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Microhabitat use by stream-dwelling spirlin *Alburnoides bipunctatus* and accompanying species: implications for conservation

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Abstract. Microhabitat use in the endangered cyprinid species spirlin *Alburnoides bipunctatus* and accompanying species was examined in three water courses of Slovakia to determine the species' environmental requirements as a basis for informing conservation policy and management. In all three rivers, water velocity, water depth and substratum character were central features of spirlin microhabitat use, regardless of year or season of sampling, with only limited variation in microhabitat associations as a function of time of day. Clear differences in microhabitat use and intra-specific associations during development were observed in two of the rivers. In particular, a shift in velocity preference towards faster flowing waters appears characteristic of spirlin during their larval and juvenile development, and possibly also that of gudgeon *Gobio gobio*, European minnow *Phoxinus phoxinus*, and chub *Leuciscus cephalus*, which are all species that may be significantly associated with young spirlin. Disproportionate use of deeper waters tended to increase with age in spirlin, and in gudgeon and barbel *Barbus barbus*, but spirlin preference for substratum was less uniform, with affinities ranging from indifference to strong preference. This contrasts the clear preferences for sand in gudgeon and for cobbles in European bullhead *Cottus gobio*. Of particular importance to young-of-the-year (YOY) spirlin are lentic zones with some sort of ligneous debris – habitat also used by YOY gudgeon and minnow. Contrary to previous reports elsewhere, spirlin did not avoid in-stream vegetation where present, and in one river it was preferred by YOY and 1+ spirlin. To avoid declines in spirlin and accompanying stream-dwelling species, such as reported elsewhere in Europe, river management in water courses such as these should be limited to the rehabilitation of regulated sections to achieve a natural, heterogeneous channel character.

Key words: *Cottus gobio*, *Vimba*, *Barbus*, vulnerable, threatened species, point abundance sampling

Introduction

Microhabitat use is an important aspect in the life history of fluvial fishes, providing essential information for the conservation of ecological integrity of water courses (Copp et al. 1994, Tharme 2003). The study of threatened species is of particular relevance because they have suffered from the loss of essential habitat, which is not readily apparent in the more abundant, generalist species. Even if a threatened species is of little or no economic importance, they are said to play an integral part of the socio-economic relationship between biodiversity and per-capita gross national product (Naidoo & Adamowicz 2001). Amongst the freshwater fish species of low economic importance but of conservation value is the spirlin *Alburnoides bipunctatus* (Bloch) (Peňáz 1995), a sub-montane species that inhabits the transition zone between the so-called 'grayling' *Thymallus thymallus* and 'barbel' *Barbus barbus* zones (sensu Huet 1959). The spirlin's threatened status in Europe was first highlighted by Lelek (1987), followed by recognition in the Bern Convention (Annex III). More recently, spirlin is listed in the IUCN (2008) Red Book as a species of "Least Concern" but locally threatened, such as in Poland (e.g. Kotusz et al. 2006), Slovakia (Holčík 1989, 2003, Maitland 1991, Kováč 1994, Hensel & Mužík 2001, Kováč et al. 2006), the Czech Republic (Jurajda et al. 2007), Austria (Schiemer et al. 2004), and in Hungary (Černý & Kvaszová 1999, Erős 2007) where the species has legally protected status.

Perhaps as a consequence of its rarity and low abundance (e.g. Lamouroux et al. 1999, Erős et al. 2003), the microhabitat of spirlin is relatively little known except in general terms (e.g. Breitenstein & Kirchhofer 2000, Tales et al. 2004, Jurajda et al. 2007, Kruk 2007, Erős et al. 2008). Although not listed in Annex II of the European Commission's Habitats and Species Directive (92/43/EEC (1) of 21 May 1992), the spirlin is listed in Annex II of the Bern Convention (e.g. Lasne et al. 2007a). These are often the same sections in which Annex II listed species also occur (e.g. bullhead *Cottus gobio*, spined loach *Cobitis taenia*, Ukrainian brook lamprey *Eudontomyzon mariae*, burbot *Lota lota*). A rheophilous species, the spirlin is sensitive to the changes in the structural diversity of rivers (Breitenstein & Kirchhofer 2000, Valová et al. 2006, Kruk 2007) and risks local extinction in some parts of its range due to river regulation. Therefore, spirlin could be used as a functional describer (*sensu* Copp et al. 1991), or 'indicator species' (Lasne et al. 2007b), of sub-montane streams (Krno et al. 2001, Kováč & Siryová 2002) where these Annex II listed fish species are characteristic.

The aim of the present study was to examine the microhabitat use requirements in spirlin (with regard to its ontogeny) and accompanying species in three water courses of Slovakia in which spirlin is relatively abundant. Microhabitat profiles generated in this study will provide essential information for conservation of the species in other water courses in which its status may be constrained by modification or degradation of in-stream habitat (e.g. Valová et al. 2006, Kruk 2007). The present study represents part of a wider ecomorphological examination of the spirlin (e.g. Siryová 2004, Kováč et al. 2006).

Study sites

Sampling was carried out from early March to mid November 2001–2003 in three rivers systems in Slovakia: Rudava, Turiec and Vlára (Fig. 1). The River Rudava is a small tributary of the River Morava (Western Slovakia), with a total length of 45 km. The river flows through a complex of inland sand dunes established during inter-glacial periods. The climate of the area is relatively dry and moderate, with a mean annual temperature that varies inter-annually between 9 and 10°C, and an mean annual rainfall of 600–700 mm. Mean stream width was 6 m. Water

