. Water velocity was measured using a calibrated dip-net; no movement of the net indicated no flow,
32 slow ballooning of net indicated weak flow (<5 cm s⁻¹), and moderate to fast ballooning of the net indicated faster
33 flow (>5 cm s⁻¹).

34 Fish relative density was calculated as the number of specimens captured per total surface area sampled (Copp,
35 1989a,b; Copp *et al.*, 1994). The ecological classification of the species followed Schiemer and Waidbacher
36 (1992); see Table I. Potential changes in the size-structure of populations were examined using the Student's
37 unpaired *t*-test. From the relative densities and numbers of species for each site, we calculated the mean relative
38 densities and the numbers of species for each site (total species richness, *S*). To adjust for the effect of density on
39 species richness, we calculated the mean adjusted species richness ($S' = S \div \ln$ of relative density) for each channel
40 type (lotic, abandoned, weir, wing-dam) as well as the percentiles of the residuals for each channel type derived
41 from species richness (*S*) regressed against natural-log (\ln) of density at the 12 sites for the two study years.
42 Between-year comparisons for each channel type were made with the Student's paired *t*-test.

43 To assess changes in the character of the 12 channels after the start of dam operations, the raw environmental
44 data (all variables except distance from bank, a microhabitat variable, and temperature, which varies according to
45 climatic conditions) for the years 1992 and 1996 (744 samples \times 13 variables) were submitted to principal com-
46 ponents analysis (PCA), with 90% ellipses (Green, 1971) generated for each channel type and year of study.
47 Changes in 0+ fish assemblage structure at the sites were also assessed using PCA of the sites-by-species matrix
48 (24 sites \times 22 species) for 1992 (12 sites) and 1996 (same 12 sites) converted to absence/presence, reduced to con-
49 tain only those species occurring in two or more sites, and submitted to PCA, with 90% ellipses (Green, 1971)
50 generated for each channel type and year of study. PCA is of particular interest in this case as the absence of a
51 species is accorded equal weight to its presence (e.g. Copp, 1989b). Changes in composite microhabitat use were
52

Table I. Latin and common names, code, ecological classification (Ra, rheophilous A; Rb, rheophilous B; Eu, eurytopic; Li, limnophilous), mean relative densities (in ind m⁻², areas sampled given in Table II), relative abundance (in % as well as number (*n*)), mean standard length (SL, in mm), with standard error (SE) and Student's unpaired *t*-value (*t*) and probability (*P*) results for comparisons of fishes of all ages captured at 12 water bodies of the Danube floodplain in Slovakia before and after the start of operation of the Gabčíkovo hydropower scheme

Latin name	Common name	Code	Ecolog. class. ^a	Rel. densities		Rel. abundance		1992 survey			1996 survey			Student's <i>t</i> -test			
				1992	1996	1992	1996	<i>n</i>	SL	SE	<i>n</i>	SL	SE	<i>t</i>	<i>P</i>		
<i>Abramis ballerus</i>	blue bream	Al	Eu*	0.11	0.06	0.11	0.08	2	96.5	0.50	41.8	7.00	2	41.8	7.00	7.794	0.02
<i>Abramis brama</i>	common bream	Ab	Eu	1.77	0.47	1.68	0.71	32	41.8	4.36	37.8	5.47	17	37.8	5.47		
<i>Alburnus alburnus</i>	bleak	Aa	Eu	36.83	16.09	35.07	24.05	667	25.2	0.52	29.7	0.83	577	29.7	0.83	-4.735	0.0001
<i>Aspius aspius</i>	asp	As	Rb	0.11	0.31	0.11	0.46	2	71.3	1.25	53.0	2.45	11	53.0	2.45	3.066	0.02
<i>Barbus barbus</i>	barbel	Bb	Ra	1.21	0.31	1.16	0.46	22	42.3	1.83	44.7	3.15	11	44.7	3.15		
<i>Blicca bjoerkna</i>	silver bream	Bj	Eu	3.04	3.32	2.89	4.96	55	40.7	4.00	31.5	1.27	119	31.5	1.27	2.788	0.006
<i>Carassius auratus</i>	Prussian carp	Ca	Li	5.47	3.26	5.21	4.88	99	87.4	3.71	40.3	4.80	117	40.3	4.80	7.556	0.0001
<i>Chondrostoma nasus</i>	nase	Cn	Ra	0.17	0.31	0.16	0.46	3	59.2	2.95	43.7	1.69	11	43.7	1.69	4.309	0.001
<i>Cobitis taenia</i>	spined loach	Ct	Rb	0.06	—	0.05	—	1	60.0	—	—	—	—	—	—	—	—
<i>Cottus gobio</i>	bullhead	Cg	Ra	0.72	—	0.68	—	13	60.8	5.87	—	—	—	—	—	—	—
<i>Exocoetis lucius</i>	northern pike	El	Eu	0.22	0.50	0.21	0.75	4	259.0	76.06	181.0	20.29	18	181.0	20.29		
<i>Gasterosteus aculeatus</i>	three-spined stickleback	Ga	Eu*	—	0.06	—	0.08	—	—	—	26.0	2.60	2	26.0	2.60		
<i>Gibio alpinus</i>	alpine gudgeon	Gp	Ra	0.99	0.03	0.95	0.04	18	37.4	1.56	31.5	—	1	31.5	—		
<i>Gymnocephalus baloni</i>	Balon's ruffe	Gb	Ra	0.11	0.03	0.11	0.04	2	71.0	0.00	75.0	—	1	75.0	—		
<i>Gymnocephalus cernuus</i>	ruffe	Gc	Eu	0.06	0.59	0.05	0.88	1	85.0	—	56.5	3.67	21	56.5	3.67		
<i>Lepomis gibbosus</i>	pumpkinseed	Lg	Li*	2.98	1.03	2.84	1.54	54	37.8	2.68	39.3	4.83	37	39.3	4.83		
<i>Leuciscus cephalus</i>	chub	Lc	Ra	0.66	0.86	0.63	1.29	12	88.4	18.06	90.2	9.27	31	90.2	9.27		
<i>Leuciscus idus</i>	ide	Li	Eu*	0.22	0.28	0.21	0.42	4	88.9	14.04	95.1	17.49	10	95.1	17.49		
<i>Leuciscus leuciscus</i>	dace	Li	Ra	—	0.33	—	0.50	—	—	—	40.7	1.96	12	40.7	1.96		
<i>Lota lota</i>	burbot	Lo	Rb	—	0.03	—	0.04	—	—	—	130.0	—	1	130.0	—		
<i>Misgurnus fossilis</i>	weather loach	Mf	Li	0.06	—	0.05	—	1	139.5	27.51	—	—	—	—	—		
<i>Neogobius kessleri</i>	Kessler's gobie	Nk	Ra	—	0.20	—	0.29	—	—	—	52.0	1.77	7	52.0	1.77		
<i>Perca fluviatilis</i>	Eurasian perch	Pf	Eu	2.93	1.17	2.79	1.75	53	56.4	3.36	72.9	2.89	42	72.9	2.89	-3.616	0.0005
<i>Proterorhinus marmoratus</i>	tubenose goby	Pm	Eu	7.68	8.67	7.31	12.96	139	28.8	0.77	22.6	0.63	311	22.6	0.63	5.791	0.0001
<i>Rhodeus amarus</i>	bitterling	Rs	Li	2.43	9.87	2.31	14.76	44	27.8	0.99	24.3	0.50	354	24.3	0.50	2.42	0.02
<i>Rutilus rutilus</i>	roach	Rr	Eu	36.72	18.57	34.96	27.76	665	42.8	0.95	44.7	0.97	666	44.7	0.97		
<i>Scardinius erythrophthalmus</i>	rudd	Se	Li	0.11	0.31	0.11	0.46	2	74.0	18.00	55.2	4.94	11	55.2	4.94		
<i>Silurus glanis</i>	wels catfish	Sg	Eu	—	0.06	—	0.08	—	—	—	200.0	0.00	2	200.0	0.00		
<i>Stizostedion lucioperca</i>	pike-perch (zander)	Sl	Eu	0.11	0.03	0.11	0.04	2	134.5	32.50	53.1	—	1	53.1	—		
<i>Tinca tinca</i>	tench	Tt	Li	—	0.11	—	0.17	—	—	—	20.4	4.52	4	20.4	4.52		
<i>Vimba vimba</i>	vimba	Vv	Ra	0.28	0.06	0.26	0.08	5	45.0	2.78	37.0	12.95	2	37.0	12.95		

^a According to Schiemer and Waidbacher (1992) except those marked*, which are according to Černý and Kvaszová (1999).

assessed using canonical correspondence analysis (CCA; ter Braak, 1986) of the samples-by-species matrix (744 × 16; i.e. samples devoid of 0+ fish were included), whereby species occurring in ≥ 3% of samples in both years were retained in the analyses (8 species) and considered separately according to their year-class (1992, 1996), hence 16 species/year-classes. The gradients generated were the basis for succinctly describing and visualizing the differential habitat preferences (niches) of taxa through a biplot ordination diagram (ter Braak and Verdonschot, 1995).

