Environmental Biology of Fishes **40**: 329–348, 1994.

Hierarchical analysis of habitat use by 0+ juvenile fish in Hungarian/Slovak flood plain of the Danube River

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Received 29.4.1993 Accepted 12.1.1994

Key words: Microhabitat, Typology, Gabčíkovo hydroscheme, Backwaters, Point abundance sampling, Canonical correspondence analysis, Principal components analysis, Anabranches

Synopsis

To address the lack of information on the distribution and habitat use of 0+ juvenile fishes in the Hungarian/Slovak flood plain of the middle Danube River, we undertook the first cross-border ichthyological investigation, examining three levels of ecological perception (hydrosystem, macrohabitat, microhabitat) during August 1992 using 'Point Abundance Sampling' by electrofishing. Being that the Gabčíkovo hydroscheme was about to begin diverting most of the river's discharge away from the flood plain during the winter of 1992, the present investigation represented the last chance to record the distribution and microhabitat use of 0+ fishes within the flood plain. At each sampling point, numerous environmental variables were measured quantitatively, or as percentages. At the hydrosystem level, 25 species of 0+ fishes were captured in the 1170 point samples collected from 52 sites (27 in Hungary, 25 in Slovakia), ranging from 10 to over 200 mm standard length (i.e. pike *Esox lucius*). No significant differences were found between the Hungarian and Slovak specimens with respect to standard length (ANOVA, $p > 0.31$), nor in the relative densities (ind.m^{-2}) of 0+ fish (Student's t-test: df 24, $t = 0.601$, $p = 0.553$). A typology of macrohabitats using principal components analysis of the sites X species data matrix in absence/presence revealed three groupings of sites: (1) lotic channels, weirs and wing-dams; (2) partially-abandoned channels; (3) abandoned channels; the results corroborated our assumption that weirs of the anabranch systems represent a quasi-lotic refuge for rheophilous 0+ fishes of the flood plain during late summer. At the microhabitat level, an empirical model of microhabitat use was generated using canonical correspondence analysis and association analysis (based on chi-square probabilities). Water velocity was the most influential variable, with the 0+ juveniles ordinated along the first canonical axis according to their increasing rheophily. The second most influential microhabitat variable was water transparency, followed by the percentage abundance of macrophytes and substrate composition.

Introduction

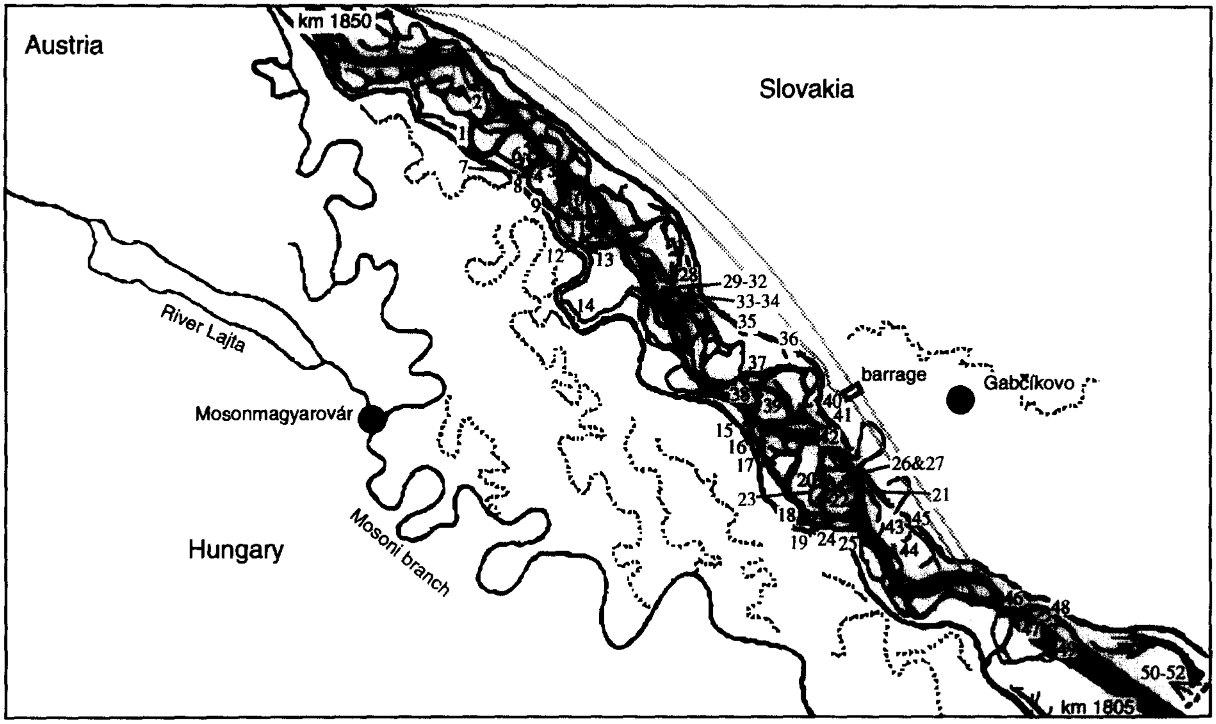
The importance of habitat heterogeneity and hydrological regime to fish production in flood plain rivers was first described in Antipa (1928), who put forward the postulate that fish production in the River Danube was positively related to the extent and intensity of flooding. Subsequent field studies further elaborated this relationship (e.g. Balon 1962a, b, 1963, 1964a, b, 1966a, 1967a, Holčík & Bastl 1976, 1977). Elsewhere, the study of ecological succession in flood plain ecosystems (Botnariuc 1967, Amoros et al. 1987) led to a greater understanding of the relationship between the successional status of flood plain ecosystems and their function as fish spawning and nursery grounds (i.e. Copp 1989b). Contrary to the linear perspective with which river systems have been often viewed in the past (Vannote et al. 1980), natural river flood plains represent an ensemble of numerous ecosystems that co-exist simultaneously at similar and different levels of ecological succession (Amoros et al. 1987). The disjunct nature of flood plains is thus reflected in the reproduction of fishes, with patches of similar spawning and nursery habitat within the flood plain representing a series of spatial-disjunct reproductive zones (Copp 1989b).

The middle section of the River Danube presents a number of flood plain hydrosystems (sensu Amoros et al. 1987) renowned for their species richness and fish productivity, despite having undergone extensive channel regulation during the end of the last century. Of these, the greatest controversy surrounds the flood plain between Bratislava (Slovakia) and Komárom (Hungary), which has undergone drastic alteration during the last 15 years as a result of deepening of the river bed. This deepening is due principally to the effects of gravel extraction in the main channel and the retention of alluvia by upstream hydroelectric scheme; construction of the Gabčíkovo hydroelectric scheme has exacerbated the situation (Boucher 1990). With the start of operations at the Gabčíkovo power scheme threatening the region's environment (Balon 1967b, Holčik et al. 1981, Tóth 1983, Bethemont & Bravard 1986, Holčík 1991, Bastl 1991, Vranovsky 1991), the general aim of the present investigation was to provide the first cross-border study of young-of-the-year fish in this international flood plain prior to operation of the Gabčíkovo hydropower scheme.

Until recently, ichthyological investigations in the Hungarian/Slovak flood plain have been undertaken mostly in Slovakia (e.g. Balon 1963, 1966a, b, 1967b, Bastl et al. 1969, Chitravadivelu 1974, Holčík & Bastl 1976, 1977, Černý 1992). Although Tóth (e.g. 1960, 1975, 1979) examined some aspects of population biology from specimens captured via commercial fisheries, Guti (1992, 1993) initiated the first field-based investigations on the Hungarian side. As the Gabčíkovo hydroscheme was about to begin diverting most of the river's discharge away from the flood plain into an above-ground retention canal during the winter of 1992, the present investigation represents the last chance to record the distribution and microhabitat use of young-of-the-year fishes within the flood plain. Young-of-the-year fishes (henceforth 0+) have proved a valuable descriptive tool for defining the ecological function of flood plain ecosystems (Copp 1989b), and an empirical model of their microhabitat use can provide essential information for any future attempts to conserve, enhance or restore the flood plain's fisheries. The specific aims of the present work were thus to undertake a hierarchical analysis, not unlike that described by Frissel et al. (1986), of 0+ fish distribution and microhabitat use in the Hungarian/Slovak flood plain hydrosystem, taking into account three levels of perception; flood plain, macrohabitat (biotope or stretch or river), and microhabitat (individual point samples).

Firstly, the overall distribution of fishes within the hydrosystem is examined in terms of relative densities (individuals·m^{-2}) and general population parameters. As the first joint study of the flood plain's 0+ fishes, the Hungarian and Slovak results are compared to determine if any significant differences exist between the relative density, frequency of occurrence, and size of the various species. Secondly, a typological investigation of 0+ fishes at the macrohabitat (or biotope) level will be undertaken to determine the function (see Copp 1989b) of the various flood plain sub-units (side-channels, partially-abandoned channels, abandoned channels) and structures (weirs, wing-dams) as nursery areas for 0+ fishes in this sector of the Middle Danube (Balon 1964a, c). As the Hungarian/Slovak flood plain undergoes an annual low-water period during late summer, with few if any channels in the anabranch systems offering lotic conditions, one of our specific aims was to reveal which macrohabitat components of the flood plain serve as lotic refuges for the young progeny of rheophilous fish.