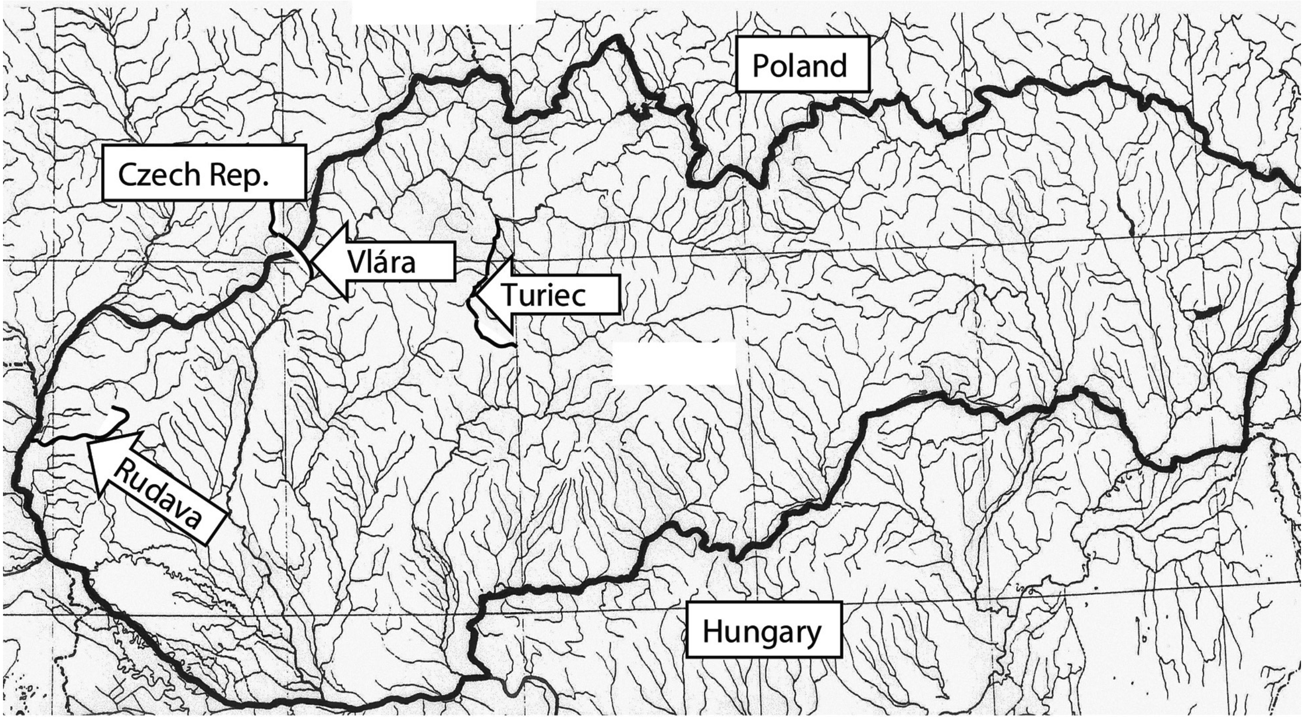

Fig. 1. *Map of Slovakia with rivers and study stretches indicated.*

depth varied according to rain events with maximum depths of 1.4 m in pools. The sampling was carried in the middle, unregulated section of the river (river km 10.5–10.8) where the substratum consisted mainly of sand, without the submerged vegetation (Spindler et al. 1992). This study stretch was selected because of its natural character with a diversity of microhabitats as well as because it has long been a reliable site as for occurrence of spirlin. The study stretch was lotic with relatively few lentic patches, with maximum water velocity 0.7 m·s^{-1}. Fish species found infrequently and in low numbers (and thus excluded from the present study) were: spined loach, burbot, Ukrainian brook lamprey, silver bream *Abramis bjoerkna*, goldfish *Carassius auratus*, European weather loach *Misgurnus fossilis,* stone loach *Barbatula barbatula,* bleak *Alburnus alburnus,* northern pike *Esox lucius,* and bitterling *Rhodeus sericeus*.

The River Turiec is an important tributary of the River Váh, the largest complete river system of Slovakia. The River Turiec is a meander-form type stream and has near-natural physical channel conditions, discharge regime and aquatic vegetation. The Turiec is over 66 km long and plays an important role in the region's hydrological balance, particularly groundwater recharge and nutrient cycling. The climate is temperate and mild, with mean air temperatures in January of -4 to -6°C, and in July of 16 to 17°C, being wet to very wet with annual rainfall varying between 780 and 1000 mm. The study stretch was mostly lotic with a maximum water velocity of 1.78 m·s^{-1} (river km 45.9–46.2). This study stretch was selected for the same reasons as in Rudava (see above). Fish species found infrequently and in low numbers (and thus excluded from the present study) were: grayling, ide *Leuciscus idus,* dace *L. leuciscus,* northern pike, nase *Chondrostoma nasus,* bleak, burbot, brown trout *Salmo trutta,* American brook trout *Salvelinus fontinalis*.

The River Vlára, another tributary of the River Váh (middle section), has a length of 47 km. In its Slovak stretch, the Vlára had a sub-montane character, with a mainly natural riverbed, discharge regime and aquatic vegetation, though the last 600 m of the Vlára have been regulated. At the village of Horné Sŕnie (indicated by the arrow in Fig. 1) the mean annual discharge was 3.31 m^3·s^{-1}, attaining its maximum in March (6.79 m^3·s^{-1}), whereas the minimum discharge occurred in November (1.05 m^3·s^{-1}). River water temperature varied between 0.0°C and 20.5°C (mean annual = 7.5°C), with minimum temperatures in January and February, and maximum temperatures in July and August. The mean annual rainfall in this mild climatic area may reach 752 mm. Sampling was carried out in an unregulated, lotic, stretch of the downstream part of the Vlára (i.e. upstream of the regulated stretch), which was characterized by rapids, river widths of 6 to 10 m, and maximum water velocities of 1.77 m·s^{-1} (river km 6.2–6.5). This study stretch was selected for the same reasons as the Rudava stretch (see above). Other fish species, which were found infrequently and in low numbers (and thus excluded from the present study), were: nase, American brook trout, brown trout, roach, ide, and golden spined loach *Sabanejewia balcanica*.

Material and Methods

Fishes and microhabitat measurements were sampled by S. Siryová using point abundance sampling by electrofishing (as per Copp & Garner 1995) on various dates in 2001 to 2003 (see Table 1) at various times of dawn, day and evening to acquire a better representation of microhabitat breadth (see Copp 2008). Point samples were collected in a haphazard manner, in an upstream direction, along the study stretch, as used in fish microhabitat studies elsewhere (Copp 1992, Copp et al. 1994, Watkins et al. 1997). Fishes were immobilized using a portable electrofishing unit (LENA, 240–310 V, 95 Hz, 100 mA) and collected with a dip net. Fish affected by the electricity, but not in the sampling point, were ignored (Copp & Garner 1995). Fish were identified to species, measured for standard length (SL) and returned to the river except for a sub-sample of captured spirlin, which were killed with an overdose of anaesthetic and preserved in 4% formaldehyde for morphological analysis (Siryová 2004, Kováč et al. 2006).

At each sampling point, 12 environmental variables were measured: distance from the bank (m); depth (cm); bed slope (depth/distance from the bank); substratum type: sand silt & clay, gravel and cobbles (as % of point sample area, e.g. Simonson 1993); vegetation (as % of point sample area), though aquatic vegetation was encountered very rarely); overhanging branches (as % of point sample area); ligneous debris and tree roots (as % of point sample area); backwater eddies (absent, present), shading (%) and water velocity (cm·s^{-1}). Water depth was measured with a graduated dip-net pole. Water velocity was measured using an Eijkelkamp mechanical flow meter, with propeller model 2030R.

For analysis and electivity profile generation, the data were categorized as follows: distance from the bank (< 1.0 m, 1.0–2.0, 2.1–3.0, ≥ 3.1 m); depth

Table 1. *List of the rivers in Slovakia sampled, with the date and the time of day of sampling: early morning (07:00–09:30), morning (08:30–11:30), midday (10:30–14:00), late afternoon (16:00–19:00), evening (18:00–21:00).*

River	Date	early morning	Morning	midday	afternoon	late afternoon	evening
Rudava	21 May 2001			X			
Rudava	27 May 2001					X	
Rudava	30 May 2001			X			
Turiec	4 July 2001						X
Turiec	28 July 2001					X	
Turiec	29 July 2001			X			
Rudava	5 August 2001					X	
Rudava	17 August 2001			X			
Rudava	17 October 2001			X			
Rudava	14 November 2001			X			
Rudava	8 March 2002			X			
Rudava	30 April 2002			X			
Turiec	18 June 2002						X
Turiec	19 June 2002					X	
Turiec	4 August 2002			X			
Rudava	6 August 2002			X			
Vlára	24 August 2002		X		X		
Rudava	29 April 2003					X	
Turiec	9 May 2003		X				
Rudava	10 September 2003					X	
Rudava	11 September 2003	X					
Turiec	18 September 2003						X
Turiec	19 September 2003		X	X			
Vlára	22 October 2003				X		

(< 30 cm, 30–40, 41–50, 51–60, ≥ 61 cm); slope (depth÷distance from bank: < 0.25, 0.25–0.5, > 0.5); sand with silt and clay (absent, 1–33, 34–66, > 67%) (except at Rudava, where 'absent' never occurred). Owing to limited variability, and/or low frequencies of occurrence, gravel, cobble, aquatic macrophytes, overhanging vegetation and backwater eddies were categorized as absent or present, but at Rudava, vegetation was not included in the analysis due to very low occurrence in samples (< 1%). The remaining variables were categorized as follows: ligneous debris and roots (absent, 1–25, 25–50, > 50%), shading (full sun, 1–33% of point sample shaded, 34–66% of point sample shaded, ≥ 67% of point sample shaded), water velocity (0 $cm \cdot s^{-1}$, 0.1–2.5, 2.51–5.00, 5.01–10.00, > 10.0 $cm \cdot s^{-1}$).