Only 11 of the 13 habitat variables were included in the CCA, as channel width was not considered to be a variable for which an individual fish could select, and depth measurements were those of the water and not of the location in the water column selected by the fish. For consistency with Copp *et al.* (1994), gravel and cobbles are combined as gravel&cobbles (>2.0 cm). The variables were categorized in preparation for analysis (Chessel *et al.*, 1987) as follows: distance from bank in meters (0–0.99, 1.00–4.99, 5.00–9.99, 10.00–20.00, >20.00 m); bank slope (≤0.04, 0.041–0.08, 0.081–0.13, 0.131–0.22, 0.221–0.36, 0.361–0.60, 0.601–1.0); clay, silt, sand, pebbles, gravel (0, 1–33, 34–66, 67–100%); ligneous debris (0, 1–3, 4–6, >6 items); macrophytes (0, 1–33, 34–66, 67–100%); water velocity (null, weak, faster); water temperature deviations from the site mean (less than –1.0, –1.0 to –0.51, –0.50 to –0.01, 0, 0.01–0.50, 0.51–1.00, ≥1.0°C). Microhabitat electivities for 1992 and 1996 were calculated as the difference between the frequency of a species in the group of samples having that category of environmental variable and the frequency of that species in all the samples.

The species richness recorded is related to the density of individuals and the number of samples (Connor and McCoy, 1979). Therefore, theoretically, the richness of 0+ fish could be predicted for 1996 using models derived from the 1992 data set. An inability to do so would be indicative of change in the reproductive function of the floodplain (*sensu* Copp, 1989b). Simple linear models were developed for each channel type using the 1992 data (Copp *et al.*, 1994) to predict 0+ fish richness and relative density (individuals (ind) m⁻²) in 1996, with the number of species at each site regressed against the relative density of 0+ fish (ln-transformed to reduce the influence of a few high values) found at each point. For each channel type, the models with the best fit were used to predict species richness from the 1996 data. Similarly, the ln-transformed data of relative density for each site in 1992 were regressed against the corresponding frequency of point samples containing 0+ fish, and this model (all channel types) was used to predict the relative densities of 0+ fish in 1996 from the frequency of point samples collected in 1996 containing 0+ fish. Predictions based on regressions for each channel type were also calculated, with a common model generated for weirs and wing-dams. Observed and expected values were compared using the Student's paired *t*-test.

Multiple regression models were elaborated for each species using the 1992 fish and habitat data in an attempt to predict the abundance of that species in 1996 from the 1996 environmental variables data. Similarly, generalized additive models (GAMs; Hastie and Tibshirani, 1990) were employed for all species combined and for each species separately to compare presence/absence of fish in 1992 and 1996, using distance from bank, depth, substratum, macrophytes, ligneous debris, water velocity and temperature as environmental predictors of fish occurrence. Substratum was calculated as an arbitrary index, based on the relative proportions of clay, silt, sand, gravel, pebble and cobble in each sample. A generalized additive logistic regression model was initially fitted to the entire 1992 data set (all species combined) as well as to each of the 1992 species-specific data subsets. The initial model included all seven predictors, with each term calculated as a smoothing (cubic) spline, with three degrees of freedom, of the form:

$$\text{Fish} = \alpha + \sum s(\text{Predictor}, 3)$$

where α is a constant intercept term, Fish (presence/absence) the (dichotomous) response variable, $s(\dots)$ the smoothing function of the predictor, and 3 represents the degrees of freedom of the smoothing. Screening of predictor variables for inclusion in the model was by analysis of deviance, which provides χ^2 -based approximate partial tests for the importance of the smoothing for each term in the model. The critical value of the partial tests was deliberately set at $\alpha = 0.10$, a choice dictated by (1) the presence, in some cases, of relatively high probability values for most, if not all, variables in the species-specific models, and (2) the need to increase the heuristic value of the model itself. Predictions for the 1996 data were then calculated based on the 1992 data-based resulting models, and the Wilcoxon rank sum test was used to compare predicted and 1992 model-based fitted values.

The principal components, canonical correspondence and other univariate analyses were undertaken on Macintosh using the ADE software package (Chessel and Thioulouse, 1998), GraphMu (Thioulouse, 1990) and StatViewSE + Graphics[©] for Mac, respectively. Multiple regression analyses were undertaken with MINITAB 13 for PC, and the GAMs using S-Plus 2000 Professional for PC.

RESULTS

At the 12 study sites extant in 1996 (Figure 1), the overall relative density (numbers per surface area sampled) of fishes (all ages) decreased from 105.0 ind m⁻² in 1992 (1902 fishes from 18.11 m², representing 25 species) to 66.9 ind m⁻² in 1996 (2399 fishes from 35.87 m², representing 28 species; Table I). The increase in area sampled reflects an increase in available water surface area at the 12 sites due to a rise in water level induced by submersible weirs. Threatened species present in 1992 but absent in 1996 were spined loach *Cobitis taenia* L., weather loach *Misgurnus fossilis* (L.), and bullhead *Cottus gobio* L. Species observed in 1996 but not in 1992 were burbot *Lota lota* (L.), dace *Leuciscus leuciscus* (L.), three-spined stickleback (L.) and Kessler's goby *Neogobius kessleri* (Günther, 1861). In terms of 0+ fishes, the only new species were ruffe *Gymnocephalus cernuus* (L.) and rudd *Scardinius erythrophthalmus* (L.). Differences in size (SL, all ages combined) between 1992 and 1996 were observed in nine species (Table I), with only two of these (bleak *Alburnus alburnus* (L.), Eurasian perch *Perca fluviatilis* L.) being significantly larger in 1996. Significantly smaller mean SL was found in blue bream *Abramis ballerus* (L.), asp *Aspius aspius* (L.), Prussian carp *Carassius auratus* (L.) and nase *Chondrostoma nasus* (L.). In some of these species, the numbers captured were low, so conclusions are tentative, but the considerable reduction of nursery areas after 1993 may be a factor in some that dropped in number between 1992 and 1996.

The overall relative density of 0+ fishes (all species combined) did not differ between 1992 and 1996 (Mann-Whitney, $P > 0.10$). Individual densities of 0+ bullhead, whitefin gudgeon *Gobio albipinnatus* Lukaš, 1933, Eurasian perch, bleak, roach *Rutilus rutilus* (L.) and bitterling *Rhodeus amarus* (Bloch, 1782) all declined significantly (Table II) in the same period. Mean relative density of 0+ fishes dropped slightly in all channel types except weirs (Figure 2), though not significantly (Student's paired *t*-test). Conversely, the number of species of 0+ fish increased in all channel types except active (lotic) channels, though again the differences were not statistically significant; this is probably due to the high variance, which is expressed in the residuals from the regression of richness versus 0+ fish density at the 12 sites in the two years of study, particularly for abandoned channels and wing-dams.