Thirdly, an empirical model of microhabitat use (see Copp 1992b) is generated to provide a means of predicting the microhabitat use of 0+ fishes during the annual low-water period, when the amount of



1	Szigeti arm	14	Burjános	27	Szilfási channel	40	Baka weir
2	Véri channel	15	Gombócosi weir	28	Bodická brána	41	Baka arm
3	Vörösfüzesi weir	16	Újszigeti weir	29	Bodíky 1	42	Baka lower mouth
4	Csákányi upper mouth	17	Halrekesztő weir	30	Bodíky 2	43	Istragov
5	Csákányi backwater	18	Halrekesztő backwater	31	Bodíky 3	44	Istragov weir
6	Muki oxbow	19	Morva arm	32	Bodíky 4	45	Ispanský oxbow
7	man-made channel	20	Szürke weir	33	Bodíky 17	46	Palkovičovo 22
8	Siszler oxbow	21	Szürke arm	34	Bodíky 18	47	Palkovičovo 21
9	Csákányi arm	22	Pókmacskási weir	35	Královská lúka	48	Palkovičovo 19
10	Disznós	23	Pókmacskási oxbow	36	Baka oxbow 13	49	Palkovičovo 20
11	Kerekesciglés	24	Asványi arm	37	Baka channel 16	50	Klučovec 23
12	Fejőmadár	25	Béka-ér	38	Baka Orliak 14	51	Klučovec 24
13	Kőhíd weir	26	Szilfási channel	39	Baka 15	52	Klučovec 25

Fig. 1. Map of the Hungarian/Slovak flood plain, middle Danube River between Bratislava and Komárom, with a list of site names and code (see Table 2). Redrawn after Bethemont & Bravard (1986).

protective cover and suitable habitat can be drastically reduced due to the receding water level (Copp 1991). In the same way that the extensive study undertaken by Balon et al. (1986) endeavoured to document the fishes of the upper Danube prior to the Rhein-Danube canal, the present investigation not only fills a gap in our knowledge of habitat use by 0+ fishes in the Middle Danube, but also will serve as a data base against which the impact of the Gabčíkovo scheme can be evaluated in the future.

Study area and sites

The hydrology and geomorphology of the Hungarian/Slovak flood plain (Fig. 1) have been reported in detail elsewhere (Holčík & Bastl 1976, Holčík et al. 1981, Bethemont & Bravard 1986, Boucher 1990). Briefly, in the average year the Danube at Bratislava carries a median discharge of 1810 $m^3 \cdot s^{-1}$, and an average discharge of 2035 $m^3 \cdot s^{-1}$, with a mean daily flow of 3300 exceeding this latter value 10% of an average year (OVIBER[1]). The lowest recorded daily flow is 570 $m^3 \cdot s^{-1}$, with a mean daily flow of 882 $m^3 \cdot s^{-1}$ exceeding this value for 95% of an average year. With respect to flooding, a mean daily flow of 8750 $m^3 \cdot s^{-1}$ exceeds the average discharge 5% of the average year. The estimated 100-year return flow is 10 600 $m^3 \cdot s^{-1}$ and the estimated 1000-year return flow is 13 000 $m^3 \cdot s^{-1}$. The maximum peak discharge on record is 10 400 (OVIBER[1]). In 1992, spring inundations of the Hungarian-Slovak flood plain continued well into May, followed by a progressive decline in discharge during subsequent months. During the study period, the Danube had an extremely low discharge (mean monthly discharge at Bratislava in August: 1280 $m^3 \cdot s^{-1}$), and the surface area of most channels was drastically reduced. As well, many of the abandoned channels suffered from extreme desiccation, containing little or no water.

The study sites (Fig. 1) consisted of the five types of macrohabitat mentioned above. In lotic side-channels, generally too large in surface area to permit study of the complete biotope, a 'representative' stretch was selected for study; this consisted of a concave/convex stretch, with the shallow aggrading bank faced opposite a deeper eroding bank. Partially-abandoned side-channels, i.e. isolated from upstream channels by an alluvial plug, were sub-sampled in a similar manner, except where their total surface area was small enough to permit study of the entire biotope; these types of macrohabitat are generally lotic during periods of elevated discharge but become partially abandoned when river flows decrease. In general, abandoned channels were sampled in their entirety, though in some cases their surface area was too great and a representative stretch was selected as above; these locations were mostly former channels isolated from other channels of the flood plain except during elevated discharge, when they may be reconnected to other channels at either or both of their extremities (upstream and downstream).

The downstream vicinity of weirs was identified as a potential refuge for the progeny of rheophilous fishes, with the seepage through and between the boulder weirs providing localised flow. The investigation of weir sites generally consisted of sampling along the weir and downstream thereof for a distance of 50–100 m, depending upon the width of the channel. Sampling in the main channel of the Danube was both impossible and impractical with the equipment available, therefore the area downstream of wing-dams was studied as the probable refuge of any 0+ fish occurring in the main channel. Only wing-dams on the Slovak side were investigated.

[1] OVIBER. 1980. The Gabčíkovo-Nagymaros River Barrage System. Országos Vizügyi Beruházási Vállalat, Nat. Inv. Ent. Hydraulic Project, Budapest (from Boucher 1990).

Material and methods

In each of 52 sites (Fig. 1), fish and environmental variables were sampled at numerous small 'sampling points' (usually 30, but less for sites with less surface area) during the month of August 1992. Rather than attempting to estimate the 'absolute' density of juvenile fishes (e.g. Černý 1991), sampling was undertaken according the Point Abundance Sampling (Nelva et al. 1979, Copp & Peňáz 1988, Persat & Copp 1989, Copp 1992b), a stratified random strategy combined with electrofishing that provides estimates of 'relative density'. Sampling points were selected within each site via a point of the finger with eyes closed. We attempted to undertake an approximately equal sampling effort at each site (about 1 point per 100 m^2), except in channels of extremely large surface area, where this intensity of sampling effort was not always possible due to time and manpower constraints. Similar fractional sampling strategies have been used by others (e.g. Mann 1971, Heggenes 1988), though the underlying statistical requirement to reduce bias is that sampling is undertaken according to a predefined strategy (Persat & Copp 1989, Bain & Finn 1991).

Sampling was undertaken from a dingy, though some wing-dams sites were so shallow that sampling was undertaken on foot, using a portable electrofishing apparatus with an anode of 10 cm diameter to capture the fish; the approximate area of the anode's effective field at each point sample has been previously measured as ≈ 0.071 m^2, though this area will vary according to water conductivity (Copp 1989a). A crouched position in the dingy permitted a discreet approach to most sampling points, except those in shallow waters, where care was taken to approach the point quietly on foot. At each point, the anode was immersed (activated) to about 0.5 m depth in the water (less in shallower locations), followed immediately by a dip net immersed 0.5 m below the anode (less in shallower locations); both were then lifted directly out of the water, and fishes were sorted from any matter (vegetation, twigs, etc.) also scooped up by the net. After capture, the fishes were preserved in 4% formalin, or measured and returned to the water (i.e. fishes ≥ 1 +).

Microhabitat character was then evaluated using five quantitative and seven semi-quantitative environmental variables: distance from bank, slope of bank, percentage of clay (< 0.06 cm), % silt (< 0.06 cm), % sand (0.06–0.2 cm), % pebbles (0.2–2.0 cm) and % gravel (< 2.0 cm), water transparency, ligneous structures, macrophytes, water velocity and water temperature. Distance from bank and depth were measured with a graduated dip-net pole, except for distances > 3 cm, when visual estimates were made; bank slope was calculated from the depth divided by the distance from bank; depth was not retained in further analyses as it describes the depth of the channel and not the depth within the water column at which fish occurred at the moment of sampling. Bottom substrate (clay, silt, sand, pebbles, gravel) was evaluated as a percentage of the sample area (i.e. 0.071 m^2), with clay and silt distinguished by the greater between-particle adhesion in clay than silt. Water transparency was measured in cm using a small Secci-type disk (a 6 cm-diameter, weighted, white jar top attached to a centimetre-graduated nylon rope). Ligneous structures (branches, logs, trunks, roots) within the sample area were counted in a manner similar to that described by Kinsolving & Bain (1990) but on a scale of 1–10, with all values over 10 attributed a value of 10. Submerged, floating and emergent macrophytes were measured to the species level as a percentage of the area sampled at the point (i.e. 0.071 m^2). Water velocity was measured semi-quantitatively using a calibrated dip-net; no movement of the net indicated no flow, slow ballooning of net indicated weak flow (< 5 cmS^{-1}), and moderate to fast ballooning of the net indicated faster flow (> 5 cmS^{-1}).

Many of the environmental variables presented distributions skewed to the right; two of these (distance from bank, slope of bank) were directly natural-log transformed in an attempt to achieve normal distribution, then converted into qualitative categories for analysis (Ter Braak 1986). The various sizes of substrate and various macrophyte taxa often occur in very low frequencies (Copp 1992b), so these were converted to semi-qualitative categories (absence, 1–33%, 34–66%, 67–100%).

In the laboratory, the specimens were measured and counted. The preserved specimens have been deposited at the Danube Research Station, Hungarian Academy of Sciences. From the material collected, a data matrix of 1170 samples-by-25 fish species (0+) was created, and the mean number of fish per sample and the index of dispersion (variance divided by mean) were calculated for each species. From this data set, two other matrices were derived.