Fishes were attributed to age classes (Table 2) using the Peterson curve method (Barnes & Hughes 1999) applied to the SL frequency-at-age distribution data acquired from specimens captured (S. Siryová, unpublished) and in consultation of bibliographic sources for spirlin summarized in Breitenstein & Kirchhofer 2000 (for Rudava specimens, see Kováč et al. 2006). The mean number of fish per sample and frequency of occurrence was calculated for each size class. Fish species occurring in < 3% of samples were excluded from microhabitat analysis, an exception was made in case of gudgeon (2%) at Turiec because it is the only species to occur consistently with spirlin at all sites in > 2% of samples (site 2). The data were arranged in two matrices for each site (samples-by-species and sample-by-variables) and these were subjected to canonical correspondence (CCA; ter Braak 1986) and electivity analyses using software by Chessel & Thioulouse (1998), with software by Thioulouse (1990) used to render the microhabitat electivity profiles. CCA was used to evaluate microhabitat use for each size/age class of fish and render a triplot that combines the ordinations for samples, species and microhabitat variable vectors (ter Braak 1986).

***Table 2.** List of fish species and codes studied in the rivers Rudava, Turiec and Vlára (Slovakia) and their corresponding standard length (SL) classes in mm using the Peterson curve method (Barnes & Hughes 1999) and some bibliographic sources.*

Species common and Latin names	Code	Age classes	SL classes
spirlin *Alburnoides bipunctatus*[1]	Ap0+	larva	≤ 30
	Ap0+J	0+ juveniles	31–45
	Ap1	1+	46–55
	Ap2	2+	56–65
	Ap3	3+	66–75
	Ap4	4+	76–85
	Ap5	5+	86–95
	Ap6	6+ and older	≥ 96
barbel *Barbus barbus*[2]	Bb1	1+	100–120
	Bb2	2+	130–150
	Bb3	3+	160–200
	Bb4	4+	≥ 210
European bullhead *Cottus gobio*	Cg0	0+ juveniles	25–40
	Cg1	1+	40–65
	Cg2	≥ 2+	70–140
gudgeon *Gobio gobio*	Gg0 -Vlára	larvae & 0+ juveniles	≤ 50
	Gg1 -Vlára	1+	70–100
	Gg2 -Vlára	2+	≥ 90
	Gg1 -Rudava	0+ and 1+	20–80
	Gg2 -Rudava	2+ and 3+	90–140
chub *Leuciscus cephalus*	Lc0	0+juveniles	40–60
	Lc1	1+	70–110
	Lc2	2+	120–180
	Lc3	≥ 3+	190–400
dace *Leuciscus leuciscus*	Ll0	larvae & 0+ juveniles	10–60
European minnow *Phoxinus phoxinus*	Pp0	larvae & 0+ juveniles	15–45
	Pp1	1+ and 2+	45–80
vimba *Vimba vimba*	Vv1	1+	80–140
	Vv2	≥ 2+	150–320
stone loach *Barbatula barbatula*	Nb1	0+ and 1+	35–70
	Nb2	2+	75–110
Eurasian perch *Perca fluviatilis*	PfA	all ages	all sizes[2]

[1] Breitenstein & Kirchhofer (2000)

[2] mean = 107.5 mm SL, n = 51, min. = 50 mm, max. = 190 mm

To determine the preferences/avoidances of each size class of each species for environmental variables for each site separately, electivity indices were calculated as the difference between the frequency of that species in the group of samples having the category of environmental variables and the frequency of that species in all samples for each site (see Copp 1992 or Watkins et al. 1997). Negative values approaching -0.5 indicate avoidance and positive values +0.5 indicate preference. Owing to low expected frequencies, the deviations from expected occurrence of fish and environmental categories were determined with the Fisher Exact test, as were the species-species associations.

Results

A total of 1484 samples were collected of which 1111 contained 5843 specimens of fish belonging to 26 species. The greatest mean number of specimens was found to be larvae and 0+ juveniles of spirlin, followed by 0+ minnows. The greatest tendency to aggregate in shoals was observed in larvae and 0+ juvenile fishes. For example, in the River Vlára, vimba were found exclusively as ≥ 1+ except for 100 specimens of 0+ fish, which were found at one sampling point where channel width was 12 m, channel slope was 0.17, distance from bank was 0.3 m, water depth was 5 cm, velocity was 0 cm·s^{-1}, temperature was 18°C; substratum was 55% silt, 40% gravel, and 5% pebble, with no aquatic or over hanging vegetation, no roots and branches, no shade.

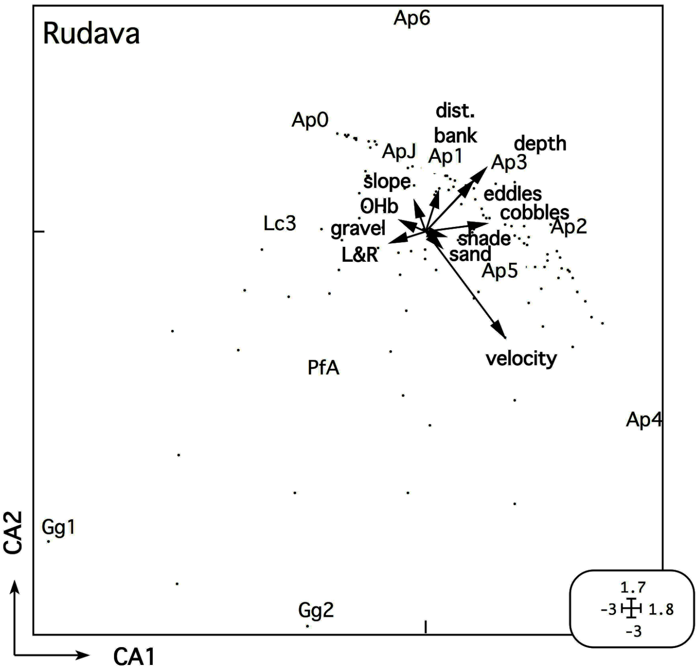

Fig. 2. *Canonical correspondence analysis (ter Braak 1986) triplot for age/size classes of fish and 12 environmental variables in the River Rudava (Slovakia). See Table 1 for dates and times, Table 2 for fish species/ class codes, and Table 3 for intra- and interspecific associations.*