In terms of environmental character (Figure 3), weirs and wing-dams underwent the most profound changes (90% ellipses having the least overlap). Weirs became much shorter, since approximately 60% of each weir emerged out of water due to massive decline in water level. Changes in wing-dams were characterized by increases in both lentic (silt, clay, macrophytes) and lotic (velocity, gravel, pebbles) components. Flowing and abandoned channels extant in 1996 changed the least after the start of hydrodam operations (90% ellipses having the greatest overlap). All channel types had a more lentic character in August 1996 than in 1992, with increased width, a shift to smaller-sized alluvia (silt, clay) and greater amounts of macrophytes.

The composition of 0+ fish assemblages changed in all four channel types (Figure 4), though abandoned channels appear to have been least impacted (orientation and girth of 90% ellipses). Only two flowing channels from the 1992 study were extant in 1996, hence the ellipses are represented by a straight line between the two ordination scores, and these reflect a decline in frequency (Table II), or the disappearance, of some rheophilous species (asp, barbel *Barbus barbus* (L.), vimba *Vimba vimba* (L.), whitefin gudgeon, chub *Leuciscus cephalus* (L.)) or eurytopic piscivores (Eurasian perch, northern pike *Esox lucius* L.) as well as the appearance of a limnophilous species (rudd). Abandoned channels increased their scope with the arrival or increased frequency of limnophilous (rudd) and eurytopic (ide *Leuciscus idus* (L.), common bream *Abramis brama* (L.), blue bream) species, but also included the occurrence of barbel, a rheophilous species. Weirs underwent a relatively strong shift in species composition, with the arrival or increased frequency of Eurasian perch, asp, dace and tubenose goby *Proterorhinus marmoratus* (Pallas, 1814) as well as the loss or decline of ide and chub. Similarly, wing-dams saw the appearance or increased frequency of some rheophilous (dace, vimba, asp) or eurytopic (tubenose goby, three-spined stickleback) species, and the loss or decline in frequency of the rheophilous bullhead or the eurytopic species such as silver bream *Abramis bjoerkna* (L.) and piscivorous species (Eurasian perch, pike-perch *Stizostedion lucioperca* (L.)).

Table II. Year of sampling, sample site, number of sampling points (pts.), surface area of water sampled (m²), channel type (fc = flowing channel, ac = abandoned channel, we = behind weir, wd = behind wing-dam in main channel), and the mean^a density (ind m⁻²) of 0+ fish in the Slovak part of the River Danube (see Copp *et al.*, 1994). See Table I for fish code

Year	Site	Pts.	Area	Type	Cg	Bb	Cn	As	Li	Lc	Gp	Vv	Al	Li	Sl	Pf	Gc	Aa	Rr	Rs	Bj	Ab	Ca	Pm	El	Lg	Se
1992	28	30	2.13	we	0	0	0	0	0	0	0	0	0	0	0	0	0	6.60	17.40	0	0	0	0	0	0	0	0
1992	33	15	1.07	wd	1.90	0	0	0	0	0	0	0	0	0	0	4.70	0	99.50	6.60	0	0.90	0	0	0	0	0	0
1992	34	15	1.07	wd	0	0	1.90	0	0	0	0	0	0	0	0.90	0.90	0	0	1.90	0	0	0	0	0	0	0	0
1992	35	40	2.84	ac	0	0	0	0	0	0	0	0	0	0	0.40	0.70	0	4.20	3.20	1.40	0.70	0	0.40	0.70	0	14.00	0
1992	37	20	1.42	fc	0	0.70	0	0.70	0	0.70	9.90	2.80	0	0	0	3.50	0	14.10	50.00	0	20.00	20.00	0	48.00	0	0	0
1992	38	30	2.13	we	0	0	0	0	0	0.90	0	0	0	0	0	2.80	0	30.00	2.40	0	3.30	0	0	21.0	0	0	0
1992	41	30	2.13	fc	0	0	0	0	0	0.50	0	0	0	0	0	0.50	0	15.50	7.50	0.50	0.50	0.50	0	1.40	0	0	0
1992	43	15	1.07	ac	0	0	0	0.90	0	0	0.90	0	0	0	0	2.80	0	336.00	180.00	22.00	5.60	0	32.00	0	2.80	0	0
1992	44	10	0.71	we	0	0	0	0	0	0	0	0	0	1.40	0	2.80	0	0	0	0	0	0	0	0	0	0	0
1992	45	30	2.13	ac	0	0	0	0	0	0.90	0	0	0	0	0	2.80	0	0.50	61.00	5.20	0.50	0	0.90	2.30	0	0.50	0
1992	47	15	1.07	wd	1.90	20.0	0	0	0	0.90	0	0	0	0	0	2.80	0	35.70	0.90	0	0	0	2.80	0	0	0	0
1992	50	5	0.36	ac	0	0	0	0	0	0	0	0	0	0	0	34.00	0	93.00	5.60	0	0	0	0	0	0	0	0
Mean densities 1992					0.32 ^a	1.73	0.16	0.13	0	0.25	0.90 ^a	0.23	0	0.12	0.11	4.39 ^a	0	45.18 ^a	35.33 ^a	2.89 ^a	2.63	1.71	2.78	6.35	0.23	1.33	0
1996	28	50	3.55	we	0	0	0	0.28	0	0	0	0	0	0	0	0.28	0	35.21	48.17	2.82	6.20	0	0	2.25	0.28	0	0
1996	33	30	2.13	wd	0	0	0	0	0	0	0	0	0	0	0	0	0	22.07	0.47	0	0	0	14.55	0	0	0	0
1996	34	35	2.49	wd	0	4.02	4.42	2.01	4.42	2.41	0	0.40	0	0	0	0	0	2.01	17.27	0	0	0	0	8.84	0.8	0	0
1996	35	40	2.84	ac	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.76	1.41	0	0	33.80	0.70	0	0	0
1996	37	50	3.55	fc	0	0	0	0	0	0	0	0	0	0	0	0	0	12.11	2.25	12.96	1.97	0.85	0	19.15	0.28	0	0
1996	38	40	2.84	we	0	0	0	0	0	0	0	0	0	0	0	0	0	11.27	4.58	51.06	7.04	0	0	35.56	0.35	0.35	0
1996	41	50	3.55	fc	0	0	0	0	0	0	0	0	0	0	0	0	0	18.59	12.39	9.30	9.58	1.69	0	1.69	0.28	0	0.28
1996	43	25	1.78	ac	0	0	0	0.56	0	0	0.56	0	0	3.37	0.56	2.81	8.99	7.30	39.89	0	3.37	0	0	0	0.56	0	0
1996	44	30	2.13	we	0	0	0	0.47	0.47	0	0	0	0	0	0	5.63	0	15.02	25.82	0.94	0	0	0	0	0.94	0	0
1996	45	55	3.91	ac	0	0.26	0	0	0.26	0	0	0	0	0	0	0	0	6.14	11.76	19.44	0.51	0.26	1.53	12.02	0	7.16	1.02
1996	47	50	3.55	wd	0	0	0	0.56	0	0	0	0	0	0	0	0.85	0	7.61	0	0	0	0	1.41	0.28	0	0	0
1996	50	50	3.55	ac	0	0	0	0.28	0	0	0	0	0	0	0	0.56	0	23.94	9.86	2.25	5.07	1.69	0.28	3.94	1.97	0.28	0
Mean densities 1996					0 ^a	0.36	0.37	0.35	0.41	0.20	0.05 ^a	0.06	0.05	0.28	0.05	0.84 ^a	0.75	13.44 ^a	14.52 ^a	8.35 ^a	2.81	0.37	2.97	8.34	0.48	0.65	0.11

^a Significant difference within species between years (ANOVA, $P \leq 0.05$).