Firstly, in preparation for the typological analysis of macrohabitat function, all point samples from a site were summed and divided by the total surface area sampled, i.e. the total individuals captured divided by the number of samples, multiplied by the surface area of the anode's effective field (0.071 m^2, see Copp 1989a); this was undertaken to account for differences in the number of samples taken at sites of different surface area. The resulting matrix (52 × 25) contained the relative density of the 25 species of 0+ fish at each of the 52 sites; from this, the relative density of each species was calculated as totals for the Slovak and Hungarian sides, respectively, then compared using the student's t-test. Analysis of variance (ANOVA) was used to identify significant differences in the relative density of species between the five types of site.

In preparation for Principal Components Analysis, species occurring at only one study site (1 species) were eliminated; the resulting reduced matrix (52 × 24) was converted to absence/presence (see Copp 1989b) and then submitted to centred and normalised Principal Components Analysis, which reduces the influence of species variation (Dolédec & Chessel 1991) and best reveals patterns in data

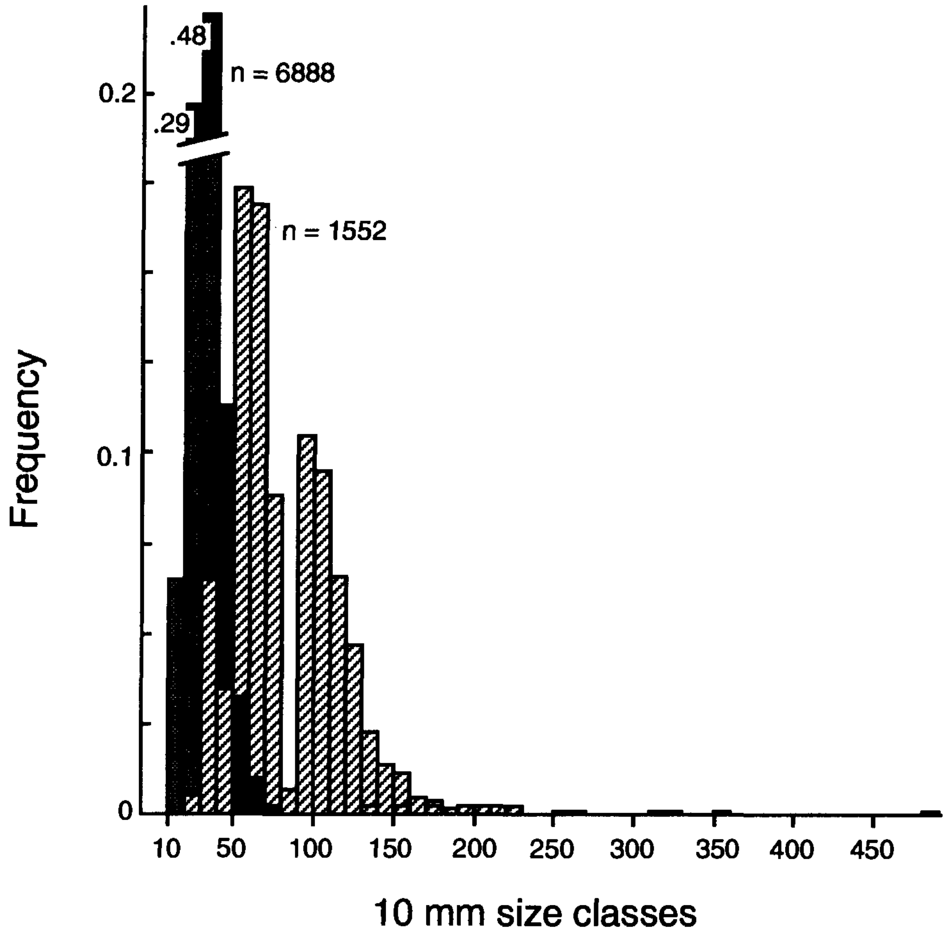


Fig. 2. Size-distribution in 2 mm size classes of 0 + and ≥ 1 + fish collected in the Hungarian/Slovak flood plain of the River Danube.

sets characterised by a short gradient and low species turnover (Gauch 1984). Chi-square analysis was then employed to reveal significant deviations from expected in the occurrence of species at the five site types.

Secondly, in preparation for direct gradient analysis of microhabitat use (Ter Braak 1986, Chessel et al. 1987), the original samples-by-species matrix (1170 x 25) was reduced to non-null samples only (567 samples-by-25 species), and rarer species (less than 3% occurrence) were reluctantly eliminated to produce the final reduced matrix (559 samples-by-16 species); this was then Log_2 transformed to reduce the over-emphasis of extremely large samples. The samples-by-environmental variables data matrix (1170 x 12) was correspondingly reduced to 559 samples-by-12 variables to contain only the environmental data (i.e. rows) corresponding to those samples (i.e. non-null) retained in the reduced samples-by-species matrix. Each variable of the reduced samples-by-variables matrix was then tested for normality (Lilliefors 1967). The two reduced data matrices were cross-tabulated (with the samples-by-species matrix converted to absence/presence) to determine the various frequencies of occurrence and species-variables associations (chi square), and to generate environmental profiles of microhabitat use for each species. The environmental profiles were calculated as the difference between the frequency of that species in the group of samples having that category of environmental variable and the frequency of that species in all samples. Because the association analysis was undertaken on the reduced matrix (i.e. void samples eliminated), calculations of the chi-square probabilities were conservative.

The two reduced matrices (559 x 12) were sub-

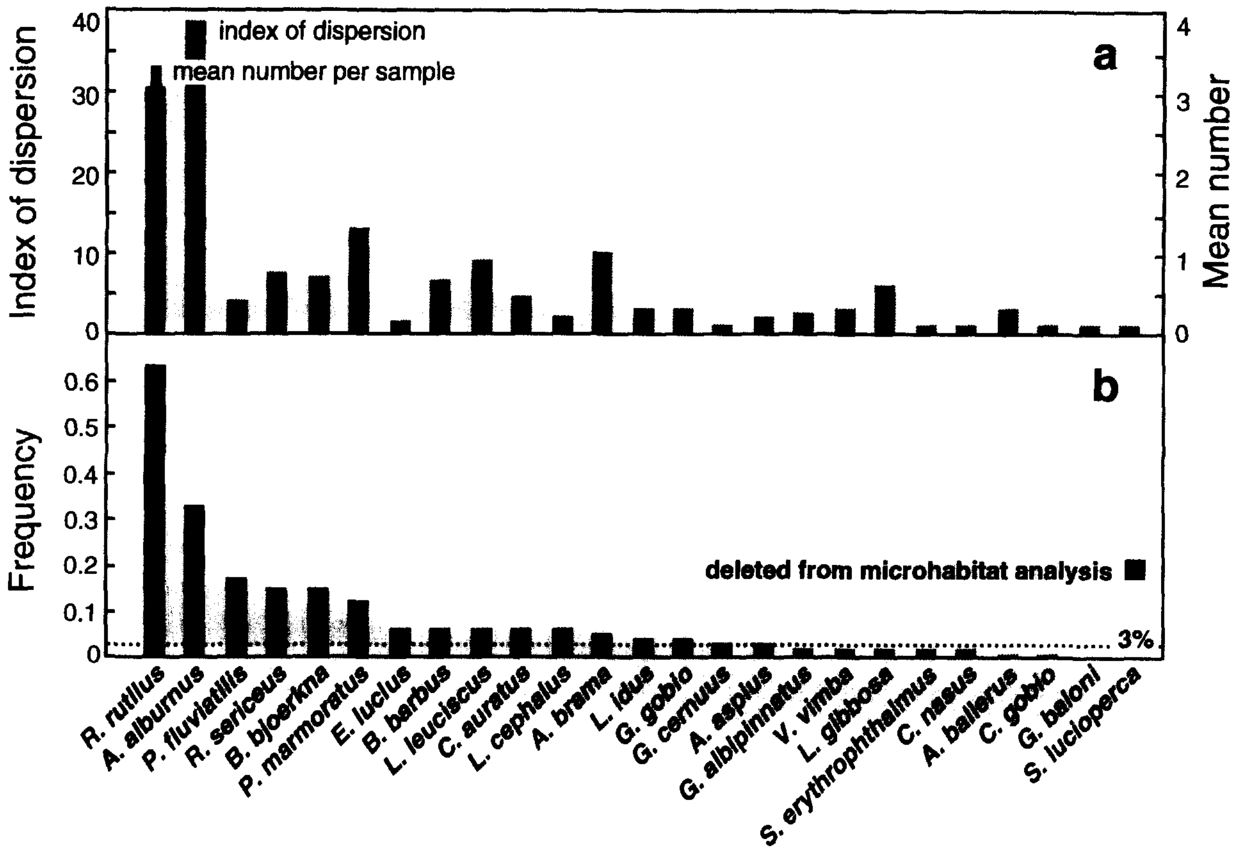


Fig. 3. a — Mean number of specimens collected per sampling point and the index of dispersion of each species in the 1170 point samples collected in the Hungarian/Slovak flood plain of the River Danube. b — Frequency of occurrence (scale: 0–1.0) of 0 + juvenile fishes in non-null samples, reduced matrix (567 × 25) in preparation for analysis. Elimination of species occurring in less than 3% of samples (shaded) produced the 559 samples × 16 species data matrix used in the Canonical Correspondence Analyses presented in Fig. 5.

sequently subjected to the Chessel et al. (1987) version of Canonical Correspondence Analysis, i.e. direct gradient analysis, using programmes by Chessel & Dolédec (1992). Direct gradient analysis was developed so that species or species assemblages could be related directly to a group of environmental variables (Ter Braak 1986). This approach identifies an environmental basis for assemblages ordination by revealing the patterns of variation in assemblage composition expressed by environmental variables. In the analysis, a biplot is generated, a diagram that illustrates the main pattern of variation in community composition as accounted for by the environmental variables, as well as the species distribution along each environmental variable.