In the River Rudava, water velocity was the most prominent microhabitat variable, followed by water depth, eddies and cobble substratum, in the comprehensive CCA of all samples (Fig. 2). All size classes of spirlin were highly associated with each other (Table 3) except 0+ spirlin (Ap0+), which occurred less often than expected with 1+ (Ap1) and 3+ (Ap3) conspecifics. However, all generally preferred areas of elevated water velocities (Fig. 3), water depths (> 40 cm), about 1–4 m from the bank, with moderately sloped banks, the presence of backwater eddies, elevated amounts of ligneous debris and some shade (i.e. overhanging vegetation). Differences between developmental/age classes were mainly in the amount of sand, whereby low proportions (1–33%) were moderately (but non-significantly) preferred by spirlin larvae (Ap0+) in contrast to most other age classes. Spirlin larvae and juveniles (Ap0+J) also demonstrated equal or nearly equal preferences for absence of water velocity and the highest category (> 10.0 cm·s^{-1}). Spirlin were generally indifferent to gravel, whereas its presence was significantly preferred by 1+ gudgeon (Gg1), which preferred relatively shallow (30–40 cm), lentic waters with elevated amounts of ligneous debris. Indeed, gravel and ligneous structures appear to account for the separation of Gg1 and 2+ gudgeon (Gg2) from the other species/age classes, which is further emphasized by weak preferences for elevated water velocity in Gg2 and steeply-sloped banks in 3+ chub (Lc3). The weak associations between 3+ chub and younger age classes of spirlin and gudgeon could reflect a predator interaction. Adult perch (PfA) demonstrated no substratum preferences, only weak

Table 3. *Deviations from expected co-occurrence for age classes in the River Rudava (Slovakia), with significant associations (Fisher-Exact test) indicated by: *, P ≤ 0.05, **, P ≤ 0.01, ***, P ≤ 0.001 (‘o‘ indicates P ≤ 0.10). All deviations are higher than expected except for those in boxes (these were lower than expected). Fish codes given in Table 2.*

	Ap0+J	Ap1	Ap2	Ap3	Ap4	Ap5	Ap6	Gg1	Gg2	Lc3	PfA
Ap0+	***	***	$\boxed{***}$	***	$\boxed{*}$	***		***			
AP0+J	—	***	***	***	***	*		*			
Ap1		—	***	***	***	***		***			o
Ap2			—	***	***	*	*				
Ap3				—	***	***		*			o
Ap4					—	***	***				o
Ap5						—	*				
Ap6							—				*
Gg1								—			*
Gg2									—		
Lc3										—	

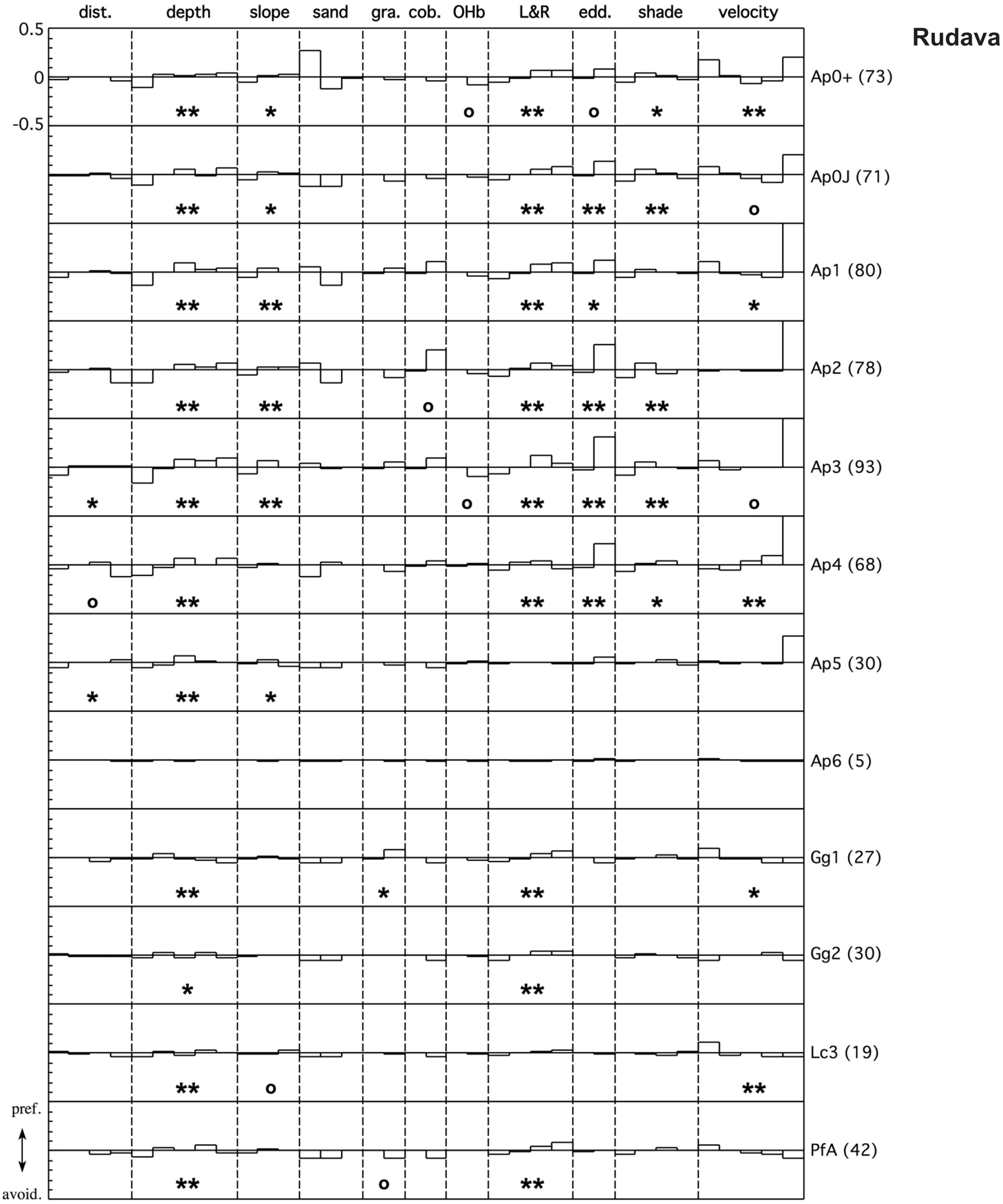

Fig. 3. *Microhabitat electivity profiles for age/size classes of fish in the River Rudava (Slovakia), with the number of samples associated with each graph given in parenthesis. See Table 2 for fish species/class codes. Variables are: dist (distance from the bank: < 1.0 m, 1.0–2.0, 2.1–3.0, ≥ 3.1 m); depth (< 30 cm, 30–40, 41–50, 51–60, ≥ 61 cm); slope (< 0.25, 0.25–0.5, > 0.5); sand (sand with silt and clay: 1–33, 34–66, > 67%); gra. (gravel: absent, present); cob. (cobble: absent, present); Ohb (overhanging vegetation and backwater: absent, present); L&R (ligneous debris and roots: absent, 1–25, 25–50, > 50%) edd. (eddies: absent, present); shade (full sun, 1–33% of point sample shaded, 34–66% of point sample shaded, ≥ 67% of point sample shaded), water velocity (0 cm·s*$^{-1}$*, 0.1–2.5, 2.51–5.00, 5.01–10.00, > 10.0 cm·s*$^{-1}$*). Negative values approaching -0.5 indicate avoidance and positive values +0.5 indicate preference, with significant deviations from expected given for P ≤ 0.10 (o), P ≤ 0.05 (*), P ≤ 0.01 (**). Note that absence of sand was not recorded at this site.*

avoidance of gravel similar to spirlin, and like most species demonstrated a strong preference for ligneous structures (Fig. 3).