Q3

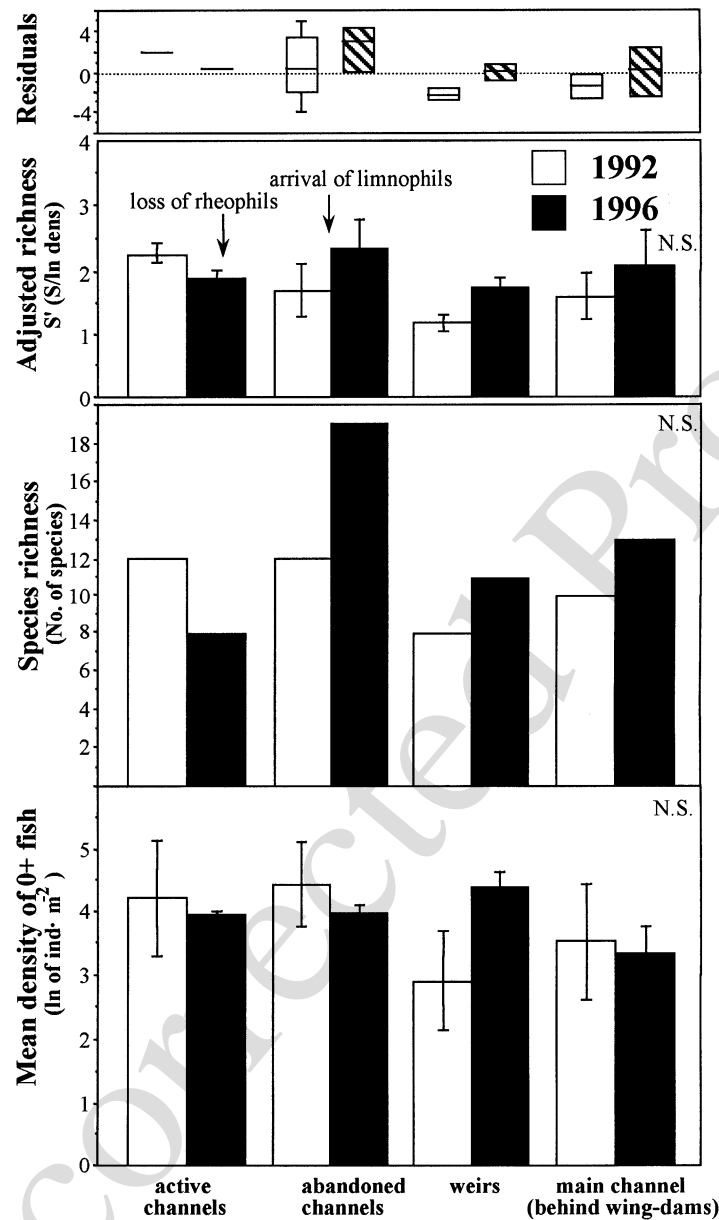


Figure 2. Mean relative densities (natural log (\ln) of ind m^{-2}), species richness (S), and adjusted species richness ($S \div \ln 0+$ fish density) of 0+ fishes in channel types of the Slovak Danube floodplain in August 1992 and August 1996. Also presented are the percentiles of residuals for each channel type from the regression of S against $\ln 0+$ fish densities for the 12 sites in 1992 and 1996

The two most important microhabitat variables (i.e. longest vectors; ter Braak and Verdonschot, 1995) were the proportions of macrophytes and gravel, though the latter was the main factor distinguishing habitat use by 0+ fishes in 1992 and 1996 (Figure 5). Indeed, most species of 0+ fish demonstrated a change in preference away from elevated proportions of gravel (Figure 5), probably reflecting the reduced availability of large, exposed alluvia in 1996 (Figure 4). In some species, such as pumpkinseed *Lepomis gibbosus* (L.) and roach, this shift in preference away from gravel was the only discernible difference in habitat use (i.e. relative positions in the CCA ordination (Figure 5) and electivities (Figure 6). In other species, such as silver bream and bleak, the shift also included the acquisition of a preference, albeit weak, for greater amounts of ligneous debris. Bleak, Eurasian perch

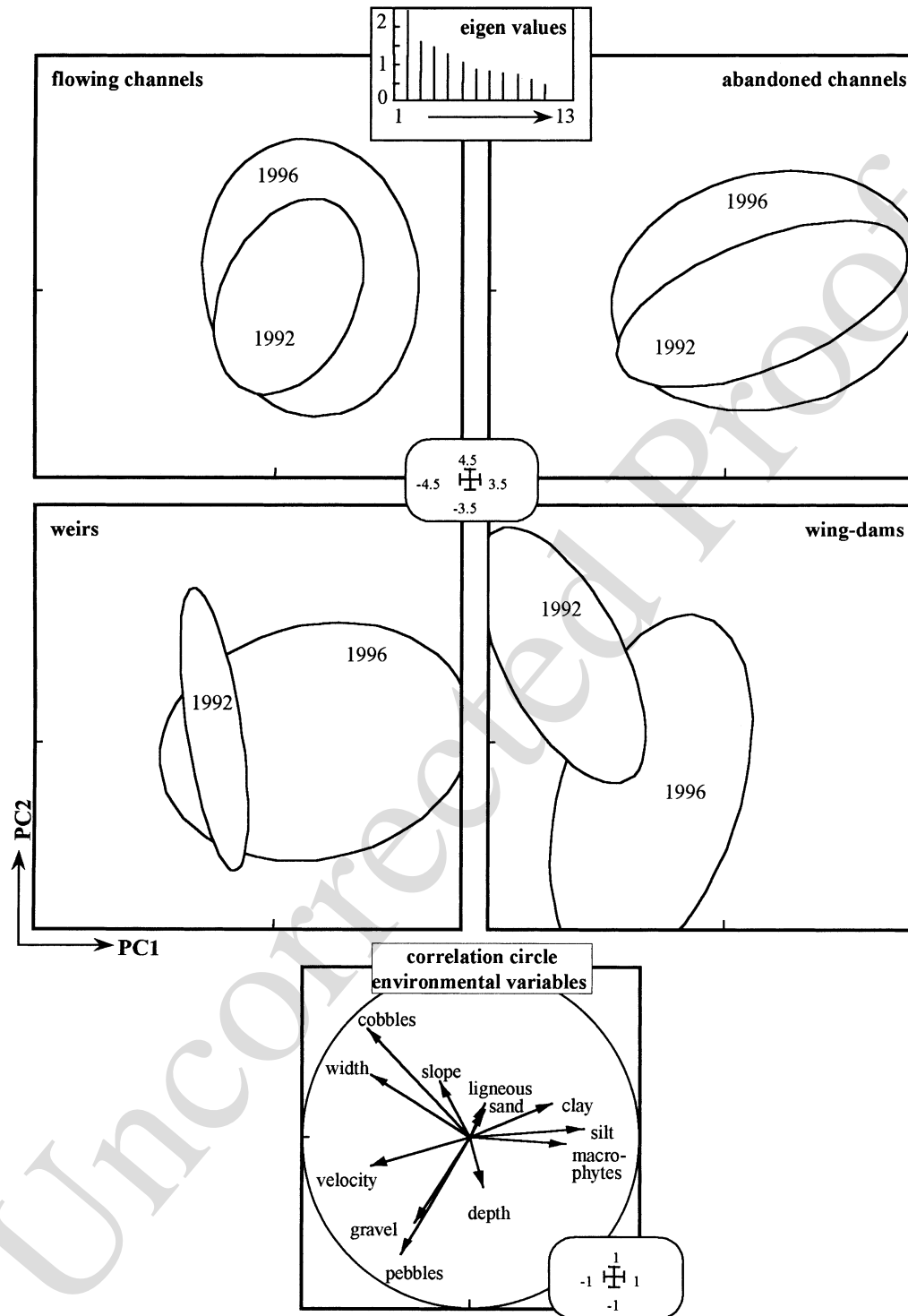


Figure 3. Principal components analysis of 12 environmental variables measured at point samples from 12 sites of the Slovak Danube flood-plain, with 90% ellipses for each channel type in August 1992 and August 1996, and the correlations for variables