The biplot presents the linear combinations of the variables from the unit variance table (from Principal Components Analysis of the environmental variables) that maximise the variance of the column means from the Correspondence Analysis table for species (Chessel et al. 1987). 'The measure of goodness of fit, 100 × (l1 + l2)/(sum of all eigen values), expresses the percentage variance of the weighted averages accounted for by the two-dimensional diagram... the length of an arrow representing an environmental variable is equal to the rate of change in the weighted average as inferred from the biplot, and is therefore a measure of how much the species distribution differ along that environmental variable' (Ter Braak 1986).

Some authors suggest the use of detrending in Corresponding Analysis (Hill & Gauch 1980, Peet et al. 1988) and Canonical Correspondence Analysis (Ter Braak 1986) to eliminate the 'Guttman' or 'arch effect'. However, evidence suggests that detrending is arbitrary in unigradient situations (Wartenburg et al. 1987) and can give a wide variety of results in multigradient situations, depending upon the number of segments into which the first axis is divided (Jackson & Somer 1991). We therefore opted for straight Canonical Correspondence Analysis. The analyses were undertaken using the ADE programme library (Chessel & Dolédec 1992), with additional graphics generated using GraphMu (Thioulouse 1989).

Results and discussion

In the Hungarian/Slovak flood plain (Fig. 1), a total of 6888 0 + fish and 1552 ≥ 1 + fish were collected during August 1992, ranging from 10 to over 450 mm in standard length (Fig. 2). Thirty species were encountered, though only 25 as 0 + juveniles (Fig. 3, Table 1); the 5 species occurring as ≥ 1 + only were *Gymnocephalus straetser, Lota lota, Cobitis taenia, Misgurnus fossilis,* and *Carassius carassius.* Some species of 0 + fish (Table 1) were not encountered in Slovakia (*Leuciscus leuciscus, Gobio gobio, Scardinius erythrophthalmus, Gymnocephalus baloni*), whereas others were not captured in Hungary (*Lepomis gibbosa, Cottus gobio, Stizostedion lucioperca*). Some species of 0 + fish expected to be encountered (e.g. *Tinca tinca, Cyprinius carpio*) were not observed during the study, though the former was found to occur in very low abundance at site 30 during a subsequent investigation (B. Rovný unpublished) as was the latter at sites 2, 5 and 8 (G. Guti unpublished).

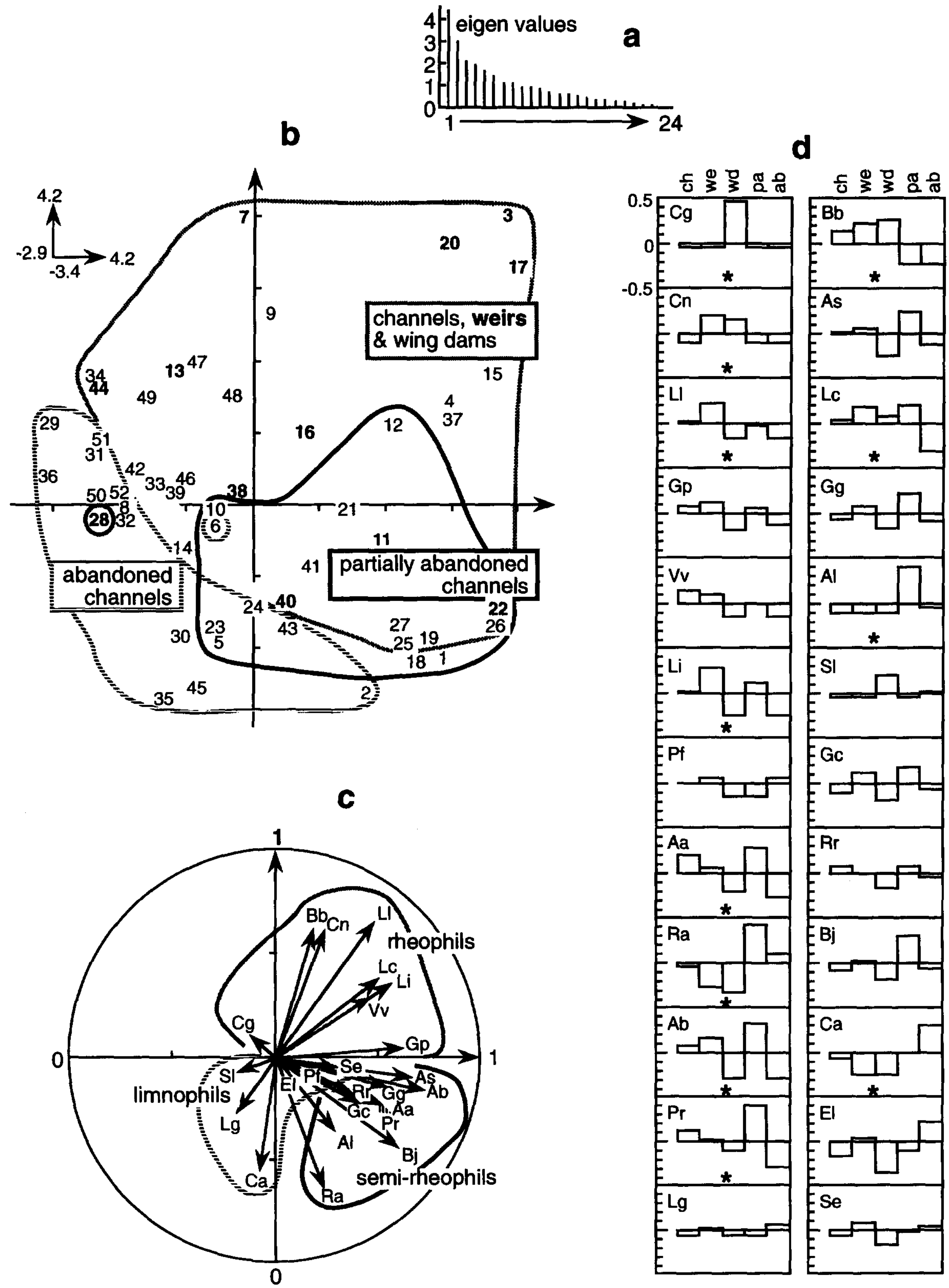
No significant differences (ANOVA) were found in standard length between the specimens captured in Hungary and those in Slovakia (Table 1). Simi-

Table 1. Number (n), mean (x SL), standard error (SE) and variance (s^2) for standard lengths of 0 + fishes captured in the Hungarian/Slovak flood plain. Analysis of variance (ANOVA) F and probability (Prob.) values between the Hungarian and Slovak groups are also given.

code	species	Hungary				Slovakia				ANOVA	
		n	x SL	SE	s^2	n	x SL	SE	s^2	F value	Prob
Rr	*Rutilus rutilus*	3253	32.9	0.08	19.9	634	31.2	0.26	43.9	0.765	1.000
Aa	*Alburnus alburnus*	414	30.6	0.41	69.7	801	23.5	0.30	71.5	0.569	1.000
Pf	*Perca fluviatilis*	146	51.7	0.70	72.4	81	52.3	1.35	146.6	0.749	0.900
Rs	*Rhodeus sericeus*	217	25.8	0.36	27.4	47	27.3	0.87	35.3	0.566	0.972
Bj	*Blicca bjoerkna*	215	28.3	0.34	24.8	61	29.9	0.56	19.4	0.866	0.711
Pr	*Proterorhinus marmoratus*	89	23.5	0.57	29.0	141	26.9	0.44	27.3	1.222	0.173
El	*Esox lucius*	29	188.0	7.55	1615.5	20	171.2	11.30	2555.5	0.744	0.738
Bb	*Barbus barbus*	44	43.1	0.89	34.8	77	45.5	1.14	99.7	1.157	0.316
Ll	*Leuciscus leuciscus*	127	45.6	0.49	30.0						
Ca	*Carassius auratus*	24	50.9	2.76	183.1	60	44.3	1.20	86.3	0.788	0.714
Lc	*Leuciscus cephalus*	40	36.3	1.40	79.2	6	39.4	1.12	7.5	0.695	0.647
Ab	*Abramis brama*	54	41.1	0.86	42.3	30	35.2	0.60	10.6	0.963	0.540
Li	*Leuciscus idus*	50	52.7	0.74	27.7	1	50.5				
Gg	*Gobio gobio*	43	37.6	0.59	14.7						
Gc	*Gymnocephalus cernuus*	17	41.1	2.00	67.5	1	54.5				
As	*Aspius aspius*	21	61.7	2.07	89.8	2	71.3	1.25	3.1	1.371	0.362
Gp	*Gobio albipinnatus*	11	37.2	1.96	42.3	15	35.7	1.51	34.2	0.995	0.499
Vv	*Vimba vimba*	19	28.3	0.44	3.7	10	44.1	0.96	9.1	0.039	1.000
Lg	*Lepomis gibbosa*					44	29.6	0.64	18.2		
Se	*Scardinius erythrophthalmus*	15	31.5	2.16	69.8						
Cn	*Chondrostoma nasus*	9	40.8	2.05	37.7	2	56.3	0.75	1.1	0.151	0.735
Al	*Abramis ballerus*	9	55.6	1.91	32.9	1	71.0				
Cg	*Cottus gobio*					4	38.1	2.73	29.7		
Gb	*Gymnocephalus baloni*	2	48.5	6.50	84.5						
Sl	*Stizostedion lucioperca*					2	134.5	32.50	2112.5		