In the River Turiec, water depth was the most prominent microhabitat variable, followed by water velocity, cobble and gravel substratum and bank slope, in the comprehensive CCA of all samples (Fig. 4). Unlike at Rudava, spirlin at Turiec demonstrated clear differences in microhabitat use during development, but overlap was apparent from the higher-than-expected co-occurrences between all spirlin age classes (Table 4). And although all age classes of spirlin generally preferred waters ≥ 40 cm or deeper (Fig. 5a), larvae (Ap0+) and juveniles (Ap0+J) significantly preferred lentic areas relatively close to moderately-sloped banks. Moderate amounts of ligneous debris were significantly preferred by Ap0+J. Spirlin of 1+ (Ap1), 2+ (Ap2) and 3+ (Ap3) age classes demonstrated few preferences, such as eddies in Ap1 and modest proportions of sand by Ap2. Whereas ages 4+ to 6+ (Ap4, Ap5, Ap6) demonstrated clear preferences for deep waters, moderately far from moderately-steep banks in the presence of backwater eddies with no vegetation or ligneous debris; these age classes appear to be indifferent to water velocity or at best preferring faster flowing areas (e.g. Ap4). 0+ bullhead (Cg0) demonstrated few preferences (Fig. 5b), whereas both 1+ (Cg1) and 2+ (Cg2) bullhead preferred high proportions ligneous debris, but unlike spirlin older bullhead significantly preferred high proportions of cobbles, which could explain the lower-than-expected co-occurrence between older bullheads and younger spirlin (Table 4). Whereas, the weak preference for cobble in 1+ stone loach (Nb1) and Cg0 (Fig. 5a, b) resulted in associations with older spirlin (Table 4). Age 2+ gudgeon (Gg2) preferred moderately-elevated

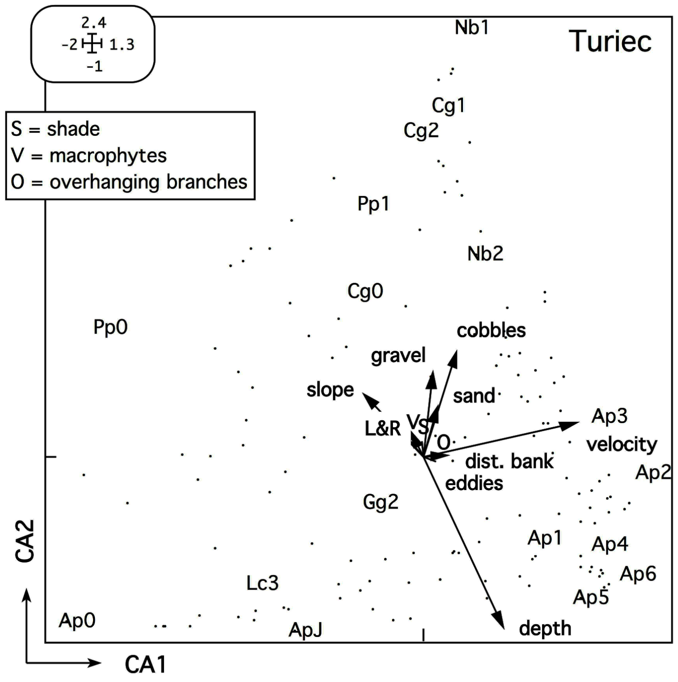

Fig. 4. *Canonical correspondence analysis (ter Braak 1986) triplot for age/size classes of fish and 12 environmental variables in the River Turiec (Slovakia). See Table 1 for dates and times, Table 2 for fish species/class codes, and Table 4 for intra- and interspecific associations.*

Table 4. *Deviations from expected co-occurrence for age classes in the River Turiec (Slovakia), with significant associations (Fisher-Exact test) indicated by: *, P ≤ 0.05, **, P ≤ 0.01, ***, P ≤ 0.001 ('o' indicates P ≤ 0.10). All deviations are higher than expected except those in a box; these were lower than expected. Fish codes given in Table 2.*

	Ap0+J	Ap1	Ap2	Ap3	Ap4	Ap5	Ap6	Cg0	Cg1	Cg2	Gg2	Lc3	Nb1	Nb2	Pp0	Pp1
Ap0+	***	***	**	***	**	***	*		$\boxed{o}$	$\boxed{o}$		**			***	***
Ap0+J	—	***	***	***	***	***	***	*	$\boxed{o}$						**	***
Ap1		—	***	***	***	***	***				o					
Ap2			—	***	***	***	*									
Ap3				—	***	***	***	**	$\boxed{*}$		o				**	***
Ap4					—	***	***	***								o
Ap5						—	***	o					o	o		
Ap6							—					*				*
Cg0								—								
Cg1									—	**			***			
Cg2										—					o	
Gg2											—					
Lc3												—				
Nb1													—			
Nb2														—		
Pp0															—	***