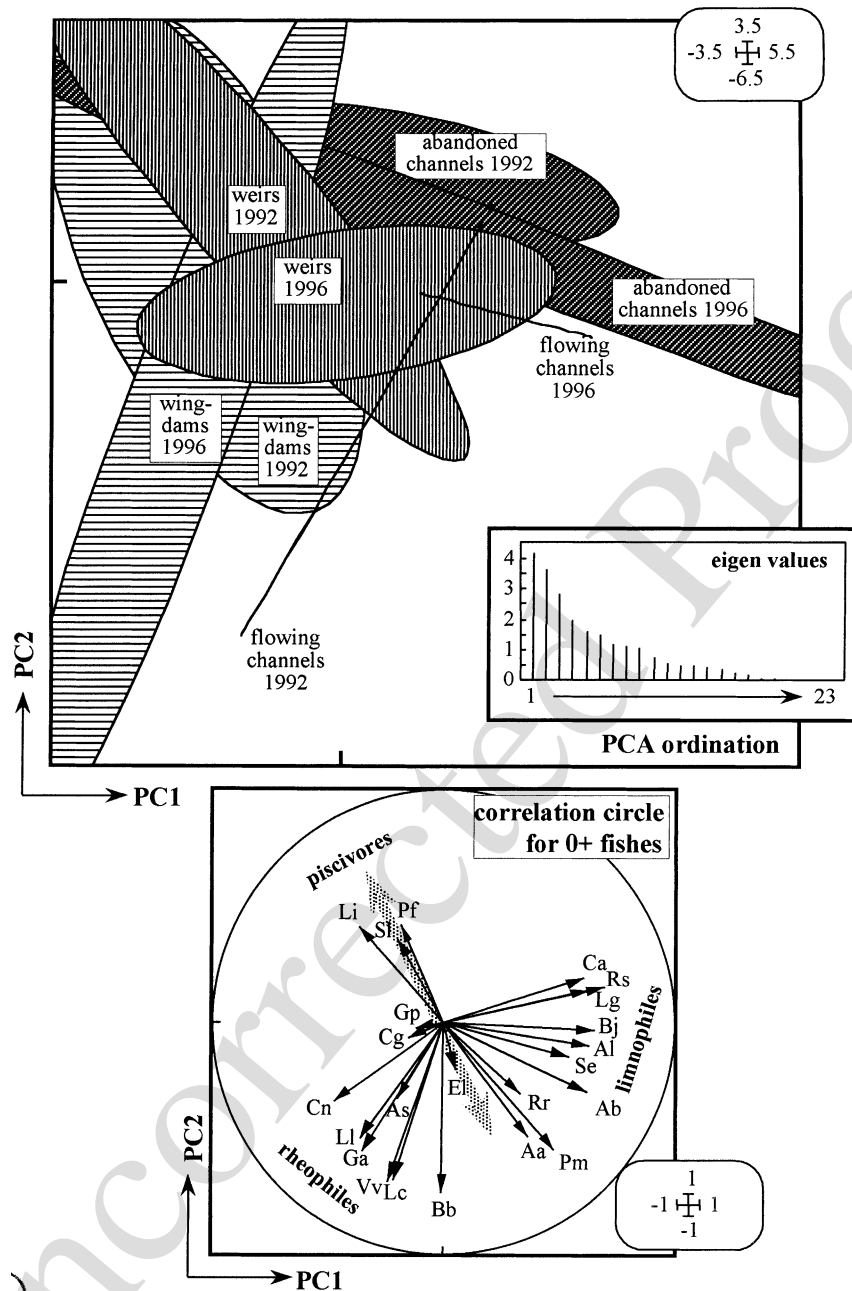


Figure 4. Principal components analysis of 0+ fish data (absence/presence) from 12 sites of the Slovak Danube floodplain, with 90% ellipses (straight lines connect two flowing channels for each year) for each channel type in August 1992 and August 1996, and the correlation vectors for species of 0+ fish

and bitterling also demonstrated weak preferences for macrophytes in 1996—again possibly reflecting the greater availability of elements characteristic of lentic environments. In 1996, 0+ tubenose goby demonstrated a greater preference for elevated water velocities, though this may merely reflect the greater frequency of occurrence of this species in 1996 (Table II) rather than a change in habitat preference *per se*. The greatest difference in microhabitat use between the two years was observed in 0+ Prussian carp (Figure 5), which shifted from a weak preference for clay in 1992 to a moderate preference for high proportions of macrophytes in 1996 (Figure 6).

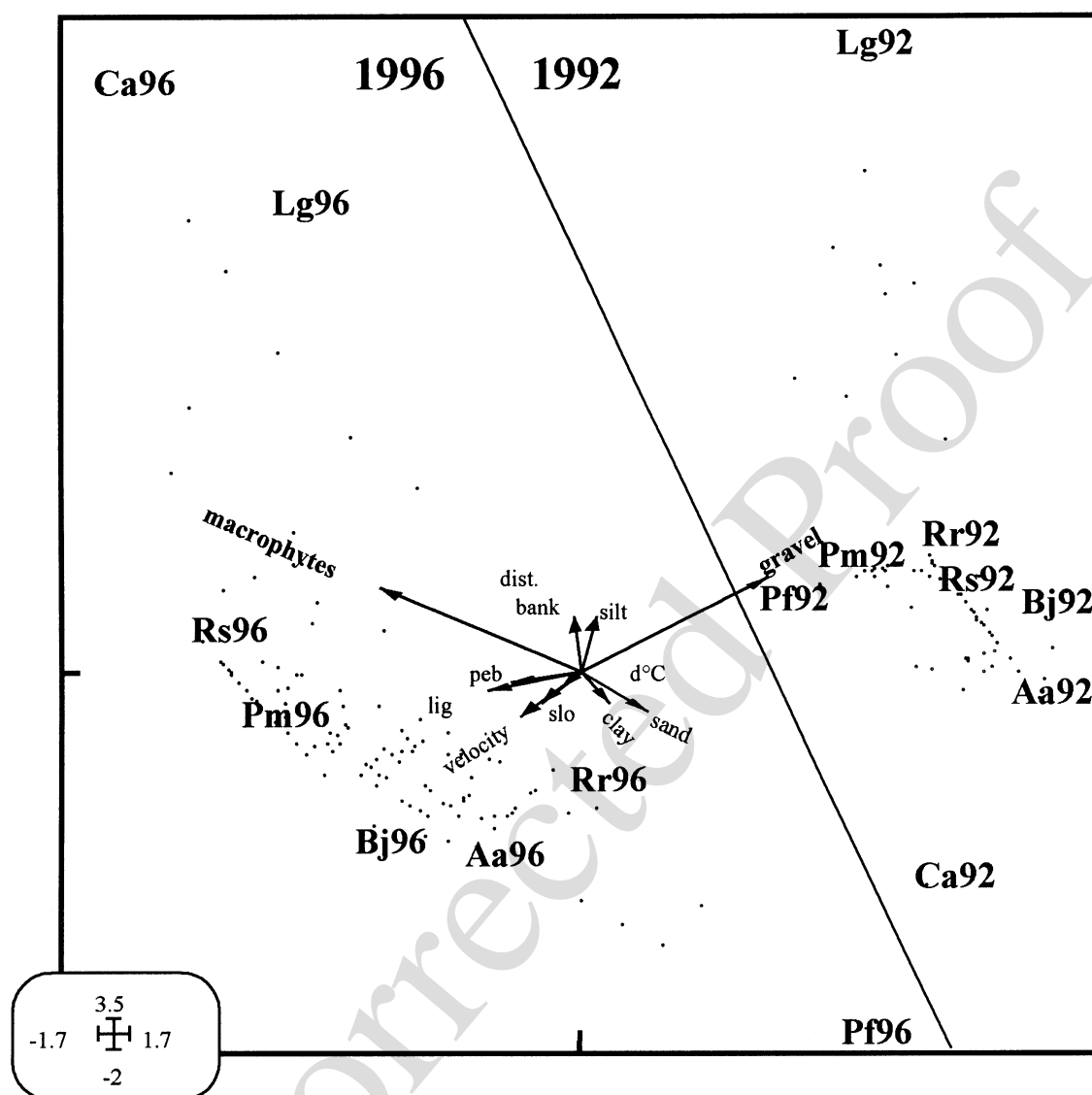


Figure 5. Canonical correspondence analysis of data (\log_2 transformed) for the most frequently encountered species of 0+ fish at point samples from 12 sites in the Slovak Danube floodplain (August 1992 and August 1996). Species codes: Aa = bleak, Bj = silver bream, Ca = Prussian carp, Lg = pumpkinseed, Pf = Eurasian perch, Pm = tubenose goby, Rr = roach, Rs = bitterling. Variables: dist. bank = distance from bank, slo = bank slope, lig = ligneous debris, peb = pebbles