Table 2. The total number of specimens and relative density (ind.m^{-2}) of 0 + fishes at various sites in the Hungarian and Slovak parts of the River Danube flood plain (pts = number of point samples at each site). The relative density of fish (all points from all sites combined) for the Hungarian (730 points) and Slovak (440 points) sides of the river did not differ significantly (paired t-test, df = 24, t value = 0.601, p = 0.5533). The species are listed left to right, from rheophilous to limnophilous, as derived from bibliographic sources (e.g. Holčík 1989). The type of site is indicated as flowing channel (fc), partially abandoned channel (pa), abandoned channel (ac), weir (we) and wingdam (wd).

site	pts	Cg	Bb	Cn	As	Gb	Ll	Lc	Gp	Gg	Vv	Al	Li	Sl	Pf	Gc	Aa	Rr	Ra	Bj	Ab	Ca	Pr	El	Lg	Se
Hungary		0	44	9	21	2	127	40	11	43	19	9	50	0	146	17	413	3254	217	215	54	24	89	29	0	15
1	20 pa				0.7				0.7				4.9		0.7	3.5	4.9	95.1	2.1	5.6	4.9	4.2	1.4			
2	10 ac				1.4					15.0						4.2	18.3	56.3	27.0	15.0		2.8	4.2	1.4		2.8
3	30 we		1.4	1.4			8.0	3.3	0.5		3.8		1.4		3.8		4.7	48.4		0.5	2.8		0.5			
4	30 fc						0.5	0.5	1.4		1.9		0.5				2.8	43.7	7.5	0.9			3.3			0.5
5	30 pa														0.5		43.7	7.0	1.9	0.9		0.5	0.9			
6	10 ac							1.4									5.6	111.0				1.4	1.4	1.4		1.4
7	20 we		2.8	1.4			9.2	3.5							0.7		9.9	6.3								
8	30 ac														3.3			0.9	14.0							
9	30 fc		3.3				1.4	1.4					0.5				8.9	5.6	0.5							
10	30 pa							0.5									1.4	22.1	2.8				8.5			
11	30 we								0.5		0.5					0.5	33.8	38.0	19.0		0.5		5.2			0.5
12	20 pa				3.5		3.5	6.3		1.4			2.8				17.6	33.8	4.2				0.7			
13	30 we		0.9					0.9									0.9	7.0								
14	30 fc																2.4	8.5	7.5				1.9	0.5		
15	25 we		1.1		1.7		20.0	0.6		1.1			2.8		19.0		1.1	80.0		0.6	0.6		2.3	1.1		
16	35 we		0.4			0.8		0.4					2.0		11.0	0.8		61.2	1.2				2.4	0.4		0.4
17	40 we		8.8	1.1	1.4		16.0	0.4	0.7	2.1			1.4		1.8		4.6	41.2		0.4			0.7	1.8		
18	30 pa							0.5		0.5		0.5				0.5	15.0	119.0	9.9	15.0	2.3		0.5	0.5		
19	20 pa				0.7			1.4		11.0		1.4					3.5	99.3	2.8	23.0	1.4		0.7			
20	30 we			0.5	0.5		3.8	0.5			0.9		8.0		4.7	0.9		137			1.4			6.1		0.9
21	30 fc				0.9				0.5				0.5		0.5		1.4	50.7	1.9		7					
22	30 we				0.5				0.5	0.5			0.5		0.9	0.5	6.1	117.0	0.9	14.0	1.9		0.5			
23	30 ac														1.4			39.4	1.9	14.0		3.3	6.6	0.9		1.4
24	20 ac							0.7							0.7	0.7	9.2	125.0	18.0	15.0		4.2				
25	30 fc				0.5			0.5		2.3					3.8		20.2	171.0	4.7	7.0	0.5	0.5	1.4			
26	30 pa							0.9	0.5		1.9	2.3			8.9	0.5	2.4	93.4	0.9	9.9	3.8		0.9	0.9		1.9
27	30 pa				0.5							0.5	0.5		8.5		5.2	130.0	0.5	2.8	0.5		2.3			
Slovakia		4	77	2	2	0	0	6	15	0	10	1	1	2	81	1	802	633	47	61	30	60	141	20	44	0
28	30 we																6.6	17.4							1.4	
29	5 ac																							2.8		
30	3 ac											4.7			33.0		23.5	136.0	4.7			4.7		9.4		
31	2 ac																	35.2						35.0		
32	10 ac														1.4			8.5	1.4					1.4		
33	15 wd	1.9													4.7		99.5	6.6		0.9						
34	15 wd			1.9										0.9	0.9			1.9								
35	40 ac													0.4	0.7		4.2	3.2	1.4	0.7		0.4	0.7		14.0	
36	25 ac																					12.0		2.3		
37	20 fc		0.7		0.7			0.7	9.9		2.8				3.5		14.1	50.0		20.0	20.0		48.0			
38	30 we							0.9									30.0	2.4		3.3			21.0			
39	30 fc														0.5		11.3	0.5					1.9			
40	20 we														4.2		13.4	47.9	1.4	11.0	0.7		2.1	1.4		
41	30 fc							0.5							0.5		15.5	7.5	0.5	0.5	0.5		1.4			
42	30 fc																24.9	0.5						0.9		
43	15 ac				0.9				0.9						2.8		336.0	180.0	22.0	5.6		32.0		2.8		
44	10 we												1.4		2.8											
45	30 ac														2.8		0.5	61.0	5.2	0.5		0.9	2.3		0.5	
46	15 fc		8.5												19.0	0.9		7.5				0.9	2.8			
47	15 wd	1.9	20.0					0.9									35.7	0.9					2.8			
48	15 fc		21.0								5.6				0.9		51.6	3.8					0.9			
49	15 wd		23.0					0.9											0.9				3.8			
50	5 ac														34.0			93.0	5.6							
51	5 ac														5.6			19.7								
52	10 ac														8.5			1.4	1.4							
relative densities																										
Hungary		0	0.85	0.02	0.041	0.04	2.45	0.77	0.21	0.83	0.37	0.17	0.96	0	2.82	0.33	7.97	32.78	4.19	4.15	1.04	0.46	1.72	0.56	0	0.29
Slovakia		0.13	2.46	0.06	0.06	0	0	0.19	0.48	0	0.32	0.03	0.03	0.06	2.59	0.03	25.67	20.26	1.50	1.95	0.96	1.92	4.51	0.64	1.41	0


a
eigen values
b
channels, weirs & wing dams
partially abandoned channels
abandoned channels
c
rheophils
limnophils
semi-rheophils
d
ch we wd pa ab
Cg Cn Ll Gp Vv Li Pf Aa Ra Ab Pr Lg
Bb As Lc Gg Al Sl Gc Rr Bj Ca El Se

larly, no significant difference (Student's t-test, df = 24, t = 0.601, p = 0.5533) was found in the relative densities of fishes in the Hungarian and Slovak 0 + fish assemblages (Table 2). The most important difference between the two sides of the flood plain was the absence on one side or the other of particular species of 0 + fish, as mentioned earlier. Although 0 + *Alburnus alburnus* were observed to have a four times higher density on the Slovak side than the Hungarian, this higher value results mainly from an extremely high abundance at one site.

The number of 0 + fish captured per sample was low, except for *Rutilus rutilus* and *A. alburnus* (Fig. 3a). As found elsewhere (Copp 1990, 1992a, 1992b), *R. rutilus* was the most frequently encountered species of 0 + fish (Fig. 3b), with the highest average number of specimens per sample and the highest propensity to aggregate (Fig. 3a). The index of dispersion was highest for *A. alburnus*, revealing a propensity to congregate similar to that observed in the upper River Rhône (Copp 1993) but about 10 times that observed for 0 + *A. alburnus* in the River Great Ouse basin, UK (Copp 1992b). *R. rutilus* were also very clumped, again similar to values on the upper Rhône but about twice as great as those observed in the Great Ouse catchment (Copp 1992b). Whereas for *Perca fluviatilis*, the index of dispersion resembled that of the Great Ouse catchment but was much lower than that observed on the upper River Rhône, where dense shoals 0 + *P. fluviatilis* were observed to move about in some abandoned meanders (Copp 1993). Of the other most frequent species (*Rhodeus sericeus, Blicca bjoerkna*), the index did not contrast to any remarkable degree those observed elsewhere (Copp 1992, 1993).