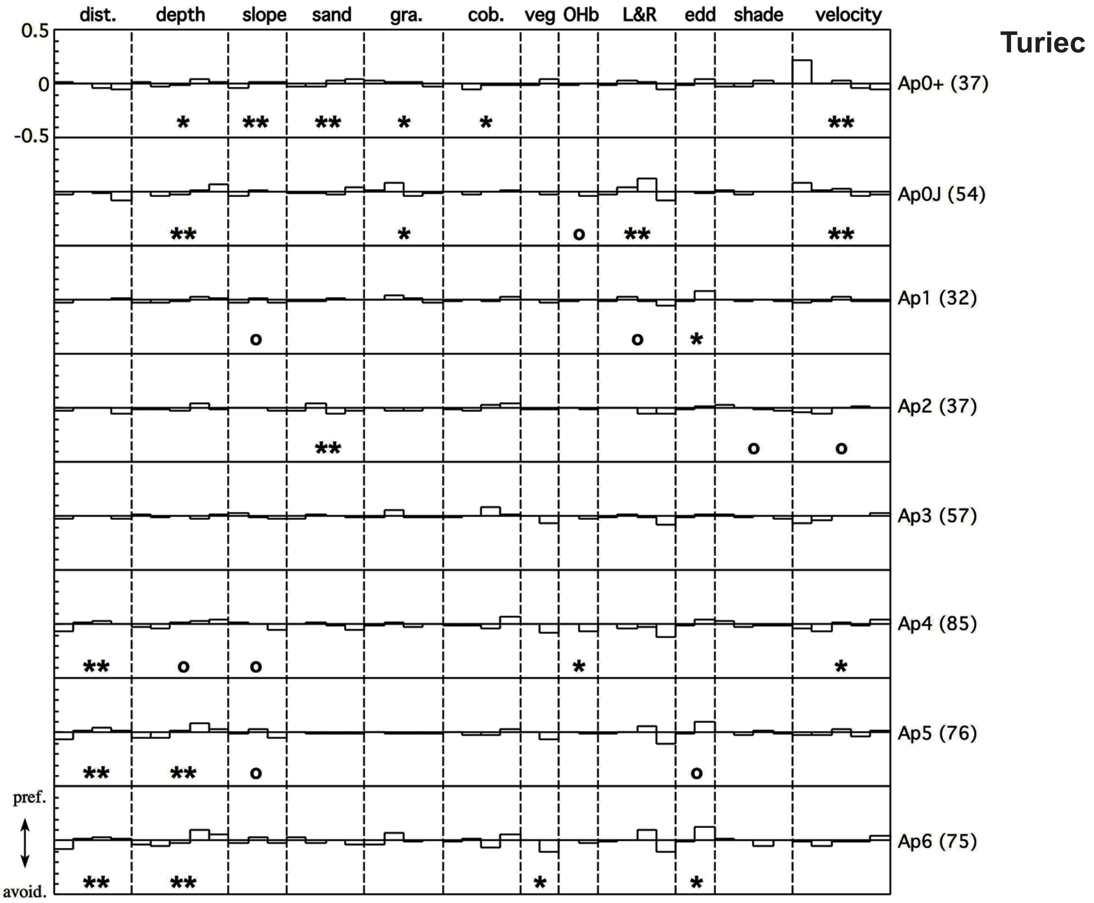

Fig. 5a. *Microhabitat electivity profiles for each size class of six species from the River Turiec (Slovakia), with the number of samples associated with each graph given in parenthesis. See Table 2 for fish species/class codes. Variables are: dist (distance from the bank: < 1.0 m, 1.0–2.0, 2.1–3.0, ≥ 3.1 m); depth (< 30 cm, 30–40, 41–50, 51–60, ≥ 61 cm); slope (< 0.25, 0.25–0.5, > 0.5); sand (sand with silt and clay: absent, 1–33, 34–66, > 67%); gra. (gravel: absent, present); cob. (cobble: absent, present); veg (macrophytes: absent, present); Ohb (overhanging vegetation and backwater: absent, present); L&R (ligneous debris and roots: absent, 1–25, 25–50, > 50%) edd. (eddies: absent, present); shade (full sun, 1–33% of point sample shaded, 34–66% of point sample shaded, ≥ 67% of point sample shaded), water velocity (0 cm·s^{-1}, 0.1–2.5, 2.51–5.00, 5.01–10.00, > 10.0 cm·s^{-1}). See Figure 3 for the electivity explanation: P ≤ 0.10 (‘o‘), P ≤ 0.05 (*), P ≤ 0.01 (**).*

proportions of sand and gravel, which resulted in weak associations with spirlin ages 1+ to 3+. The preferences of 3+ chub (Lc3) were similar to those of Cg2 except for deeper waters close to steeply-sloped banks. The similarity in microhabitat profiles for 0+ and 1+ minnows (Pp0, Pp1) and 0+ spirlin is corroborated by the highly significant associations with Ap0+ and Ap0+J (Table 4).

In the River Vlára, substratum components (sand, cobble) and water depth were the most prominent microhabitat variables, followed by water velocity, distance from bank, bank slope, and ligneous structures in the comprehensive CCA of all samples (Fig. 6). As in the other two rivers, spirlin size classes were highly associated but in this case mainly with neighbouring age classes (Table 5). As at Turiec, spirlin larvae (Ap0+) occurred less-often-than-expected with older conspecifics, which reflects differences in microhabitat use (Fig. 7a). With increasing age, spirlin preferred increasing greater distances from bank, water velocity and increasing proportions of gravel and cobbles, though the oldest age classes were showed few significant associations with substratum types. Whilst all age classes of spirlin had relatively similar preferences for water depth, older spirlin were indifferent to, or indeed avoided, aquatic vegetation, overhanging branches, and shade. Young-of-the-year spirlin (Ap0+, Ap0+J) were significantly associated

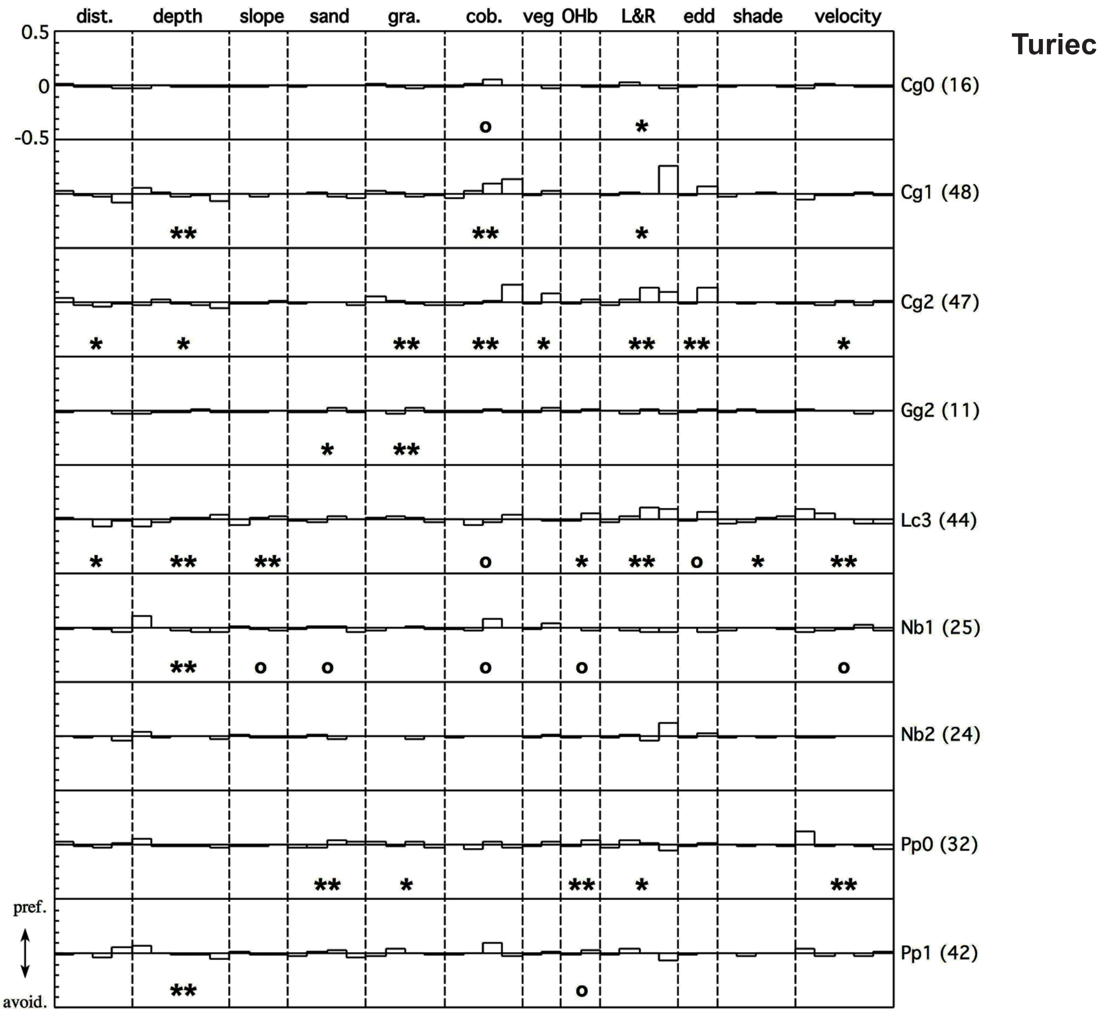

Fig. 5b. *Microhabitat electivity profiles of fish in the River Turiec (continued).*