The relationship between the species richness (S) and the \ln -density of 0+ fishes in 1992 was significant ($S = 2.252 \ln[\text{density}] - 1.712$; $r^2 = 0.483$, $F = 46.727$, $df = 50$, $P = 0.0001$), as were the relationships between S and the number of samples ($S = 0.17 \ln[\text{density}] + 3.424$; $r^2 = 0.22$, $F = 14.136$, $df = 50$, $P = 0.0004$), and \ln -density and the frequency of samples containing 0+ fish ($\ln[\text{density}] = 5.362[\text{frequency of samples with 0+ fish}] + 2.424$; $r^2 = 0.483$, $F = 46.727$, $df = 50$, $P = 0.0001$). Thus, the 0+ fish species richness in August 1996 could be predicted from the overall density of 0+ fishes in that August, and overall 0+ fish density in August 1996 could be predicted from the frequency of samples containing 0+ fishes in that August. However, the fit of expected and predicted values was better for species richness than for 0+ fish density (Figure 7).

Predictions using models developed by channel type fit less well than those from all data combined (Figure 2), and thus are not presented. Predictions of abundance of individual species in 1996 from the environmental data

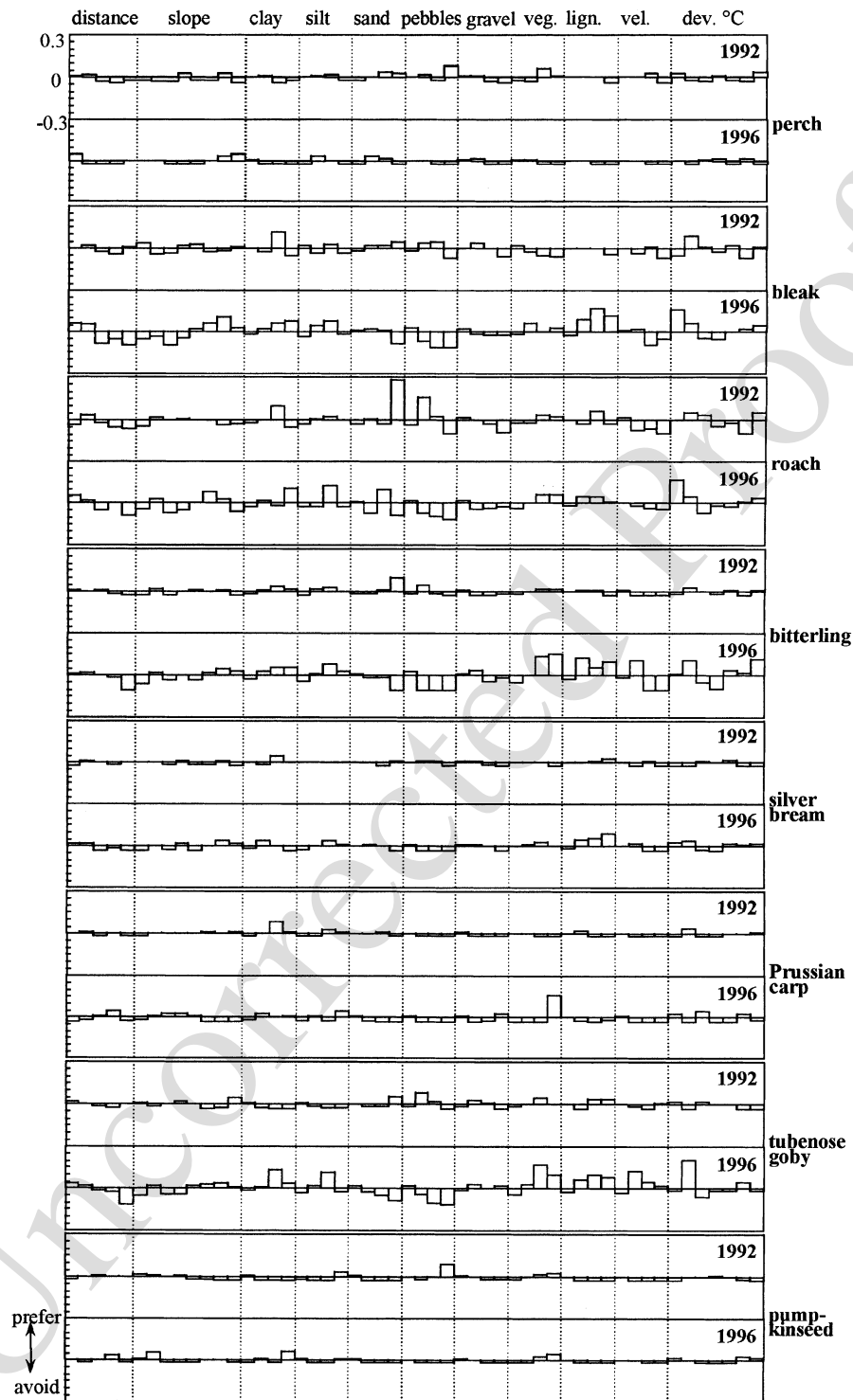


Figure 6. Microhabitat electivities for the species of 0+ fish at point samples from 12 sites in the Slovak floodplain of the River Danube, 1992 and 1996. The electivities consist of the difference between the frequency of a species in the group of samples having that category of environmental variable and the frequency of that species in all the samples. Values approaching $[0.5]$ indicate preference (+) or avoidance (-). Abbreviations: distance = distance from bank, veg. = macrophytes, lign. = igneous debris, vel. = water velocity, dev. °C = sample deviation from mean water temperature for that site. See study area, material and methods section for categories

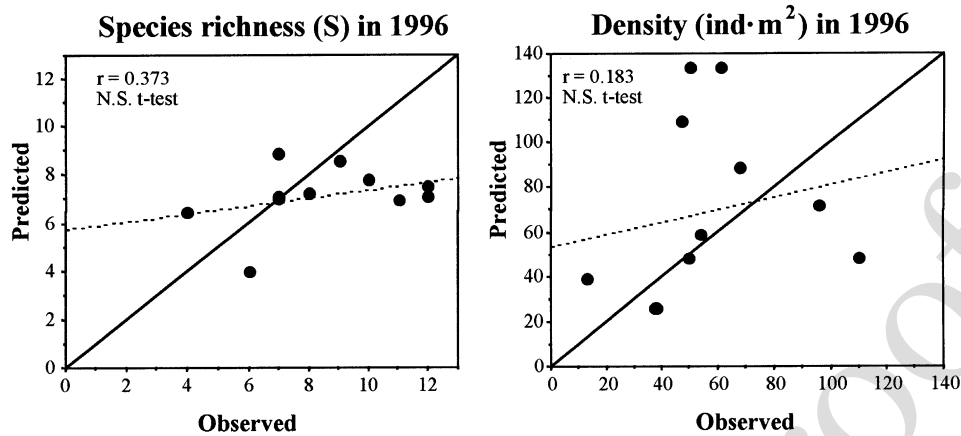


Figure 7. Predicted (from 1992 data; Copp *et al.*, 1994) and observed species richness and relative densities ($\text{ind} \cdot \text{m}^2$) of 0+ fishes in the Slovak Danube floodplain in 1996. Species richness in 1996 was predicted from species number in 1992 regressed against \ln -densities in 1992. Density in 1996 was predicted from \ln -densities in 1992 regressed against the frequency of samples in 1992 containing 0+ fishes. Solid lines represent $x = y$; dashed lines are the best-fit linear model, with correlation coefficients indicated. Observed and expected values did not differ significantly (paired Student's *t*-test)