At the macrohabitat level of perception, one of the 25 species of 0 + fish encountered (*Gymnocephalus baloni*) was present at one site only (no. 16) and could not be considered in the Principal Components Analysis of macrohabitat function. The first two components of the analysis accounted for 30% of the variation (Fig. 4a) and three major groups of sites were based on biotope character: (1) channels, weirs and wing-dams, (2) partially-abandoned channels, and (3) abandoned channels (Fig. 4b). Correspondingly, the correlation circle for species along the same axes revealed three groups of species (Fig. 4c); rheophils, semi-rheophils and limnophils. The progeny of rheophilous fishes such as *C. gobio, Barbus barbus, Chondrostoma nasus, L. leuciscus, L. cephalus* and *L. idus*) were observed more often than expected (chi-square, $p < 0.05$) at weir, wing-dams and/or lotic channel sites (Fig. 4d, Table 2); the frequency of occurrence of some other rheophils such as *Vimba vimba* and *Gobio albipinnatus* did not deviate from expected, but showed a weak preference for such sites (Fig. 4d); this corroborates our assumption that weirs of the flood plain's anabranch systems function as lotic refuges for the progeny of rheophilous fishes in late summer, when river flows through the anabranch systems are drastically reduced. Indeed, many of these species occurred in significantly higher relative densities (ANOVA) than in the lentic side-channels, partially abandoned channels and/or abandoned channels, i.e. *C. nasus* ($F = 2.90$, $p < 0.05$), *L. leuciscus* ($F = 3.57$, $p < 0.05$), and *L. idus* ($F = 2.55$, $p = 0.05$). The wing dams appear to be important areas for the progeny of some other rheophilous species, which had significantly higher relative densities (ANOVA) at wing-dam sites than all other sites, i.e. 0 + *C. gobio* ($F = 10.85$, $p = 0.0001$) and *B. barbus* ($F = 5.14$, $p = < 0.005$).

A number of species demonstrated higher-than-expected frequencies in partially-abandoned channels (Fig. 4c, d), which are in transition between lotic and lentic conditions, suggesting semi-rheophily (e.g. *Abramis ballerus, A. alburnus, R. sericeus,*

←

Fig. 4. Centred and normalised principal components analysis (Chessel & Dolédec 1991) of the Sites-by-Species matrix (52 × 24): a — eigen values, b — ordination of axes 1 and 2 for sites with sites grouped by type of macrohabitat. Weir sites are given in bold. Sites ordinated amongst a different type of macrohabitat are circled with the style of line corresponding to their respective group (see also Table 2). c — Circle of correlation of axes 1 and 2 for 0 + fishes. d — Preference/avoidance profiles for the 24 species with respect to type of channel. Significant chi-square deviations from expected between species and variables are indicated with an asterisk ($p \leq 0.05$), and the profiles were calculated as the difference between the frequency of that species in the group of sites of a given type of channel and the frequency of that species in all sites (significance is indicated by values approaching |0.5|).

Table 3. Total frequency (f_c = 146) of each category (for each environmental variable) and frequency of each species of 0 + fish (f_s) in the 559 samples from the Hungarian/Slovak flood plain. The fish abbreviations are given in Table 1.

f_c	Variable category species: f_s =	Bb 35	As 15	Ll 33	Lc 32	Gg 20	Li 22	Pf 96	Gc 16	Aa 188	Rr 360	Rs 86	Bj 86	Ab 28	Ca 33	Pr 67	El 36
	distance from bank																
28	0–0.4	1	0	1	3	2	0	8	2	6	18	7	3	1	3	10	0
213	0.5–0.90	13	3	7	10	5	8	23	2	21	52	14	9	4	2	15	10
93	1.0–2.0	8	7	14	13	10	11	44	5	63	161	42	33	15	13	28	17
85	2.1–4.0	3	3	6	2	2	2	10	4	35	65	10	17	4	7	6	4
56	4.1–9.0	1	1	4	3	1	1	0	1	37	41	9	14	1	7	4	4
56	> 9.0 m	9	1	1	1	0	0	1	2	26	23	4	10	3	1	4	1
	slope of bank																
54	0–0.04	9	1	5	3	1	1	3	1	18	27	4	13	3	3	4	2
69	0.05–0.08	0	1	3	3	1	2	4	1	19	47	13	12	2	11	4	3
79	0.09–0.13	7	3	10	3	4	3	10	3	29	43	12	10	2	4	5	4
113	0.14–0.22	2	4	7	8	7	3	20	3	47	75	17	19	7	4	13	4
88	0.23–0.36	8	2	3	6	4	1	12	4	33	62	15	17	6	4	12	6
94	0.37–0.60	5	2	4	6	3	7	20	2	27	73	18	8	8	4	15	11
43	0.61–1.0	2	2	1	2	0	4	20	1	8	26	6	7	0	2	7	5
19	> 1.0	2	0	0	1	0	1	7	1	7	7	1	0	0	1	7	1
	substratum—clay																
318	0	34	11	32	24	9	16	65	6	108	178	30	29	14	9	41	19
178	1–33	1	3	0	7	11	5	24	6	33	129	32	39	10	19	21	14
50	34–66	0	0	1	1	0	1	5	3	22	42	15	14	3	4	3	2
13	67–100%	0	1	0	0	0	0	2	1	5	11	9	4	1	1	2	1
	substratum—silt																
181	0	31	8	26	13	6	13	36	4	66	88	4	8	7	1	22	11
129	1–33	4	4	7	10	4	6	25	6	49	92	36	16	8	3	25	7
74	34–66	0	0	0	3	1	1	13	2	25	61	18	15	4	6	5	3
175	67–100%	0	3	0	6	9	2	22	4	48	119	28	47	9	23	15	15
	substratum—sand																
292	0	23	9	10	14	8	11	47	4	85	182	42	59	15	24	32	23
180	1–33	10	4	18	10	10	7	31	9	70	120	24	16	11	7	17	9
56	34–66	1	1	5	5	1	4	11	2	22	34	13	7	1	2	11	2
31	67–100%	1	1	0	3	1	0	7	1	11	24	7	4	1	0	7	2
	substratum—pebbles																
370	0	14	6	3	15	11	11	72	13	116	241	63	77	18	30	40	33
95	1–33	15	6	11	5	5	4	14	1	34	60	13	5	5	2	16	1
86	34–66	5	3	18	12	4	6	7	2	36	53	8	3	5	1	10	1
8	67–100%	1	0	1	0	0	1	3	0	2	6	2	1	0	0	1	1
	substratum—gravel																
339	0	2	6	3	16	13	7	51	13	107	246	77	77	17	29	41	24
40	1–33	2	1	8	0	4	3	6	0	17	27	3	1	1	0	3	0
71	34–66	11	4	14	10	0	4	11	2	28	43	3	2	7	2	3	3
109	67–100% area	20	4	8	6	3	8	28	1	36	44	3	6	3	2	20	9
	water transparency (cm)																
27	0–11	0	1	0	0	0	0	2	0	11	13	6	3	0	18	0	6
50	12–20	0	1	0	2	7	0	0	2	11	44	9	22	4	2	2	2
81	21–33	0	1	1	5	3	1	9	3	34	63	24	21	4	2	11	2
132	34–54	5	4	4	9	6	10	19	6	52	95	25	20	9	7	12	4
160	55–90	18	4	17	12	3	4	32	1	44	91	16	15	5	3	22	15
84	91–148	11	3	10	2	1	6	30	4	27	43	6	2	3	1	10	5
25	> 148 cm	1	1	1	2	0	1	4	0	9	11	0	3	3	0	10	2

Table 3. Continued.

f_c	Variable category species: f_s =	Bb 35	As 15	Ll 33	Lc 32	Gg 20	Li 22	Pf 96	Gc 16	Aa 188	Rr 360	Rs 86	Bj 86	Ab 28	Ca 33	Pr 67	El 36
	ligneous debris (count)																
433	0	30	13	31	22	16	13	64	12	155	265	58	60	17	27	43	24
61	1–3	3	1	1	4	4	6	14	2	17	42	11	13	5	3	7	1
30	4–6	1	1	0	1	0	3	8	2	7	23	10	5	3	2	8	7
35	> 6	1	0	1	5	0	0	10	0	9	30	7	8	3	1	9	4
	macrophytes																
428	0	30	11	27	29	18	20	67	14	163	267	53	71	26	28	38	25
48	1–33	3	2	1	2	1	1	8	1	15	34	15	4	1	1	10	2
34	34–66	2	0	2	0	0	0	8	0	6	22	7	5	0	1	8	2
49	67–100%	0	2	3	1	1	1	13	1	4	37	11	6	1	3	11	7
	water velocity																
499	null	10	13	21	25	17	18	77	15	166	342	85	85	28	32	60	36
37	weak (≤ 5 $cm \cdot s^{-1}$)	13	0	3	4	0	1	15	1	15	12	1	0	0	1	6	0
23	faster (> 5 $cm \cdot s^{-1}$)	12	2	9	3	3	3	4	0	7	6	0	1	0	0	1	0
	water temperature																
54	≤ 21° C	2	0	2	3	0	1	7	1	26	33	7	14	1	2	7	4
130	21.1–23.0	11	7	14	6	7	11	29	7	45	81	15	14	9	5	10	9
174	23.1–25.0	14	7	7	10	8	6	30	7	63	113	22	33	12	10	25	14
135	25.1–27.0	6	1	7	9	5	2	24	1	36	87	26	21	6	11	15	8
66	≥ 27° C	2	0	3	4	0	2	6	0	18	46	16	4	0	5	10	1

Abramis brama and *Proterorhinus marmoratus*). However, only *R. rutilus* had significantly higher relative densities (ANOVA, $F = 1.817$) in partially-abandoned side-channels than another type of site, in this case wing-dams ($p = 0.05$). Indeed, the low discharge of the Danube left the normally lotic anabranches in a lentic state, favourable to the progeny of some semi-rheophilous fishes; for example, *A. brama* had significantly higher relative densities (ANOVA, $F = 1.453$) in side-channels than in abandoned channels ($p = 0.05$). Relatively few limnophilous species were encountered (Fig. 3, Table 2), with only *Carassius auratus* occurring more often than expected in abandoned channels (Fig. 4d) and having significantly higher relative densities (ANOVA, $F = 1.778$) in such sites than in side-channels and weirs ($p = 0.05$).