with (Table 5), and had similar microhabitat profiles to (Fig. 7a, b), young age classes of gudgeon (Gg0), dace (Ll0), and chub (Lc1), whereas older spirlin co-exploited similar microhabitat with barbel of all age classes. The proximity of small benthic species, i.e. minnow (Pp0, Pp1), stone loach (Nb1, Nb2) and bullhead (Cg0, Cg1, Cg2), in the composite CCA (Fig. 6a) is reflected in their relatively similar microhabitat profiles (Fig. 7b) and significant co-occurrences (Table 5). Similarly, the microhabitat use of vimba (Vv1, Vv2) and chub (Lc1, Lc2) appears to overlap somewhat with that of younger spirlin but not with barbel, as is apparent in the lower-than-expected co-occurrences (Table 5).

Discussion

Slovak populations of spirlin are in the approximate latitudinal and longitudinal mid-point of their native range (Lelek 1987). The three study stretches of submontane river represent a transition in fish species composition between the so-called ‘grayling’ and ‘barbel’ zones (sensu Huet 1959), where spirlin is considered to be most abundant (Breitenstein & Kirchhofer 2000, Jurajda et al. 2007). In all three stretches, the same three habitat variables central to fish physical habitat modelling (PHABSIM; Tharme 2003), i.e. substratum character, water velocity and depth, were central features of spirlin microhabitat use (Figs. 2, 4, 6). Between spirlin of different ages, constancy in microhabitat use was observed in the River Rudava but not the rivers Turiec and Vlára (Figs. 3, 5a, 7a) and intra-specific associations (Tables 3–5). Young spirlin are said to prefer slow-flowing waters (Breitenstein & Kirchhofer 2000), as was observed in the rivers Turiec and Vlára (see also Jurajda et al. 2007). But also they have been observed to move

Table 5. *Deviations from expected co-occurrence for fish age classes in the River Vlára (Slovakia), with significant associations (Fisher-Exact test) indicated by: *, P ≤ 0.05, **, P ≤ 0.01, ***, P ≤ 0.001 ('o' indicates P ≤ 0.10). All deviations are higher than expected except for those in boxes (these were lower than expected). Fish codes given in Table 2.*

	Ap0+J	Ap1	Ap2	Ap3	Ap4	Ap5	Ap6	Bb1	Bb2	Bb3	Bb4	Cg0	Cg1	Cg2	Gg0	Gg1	Lc0	Lc1	Lc2	Lc3	Ll0	Nb1	Nb2	Pp0	Pp1	Vv1	Vv2
Ap0+	***	***				$\boxed{o}$	$\boxed{o}$								***	o		**			o						
Ap0+J	—	***	**	*											*			*		*			*	*	o		
Ap1		—	***	*														***						o			
Ap2			—	***	**	*	*			o							o		o					o			
Ap3				—	***	***	***		o	**	*									*							
Ap4					—	***	***												o					*		*	*
Ap5						—	***	***	***	***										o							
Ap6							—			*				$\boxed{*}$				$\boxed{o}$					o				
Bb1								—	***	***	***																
Bb2									—	***	***									o						$\boxed{*}$	
Bb3										—	***			$\boxed{o}$				o		*					$\boxed{*}$	$\boxed{*}$	
Bb4											—																
Cg0												—															
Cg1													—	$\boxed{o}$											**		
Cg2														—				o									
Gg0															—	**					*			o			
Gg1																—					*				*		
Lc0																	—										
Lc1																		—	**						o		
Lc2																			—	***						*	
Lc3																				—					$\boxed{*}$		*
Ll0																					—			o			
Nb1																						—	*		*		
Nb2																							—				
Pp0																								—	***		
Pp1																									—		
Vv1																										—	**

repeatedly between fast and slow water velocities (*ibidem*), which could explain the contrasting microhabitat associations in 0+ spirlin in Rudava, fluctuating between a preference for slow and for fast flowing waters. Nonetheless, a shift in velocity preference towards faster-flowing waters appears to be characteristic of early development in spirlin, coinciding with shifts in body morphology (Kováč et al. 2006). Similar shifts to more elevated water velocities were also observed in gudgeon, minnow, and chub, which were each significantly associated with young spirlin in at least one river (Tables 3–5; see also Jurajda et al. 2007).

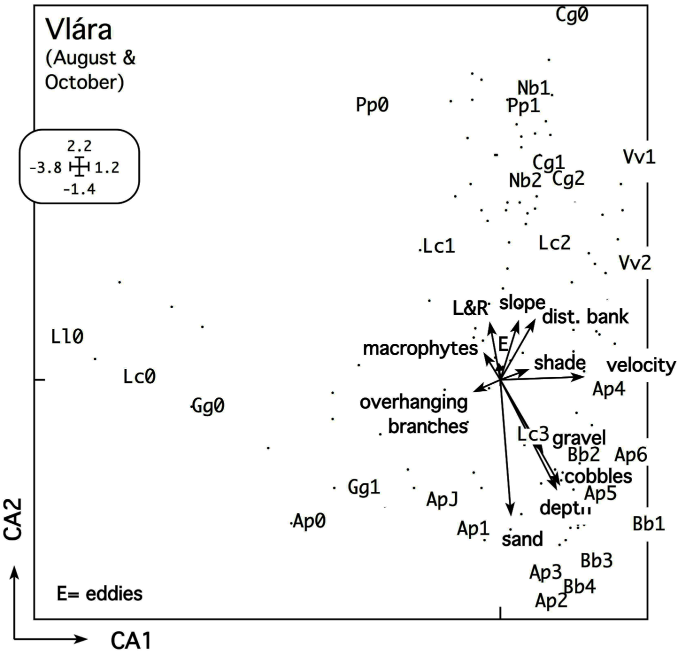

Fig. 6. *Canonical correspondence analysis (ter Braak 1986) triplot for age/size classes of fish and 12 environmental variables in the River Vlára (Slovakia). See Table 1 for dates and times, Table 2 for fish species/class codes, and Table 5 for intra- and interspecific associations.*

Preferences for deeper waters tended to increase with age in spirlin (Figs. 3, 5a, 7a), with position (depth) in the water column increasing with increasing size (Hofer 1911, Saladin 1998), though these lower layers may be occupied by chub and brown trout when present (Kainz & Gollmann 1990). This shift to deeper waters was also observed in gudgeon (Figs. 3, 7a) and barbel (Fig. 7b). Microhabitat preferences for substratum in spirlin were less uniform, with affinities ranging from indifference to strong preference (Figs. 3, 5a, 7a). This corroborates previous reports in the literature, which state preferences for sand, cobbles, pebbles, and even large stones of re-enforced banks (see Breitenstein & Kirchhofer 2000, Erős et al. 2008). Of particular importance to young-of-the-year spirlin are lentic zones with some sort of ligneous debris (Figs. 3, 5a, 7a), but stagnant areas with signs of eutrophication (e.g. dense mats of algae) are avoided (Saladin 1998).