Table III. Generalized additive logistic regression models for 0+ fish data (presence/absence) from the Slovak Danube floodplain in 1992. The asterisks indicate the environmental variables (predictors) retained in the model. *P* is the probability for comparisons between (1992 model-based) predicted and (1996 data-based) fitted values for fish occurrence (Wilcoxon rank sum test). No model could be fitted to pike-perch because of low sample sizes. Fish codes are as given in Table I

Species	Distance	Depth	Substratum	Macrophytes	Ligneous	Velocity	Temperature	<i>P</i>
All	*	*	*	*		*		0.16 NS
Bb		*	*		*	*		<0.001
Cn			*					<0.001
As	*							<0.001
Ll			*	*		*	*	<0.001
Lc	*	*	*					<0.001
Gp		*						<0.001
Vv		*						<0.001
Al	*	*						<0.001
Li					*			<0.001
Pf	*	*	*			*	*	<0.001
Gc	*							<0.001
Aa	*					*	*	0.46 NS
Rr	*						*	<0.001
Rs	*							<0.001
Bj			*	*	*		*	<0.001
Ab	*							<0.001
Ca	*		*					<0.001
Pm	*			*			*	<0.001
El		*	*		*		*	<0.001
Lg				*				<0.001
Se			*					<0.001

were not possible as the multiple regression models were not statistically significant. However, fitting of generalized additive logistic regressions to the 1992 species-specific data sets resulted in a mosaic of models in which, depending on the species, the probability of fish occurrence in that year was described by a number of environmental variables (predictors), ranging from one to five (Table III). Except for bleak, species-specific values of presence/absence predicted for 1996 from the 1992 data set and the values actually observed in 1996 were always

Table IV. Analysis of deviance for a generalized additive logistic regression model fitted to 0+ fish data (fish presence/absence; all species included) from the Slovak Danube floodplain in 1992 (cf. Table III). s(Predictor, 3) indicates a smooth function (spline with three degrees of freedom) of the predictor. In bold type are significant ($\chi^2 = 0.10$) χ^2 -based approximate (non-parametric) partial tests (Npar), highlighting the environmental variables retained in the final model

Term	df	Npar df	Npar χ^2	P
Intercept	1			
s(Distance, 3)	1	2.0	35.41	<0.001
s(Depth, 3)	1	1.9	15.64	<0.001
s(Substratum, 3)	1	2.0	5.75	0.056
s(Macrophyte, 3)	1	2.0	4.59	0.099
s(Ligneous, 3)	1	2.0	2.28	0.317
s(Velocity, 3)	1	2.0	6.80	0.032
s(Temperature, 3)	1	2.0	3.91	0.139

significantly different, indicating that the 1992 data-based predictions could not be used to model species-specific occurrences in 1996. However, the overall model (all species combined) for 1992 (including distance, depth, substratum, macrophytes and velocity) did successfully predict overall fish occurrence in 1996 (Table IV), and was of the form: Fish = Intercept + s(Distance, 3) + s(Depth, 3) + s(Substratum, 3) + s(Macrophyte, 3) + s(Velocity, 3). In this model, depth and distance were the two most influential predictors, indicating that: (1) the majority of fish would be found in shallow areas, generally close to the bank, their occurrence decreasing sharply along the first 20 m of distance and progressively increasing (Figure 8, top row); (2) that, to some extent (owing to the marginal contribution of substratum and macrophytes in the model), fish would be confined to finer substrata and areas with high macrophyte cover (Figure 8, middle row); and (3) that a peak in fish occurrence would be present at relatively high velocities (Figure 8, bottom row).

DISCUSSION

The initial impact of the Gabčíkovo hydropower scheme on the floodplain's fisheries was already being felt as this paper was being prepared (see Balon and Holčík, 1999), realizing the negative effects predicted prior to the scheme's operation (Balon, 1957; Holčík *et al.*, 1981; Holčík, 1991). However, our results may seem equivocal as neither relative density nor species richness differed significantly for 0+ fish between 1992 and 1996. Local extinction (in reproductive terms) of rheophilous and limnophilous fishes since 1992 was matched by the arrival of other (mainly eurytopic and some limnophilous) species. However, the densities of several species of 0+ fishes did decrease between 1992 and 1996. Declines in density and size have also been observed in separate, long-term monitoring studies of older fishes in the same study area, though other factors have contributed to this, such as excessive angling and poaching with electrofishing equipment, various nets and explosives (Černý, 1999). Similarly, previously lotic habitat for rheophilous species also declined, with weirs and wing-dams becoming more silted and vegetated (Figure 3). This change in available habitat is reflected in the microhabitat use, with water velocity and transparency being the main defining variables in 1992 (Figures 5 and 6), whereas macrophytes and gravel were the main variables in 1996 (Copp *et al.*, 1994).

Weirs were the only channel type to experience increases in both 0+ fish density and species richness, which corroborates with the assumption that such mesohabitats are important refuges for 0+ fishes in late summer, particularly for rheophilous species, when river discharge is usually at its lowest (Copp *et al.*, 1994). The apparent decline in overall density at the majority of sites reflects the dramatic changes that occurred once hydroscheme operations began: (1) a change in hydrological regime from dynamic to regulated, in particular the virtual elimination of floods during favourable periods of year, i.e. spring or summer when floods used to be intrinsic for functioning of the floodplain ecosystem; (2) the loss of both longitudinal and lateral connectivity, with upstream migrations virtually impossible and movement through the inland delta restricted—the original network of