At the microhabitat level of perception, only 16 of the 25 species of 0 + fish occurred in ≥ 3% of non-null samples (Fig. 3b) and these were eliminated prior to direct gradient analysis of microhabitat use. Of the 12 environmental variables (Table 3), only channel width, bank slope, percentage of silt substrate and water temperature passed Lilliefors' (1967) test of normality, which is known to be very conservative (Connover 1971). Fortunately, Canonical Correspondence Analysis is robust with respect to violated assumptions (Ter Braak 1986), a frequent occurrence in the study of natural systems (Gauch 1984), as the removal of too many or the wrong variables can result in statistically significant decreases in the eigen values (Ter Braak 1986, Copp 1992).

The first two axes of the Canonical Correspondence Analysis accounted for 65% of the variability (inset Fig. 5), with the first axis accounting mainly for water velocity; in the samples ordination, a gradient of increasing water velocity can be perceived, from left to right, in the three distinct groups of samples, with the corresponding ordination of species from left to right (rheophilous to limnophilous). And the second axis accounted mainly for water transparency (Fig. 5). Note that the vector length for a variable represents the relative importance of that variable for predicting (in the sence of multiple regression) fish habitat use (Chessel et al. 1991).

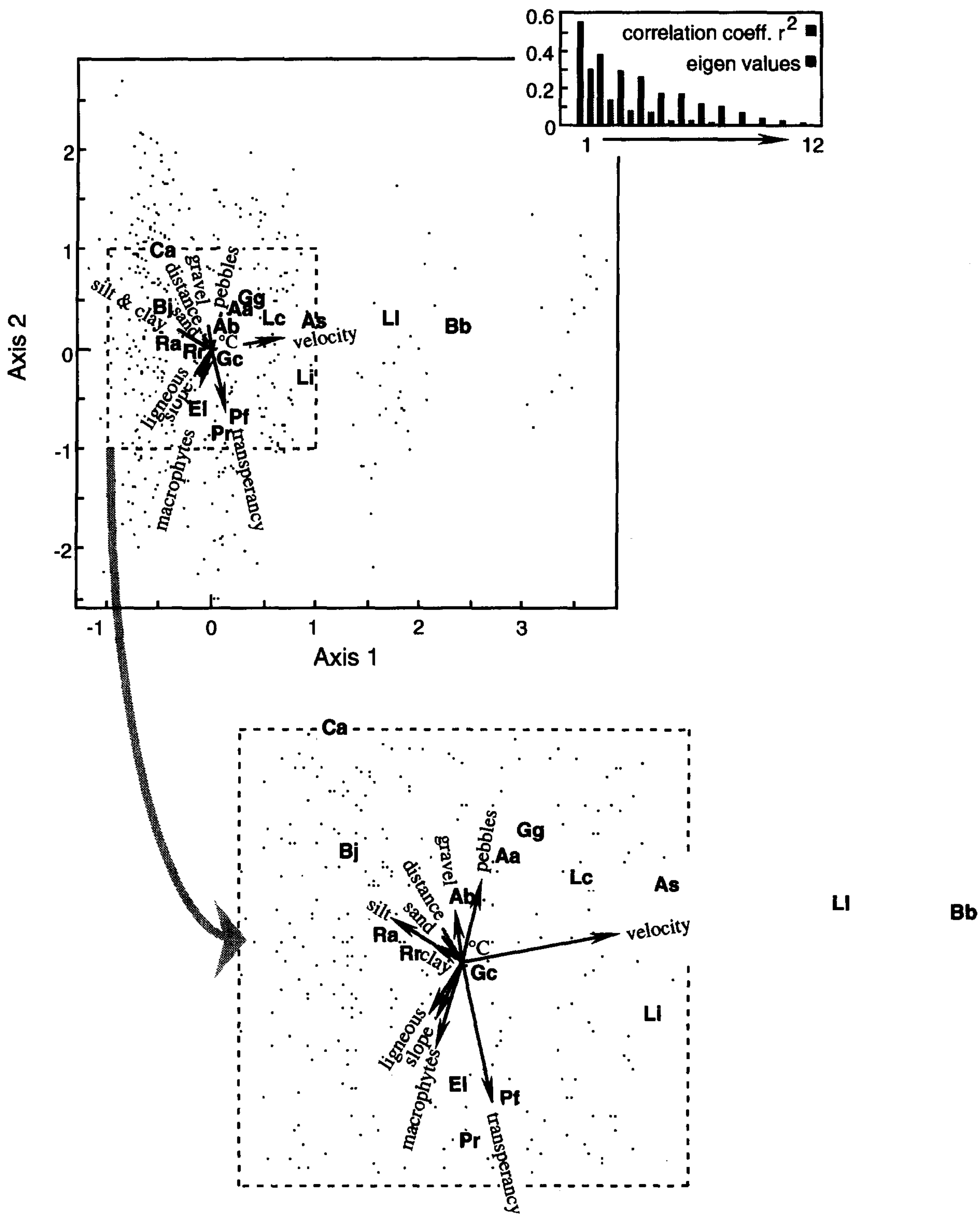


Fig. 5. Canonical Correspondence Analysis (Chessel et al. 1987) biplot for the 16 juvenile fish species (0 +) and 12 environmental variables, axes one and two. The eigen values and correlation coefficients are illustrated graphically (inset) to facilitate evaluation. The dots represent the ordination of individual samples, whereas the abbreviations for each fish species is placed at that species' co-ordinates. The length of arrow for each environmental variable is relative to that variable's importance in the ordination of the samples and species. The location of a species along a given environmental vector, which can be extended beyond the origin, represents that species' ordination along that environmental gradient relative to other species. The centre portion of the biplot is magnified to assist interpretation.

The vectors can be extended in either direction to identify the position of a species relative to other species along that environmental gradient (Ter Braak 1986).

Some of the 0 + fishes (*B. barbus, L. leuciscus* and *G. gobio*) demonstrated rheophily through a statistically significant preference for weak or moderate/fast water velocities (Figs 5, 6), with *B. barbus, L. leuciscus, L. cephalus* and *L. idus* also occurring more often than expected over the predominantly pebbel and gravel substrates that are characteristic of lotic microhabitats. Similar to results reported by Schiemer & Spindler (1989), some rheophilous species (*B. barbus, L. idus, L. cephalus*) were found more often than expected close to weakly-sloped banks with greater water transparency (*B. barbus, L. leuciscus, L. idus*). It follows then that these two species were found to co-occur more often than expected (Table 4). Only *G. gobio* occurred more often than expected in more turbid waters (Figs 5, 6), and only *L. idus* was significantly associated with ligneous structures. Although 0 + *Aspius aspius* was originally considered to be rheophilous (Table 2), its 0 + juveniles were observed almost entirely in the absence of water current (Table 3, Fig. 6). However, the higher-than-expected co-occurrence of *A. aspius, L. leuciscus, G. gobio* and *L. idus* in samples suggests some overlap in their microhabitat use (Table 4). Previous investigations of microhabitat use by 0 + fish in the upper River Rhône (France), which is of roughly similar geomorphological origin (J.P. Bravard personal communication), have revealed a similar pattern of refuge co-exploitation by numerous species of 0 + fish during periods of low discharge (Copp 1991, 1992a).

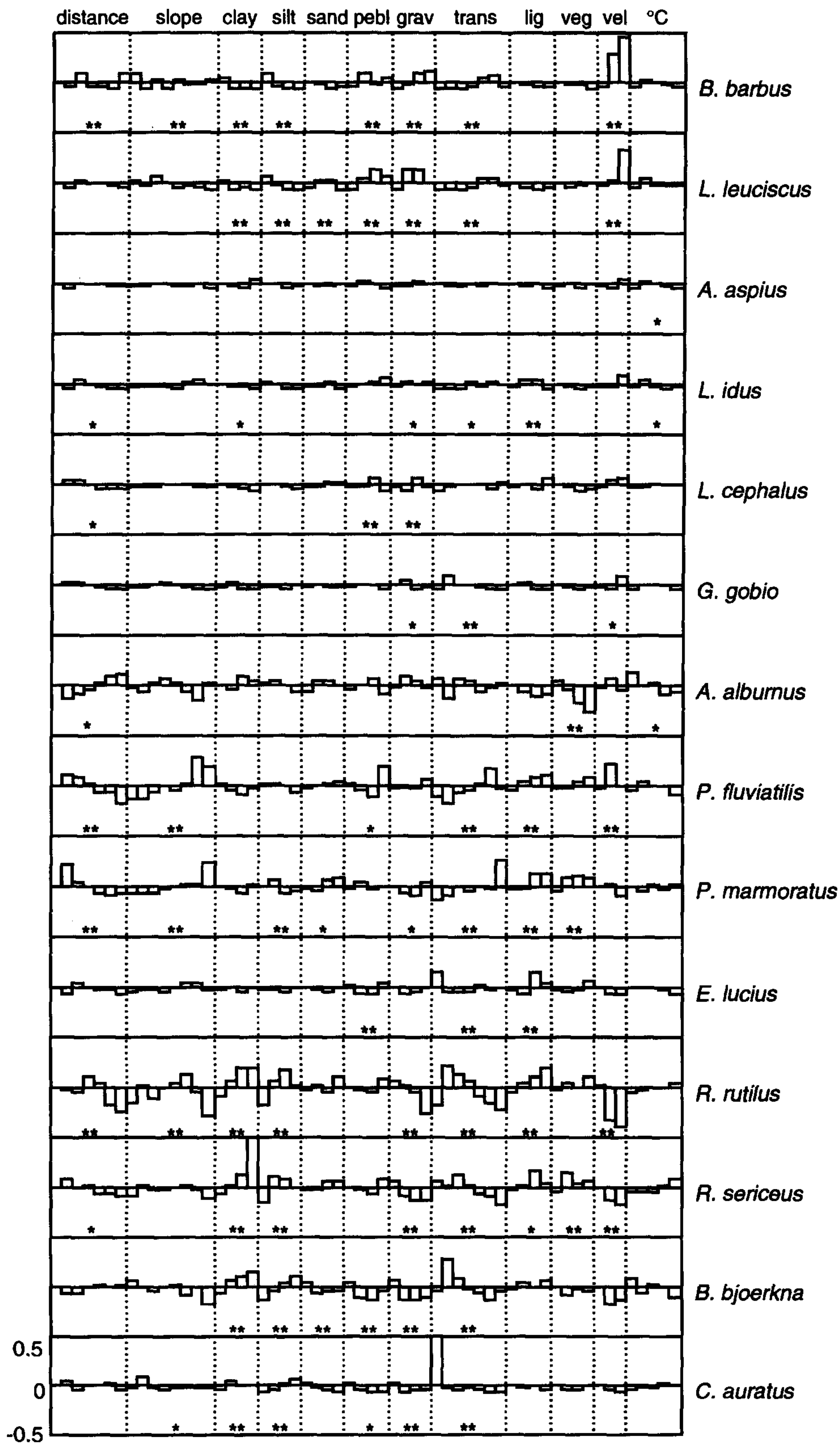
Amongst the progeny of semi-rheophilous fishes, only *P. fluviatilis* demonstrated a preference for water currents, but *P. marmoratus* preferred a very similar microhabitat, both occurring more often than expected in high transparency waters close to strongly-sloped banks with ligneous structures (Figs 5, 6); although *P. fluviatilis* occurred frequently amongst macrophytes (Table 3), of the two only *P. marmoratus* demonstrated a significant association (Fig. 6). Despite the similarity in microhabitat, these species appear to avoid overlap, as the frequency of their co-occurrence in samples did not deviate from expected (Table 4). In contrast, *A. alburnus* preferred greater distances from the bank, and significantly avoided macrophytes.

The 0 + juveniles of other semi-rheophilous species either significantly avoided water flow (*R. rutilus, Rhodeus sericeus amarus*), or were almost never observed to occur in its presence (*Esox lucius, A. brama, B. bjoerkna;* Table 3). *R. rutilus* and *R. sericeus* preferred very similar microhabitats (Figs 5, 6), occurring more often than expected amongst macrophytes and ligneous structures in turbid waters about 2 m from clay and/or silty banks.

Previous investigations have demonstrated that *R. rutilus* often occur amongst macrophytes (Lightfoot & Jones 1979, Copp 1992a), which provide protective cover against predation (Killgore et al. 1989). Although the occurrence of *B. bjoerkna* with respect to macrophytes, ligneous structures or distance from bank did not deviate from expected (Fig. 6), its frequencies (Table 3) were rather similar to those of *R. rutilus* and *R. sericeus*, suggesting a generally similar microhabitat; this assumption is corroborated by the higher-than-expected co-occurrence in samples of the three species (Table 4) and their close proximity in the canonical ordination biplot (Fig. 5). *R. rutilus* did not, however, co-occur more than expected with *P. fluviatilis*, two species that are known to interact in both riverine (G.H. Copp unpublished) and lake systems (Persson 1991).

The only limnophilous species to occur in sufficient frequency to warrant inclusion in the analysis, *C. auratus*, demonstrated preferences for the silty, turbid waters characteristic of shallow, desiccating abandoned channels (Figs 5, 6). The low frequency or absence of limnophilous, plant spawning fishes (e.g. *T. tinca, S. erythrophthalmus*) is probably an artifact of the year's climate, given that extreme desiccation limited the number of abandoned channels available for study.

The fact that some species were not encountered on the Hungarian side (*G. gobio, S. lucioperca, L. gibbosa*) and others not on the Slovak side (*Gobio albipinnatus, G. gobio, L. leuciscus, S. erythrophthalmus*) does not necessarily indicate their absence, but suggests a very sparse distribution if the species did indeed exist. That this species were


distance
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silt
sand
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lig
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vel
°C
B. barbus
L. leuciscus
A. aspius
L. idus
L. cephalus
G. gobio
A. alburnus
P. fluviatilis
P. marmoratus
E. lucius
R. rutilus
R. sericeus
B. bjoerkna
C. auratus
0.5
0
-0.5

←

Fig. 6. Microhabitat profiles and chi-square associations (Chessel & Dolédec 1992) between 14 species 0+ fish and 12 environmental variables in the Danube River flood plain. For *G. cernuus*, *A. brama*, there were no deviations from expected. Each histogram represents the difference between the frequency of that species in the group of samples having that category of environmental variable and the frequency of that species in all samples. Significant deviations from expected between species and variables are indicated with an asterisk (*, $p = 0.05$; **, $p < 0.01$), and between species and individual categories by values approaching 10.51. Abbreviations: pebl = pebbles, grav = gravel, trans = water transparency, lig = ligneous debris (e.g. branches, roots), veg = macrophytes, vel = water velocity. See Table 3 for categories.

found somewhere in the flood plain emphasises the importance of maintaining the co-existence of numerous aquatic biotopes (lotic, semi-lotic, stagnant channels) at similar and at different phases of ecological succession (Amoros et al. 1987, Copp 1989b). The resilience of flood plain systems, such as those of Middle Danube, depends upon such a variety of macro and microhabitats, which offer fish populations a sufficient range and number of favourable spawning sites; this ensures reproductive success somewhere in the system, even in the event of a pollution incident or other major environmental perturbation such as the drought experienced prior to and during the present study.

The initial impact of the Gabčíkovo hydropower scheme on the flood plain's fisheries was already been felt as the present article was being prepared, realising the negative effects predicted prior to the scheme's operation (Balon 1967b, Holčík 1991, Holčík et al. 1982). In November 1992, the water flow through the anabranch systems on the Hungarian side was reduced to a trickle compared with the previous discharge, reducing the level of the main channel to such an extent that one can traverse it on foot in some locations and the more elevated side-channels of the anabranch systems were completely dry (personal observation). However, since that time there has been some mitigation on the Slovak side, with extra water diverted to the flood plain. However, a political impasse between the Hungarian and Slovak governments has impeded the resolution of the question of how much water will be diverted towards the Hungarian flood plain. In areas worst effected by the reduction in discharge, we expect to see local extinction of fish populations as the beds of former channels no longer contain water except during extreme flooding. As fish production is proportional to the area of land inundated (Antipa 1928), the hydroscheme development is expected to result in a decrease in fish production. The change in hydrological regime is expected to bring on this decrease in two ways. Firstly, inundation of

Table 4. Chi-square significance of deviations from expected co-occurrence of 0+ fishes in the River Danube flood plain (Hungary/Slovakia), calculated from the non-null sample matrix (559 × 16): *, $p = 0.05$: **, $p = 0.01$; ***, $p = 0.005$; ****, $p = 0.001$; *****, $p < 0.001$. No significant deviations were observed between Ab, Ca, Pr and El. The frequency of each species in the 559 samples is given in Table 3, the fish abbreviations in Table 1.

	As	Ll	Lc	Gg	Li	Pf	Gc	Aa	Rr	Ra	Bj	Ab	Ca	Pr	El
Bb		*****	***		****				*****	*	*				
As	—	*****		*****	***										
Ll		—	***	**	*****										
Lc			—									*			
Gg				—		*	*				*				
Li					—	*									
Pf						—		*****							**
Gc							—			*	*	*****			
Aa								—	*					*****	*****
Rr									—	*****	*****	*	*		
Ra										—	***			*****	
Bj											—	*****			

the flood plain will be limited to extreme flooding events, which will be buffered to some extent by filling of the reservoir. Secondly, as the magnitude of change in the water level has been increased by diversion of the river to the reservoir, the period of time flood plain channels hold water will be shorter, leading to a more rapid desiccation of the various flood plain biotopes (particularly the abandoned braided channels that were already of temporary character prior to the hydroscheme's operation). Unusually low river discharges during the period prior to the investigation are probably the reason for the low abundance of limnophilous, plant spawning fishes (e.g. *T. tinca, S. erythrophthalmus*); this pattern of species impoverishment is expected to continue. The fate of rheophilous species is less certain; although species richness may not decline, the change in discharge rate will probably effect production by inhibiting recruitment, such as observed in *Chondrostoma nasus* in a by-passed section of the upper Rhône River in France (Persat & Chessel 1989). Should an environmentally acceptable compromise be reached concerning the repartition of the Danube's flow between the hydroelectric scheme and the adjacent flood plain, the empirical model elaborated in the present study could assist in the mitigation of the scheme's impact on local fish populations.

Acknowledgements

This investigation was funded through a Royal Society (UK) travel grant to GC and post-doctoral fellowship to GG, by the Hungarian Academy of Sciences, the National Science Research Foundation (Hungary), and by the Slovak Academy of Sciences (grant nrs 333 & 336). We thank all these organisations for their support. Special thanks are extended to Á. Berczik and M. Lisicky for their help behind the scenes, and to S. Johnson and C. Hainsworth for technical assistance.

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