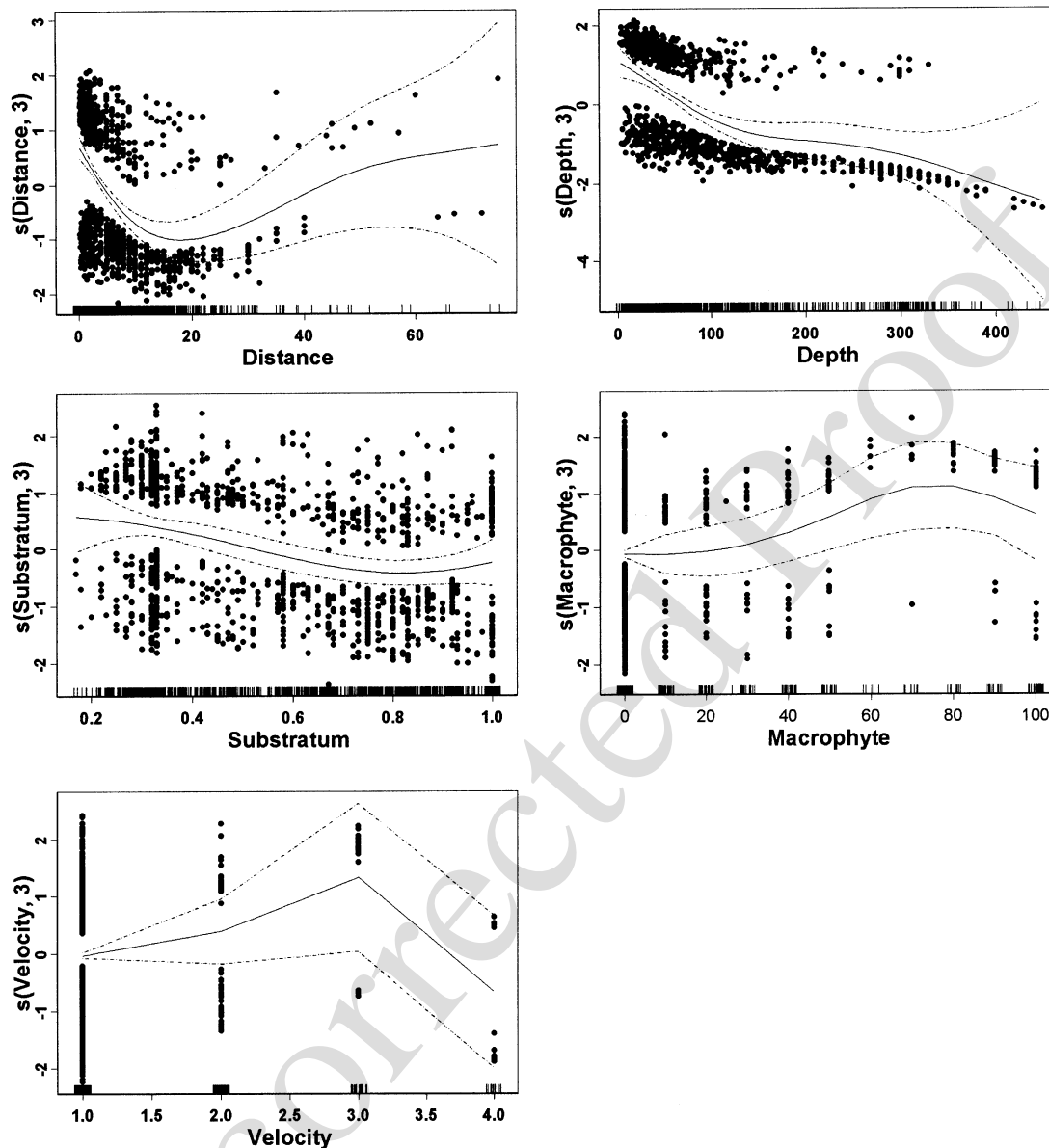


Figure 8. Partial fits for a generalized additive logistic regression model of 0+ fish presence/absence (entire, species-combined 1992 dataset) in the Slovak part of the River Danube, with the environmental variables distance from bank, depth, substratum, macrophytes and velocity as predictors. The resulting model is: Fish (presence/absence) = $s(\text{Distance}, 3) + s(\text{Depth}, 3) + s(\text{Substratum}, 3) + s(\text{Macrophyte}, 3) + s(\text{Velocity}, 3)$. The points plotted are partial residuals for fish occurrences versus the raw data for each environmental variable (predictor) retained in the model (cf. also Table IV). Smooth functions (cubic splines with three degrees of freedom) of the predictors (notation as in Table IV) are plotted on a common y-axis scale along with point-wise standard errors and the corresponding rug-plot (raw data points) on the x-axis. In each plot, changes in probability of fish occurrence are indicated by the shape of the smoothing

side-arms became a series of isolated subnetworks with the fish metapopulation units virtually isolated from one another; and (3) a reduction in both number and availability of spawning grounds and nursery areas.

Some of the channels on the Slovak side of the floodplain, which were studied in 1992 (Copp *et al.*, 1994) but no longer existed in 1996, disappeared as the result of engineering work, but most were lost due to the change in hydrological regime. The increase in surface area sampled is partially reflective of increases in water level at some sites due to new weirs, which were constructed to retain water and compensate for the reduced discharge through

1 the floodplain that results from water diversion to the hydroelectric turbines. Of the species which are currently
2 objects of conservation attention (Schiemer and Waidbacher, 1992; Schiemer, 1999), spined loach, weather loach
3 and bullhead were absent in 1996. This may simply be because all the locations where these species had been
4 found in 1992 no longer existed in 1996. However, this is not to say that spined loach, weather loach and bullhead
5 disappeared from the inundation area: bullhead occurred only as 0+ juvenile in 1992 and weather loach is not
6 likely to be captured as 0+ juvenile by point sampling (Copp, 1989b). Moreover, all these species occur regularly
7 in our samples taken from other locations (Černý, 1999). On the other hand, conditions became more favourable to
8 limnophilous species after the start of the Gabčíkovo hydroscheme operations, as most of the previously lotic side-
9 arms (eupotamal and/or parapotamal types, *sensu* Amoros *et al.* (1987)) became lentic (palaeopotamal type).
10 Therefore, rheophilous species may have moved to other suitable habitats rather than disappeared. The absence
11 of bullhead is also due to predation and competition with *Neogobius* species invading from the lower Danube
12 (Kautman, 2001).

13 The appearance of burbot, dace and three-spined stickleback in 1996 reflects the habitat changes between 1992
14 and 1996, though burbot were rare in any case. The potential habitat of burbot, which prefers deep pools and cob-
15 bles, may have expanded as a result of the construction of weirs in the side-arm system. The dace, a rare species in
16 Slovakia (Kováč, 1994), might have been absent in the 1992 samples due to greater dispersal compared to 1996,
17 when most of its population was assumed to concentrate just below the new weirs. The three-spined stickleback, on
18 the other hand, is known to exploit, albeit sporadically, new and/or temporary floodplain ecosystems of some large
19 European rivers (Copp, 1989b, 1992), and it has become a common species in the old main channel of the Danube
20 (Černý, 1999). Kessler's goby is one of a few recent migrants up from the Danube's delta (Zweimüller *et al.*, 1996;
21 Kautman, 2001); this upstream range expansion probably results from the gradual increase in mean summer water
22 temperatures caused by the numerous impoundments on the river in Germany and Austria (Kautman, 2001). The
23 occurrence of ruffe in 1996, despite its absence in 1992, is not remarkable, as ruffe are rarely captured by random
24 point sampling in rivers even when known to be present via other sampling methods (R.H.K. Mann, personal com-
25 munication). Rudd is a typically limnophilous species and was previously neither rare nor abundant in the Slovak
26 Danube. The absence in 1992 and presence in 1996 of 0+ rudd suggests an increase in reproduction, reflecting the
27 changes in available habitat, i.e. reduction of lotic and increasing dominance of lentic environments.

28 The ability to predict 1996 overall fish occurrences from the 1992 GAM of fish-habitat relationships contrasts
29 with the inability of species-based GAMs to allow reliable predictions. The overall GAM is both a descriptive and
30 predictive tool, providing a reliable approximation of fish occurrences at the floodplain scale. The occurrence of
31 0+ fish decreases progressively with increasing distance from the bank, a pattern also observed with 0+ perch in
32 lakes (Masson *et al.*, 2001). Substratum type and macrophyte cover are important predictors of 0+ fish presence in
33 our model, corroborating the two main variables in the CCA (Figure 5) as well as patterns reported elsewhere
34 (Grenouillet *et al.*, 2000, 2001). Nevertheless, the lack of species specificity renders the model of limited value.
35 The mosaic of responses resulting from fitting similar models to individual species highlights the multitude of
36 spatio-temporal parameters affecting fish habitat use. These results corroborate the concerns raised by Mathur
37 *et al.* (1985) and by experimental work on microhabitat use by 0+ juvenile barbel (L. Vilizzi and G.H. Copp,
38 unpublished), that fish-habitat assessments based on single samples are representative for that moment in time
39 only, and that composites of habitat electivities, such as the typological studies presented here, can provide an
40 approximation for a study area, but at the expense of between-site variation. Theoretically, the inability of all
41 species-based models to predict 1996 occurrences from the 1992 data set may result from the inadequacy (lack
42 of accuracy?) of the environmental variables used to evaluate habitat use. However, very similar (if not identical)
43 variables have been used successfully elsewhere with both multiple regression and neural network models (e.g.
44 Gozlan *et al.*, 1999). Thus, the lack of predictive ability of the models discussed probably results from
45 variations/changes in microhabitat use within species in response to the drastic change in ecosystem structure,
46 function and assemblage composition.

47 In conclusion, although the species richness and overall densities of 0+ fishes did not change markedly in the
48 first four years after the start of operations at Gabčíkovo, the densities of some species decreased significantly and
49 the overall composition of the 0+ fish assemblage changed dramatically, mainly in a shift to eurytopic or limno-
50 philous species. These changes probably reflect comprehensive alterations in channel character, which may have
51 been at least partially responsible for the observed differences in habitat use by 0+ fishes in 1996 relative to 1992.
52

This variation in late-summer habitat use between years is corroborated by the inability of species-based models to predict 1996 occurrences from the 1992 data set. Moreover, only 12 of 27 sites sampled in August 1992 were extant in August 1996. The monitoring of the fish and other biotic components in this floodplain (Černý, 1995; Mucha, 1995, 1999) still continues, which will provide us the opportunity to assess and understand better the long-term impact of the Gabčíkovo hydroscheme.

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