Dead branches or fallen trees have been identified as particularly important to spirlin distribution (Kirchhofer 1995, Saladin 1998), and preferences for ligneous debris were apparent in two of the rivers studies (Figs. 3, 5a). Areas with ligneous debris are often lentic, and spirlin appears to share these microhabitats with gudgeon and minnow (Tables 4, 5), which demonstrate similar preferences (Figs. 3, 5b, 7b). The removal of in-stream ligneous structure can result in reductions in biomass and thus changes in the size structure of stream fish assemblages (e.g. Copp & Bennetts 1996).

In-stream vegetation, however, is thought to be of little importance to spirlin (Breitenstein & Kirchhofer 2000), which has been reported to avoid aquatic vegetation (e.g. Lelek & Buhse 1992). This was, at best, partially supported by our results (Figs. 3, 5a): aquatic vegetation was virtually non-existent in the River Rudava; spirlin in the River Turiec were generally indifferent to aquatic vegetation, switching from non-significant mild preference as larvae to non-significant mild avoidance until Age 6+, when this avoidance was significant (Fig. 5a); whereas, spirlin in the River Vlára demonstrated definite preferences for the presence of vegetation up to Age 1 (Fig. 7a). The fact that the River Vlára was the only location of the three that was sampled twice on the same day suggests that repeated sampling of a site at different times of day may provide a more accurate picture of fish microhabitat requirements. This has been demonstrated in other studies of other stream-dwelling fishes (e.g. Johnson & Covich 2000, Copp et al. 2005, Copp 2008).

In conclusion, the data suggest that spirlin in these three Slovak water courses are numerically abundant and the population size distributions are similar to those reported elsewhere (e.g. Johal 1979, Soric & Ilic 1985). The graphical illustration of preferred microhabitat can aid managers in identifying the types of microhabitat required by the species (Figs. 3, 5, 7). Spirlin is believed to be sensitive to changes in water quality and in-stream character (see Breitenstein & Kirchhofer 2000, Valová et al. 2006), so any future management of these rivers should emphasize the enhancement of the existing situation, in particular the restoration of natural, heterogeneous channel character in parts of the water course that have previously undergone regulation

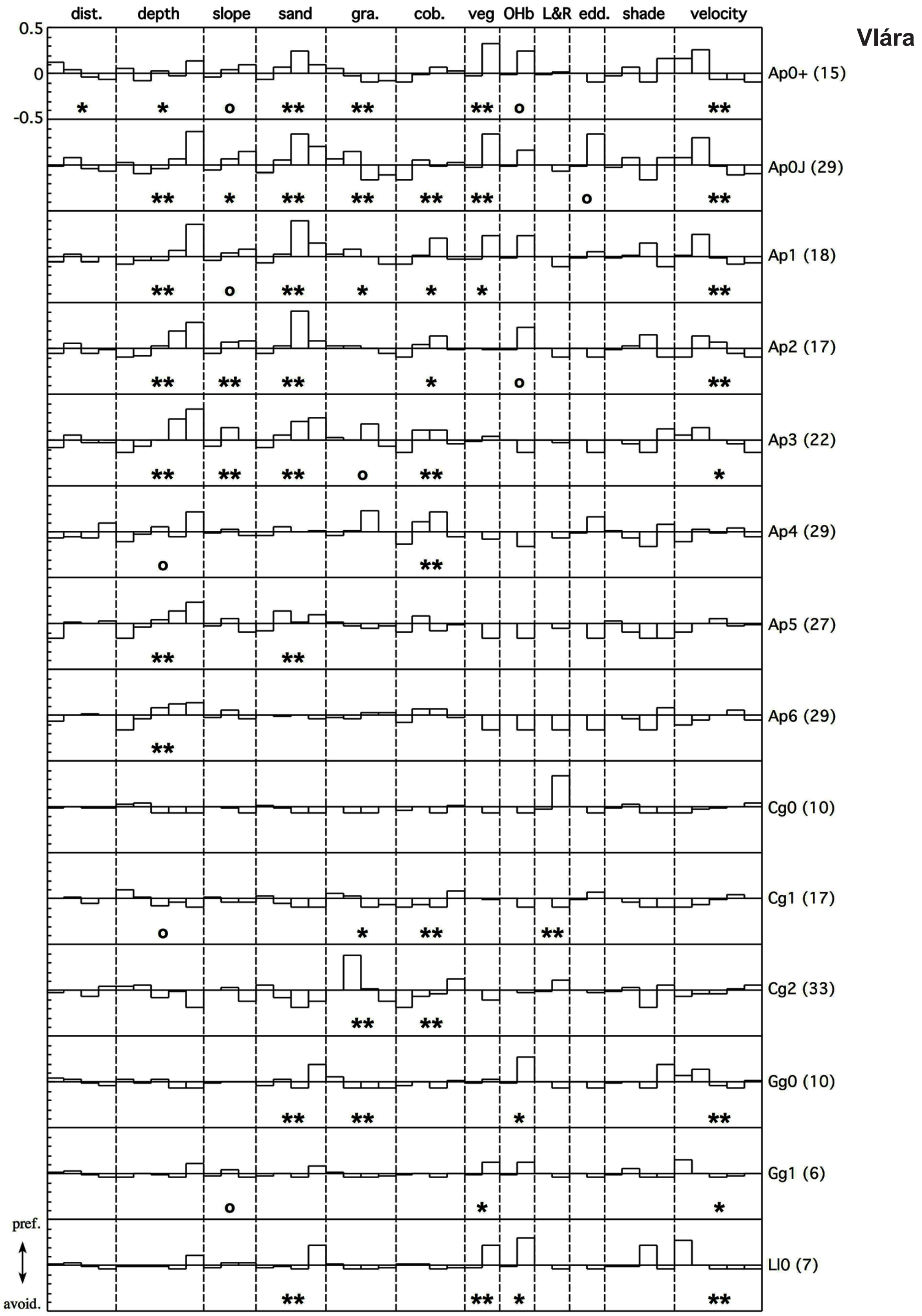

Fig. 7a. *Microhabitat electivity profiles for each size class of age/size classes of fish in the River Vlára (Slovakia), with the number of samples associated with each graph given in parenthesis. See Table 2 for fish species/class codes. Variables are: dist (distance from the bank: < 1.0 m, 1.0–2.0, 2.1–3.0, ≥ 3.1 m); depth (< 30 cm, 30–40, 41–50, 51–60, ≥ 61 cm); slope (< 0.25, 0.25–0.5, > 0.5); sand (sand with silt and clay: absent, 1–33, 34–66, > 67%); gra. (gravel: absent, present); cob. (cobble: absent, present); veg (macrophytes: absent, present); Ohb (overhanging vegetation and backwater: absent, present); L&R (ligneous debris and roots: absent, 1–25,*

25–50, > 50%) edd. (eddies: absent, present); shade (full sun, 1–33% of point sample shaded, 34–66% of point sample shaded, ≥ 67% of point sample shaded), water velocity (0 cm·s^{-1}, 0.1–2.5, 2.51–5.00, 5.01–10.00, > 10.0 cm·s^{-1}). See Figure 3 for the electivity explanation: P ≤ 0.10 (‘o‘), P ≤ 0.05 (*), P ≤ 0.01 (**).

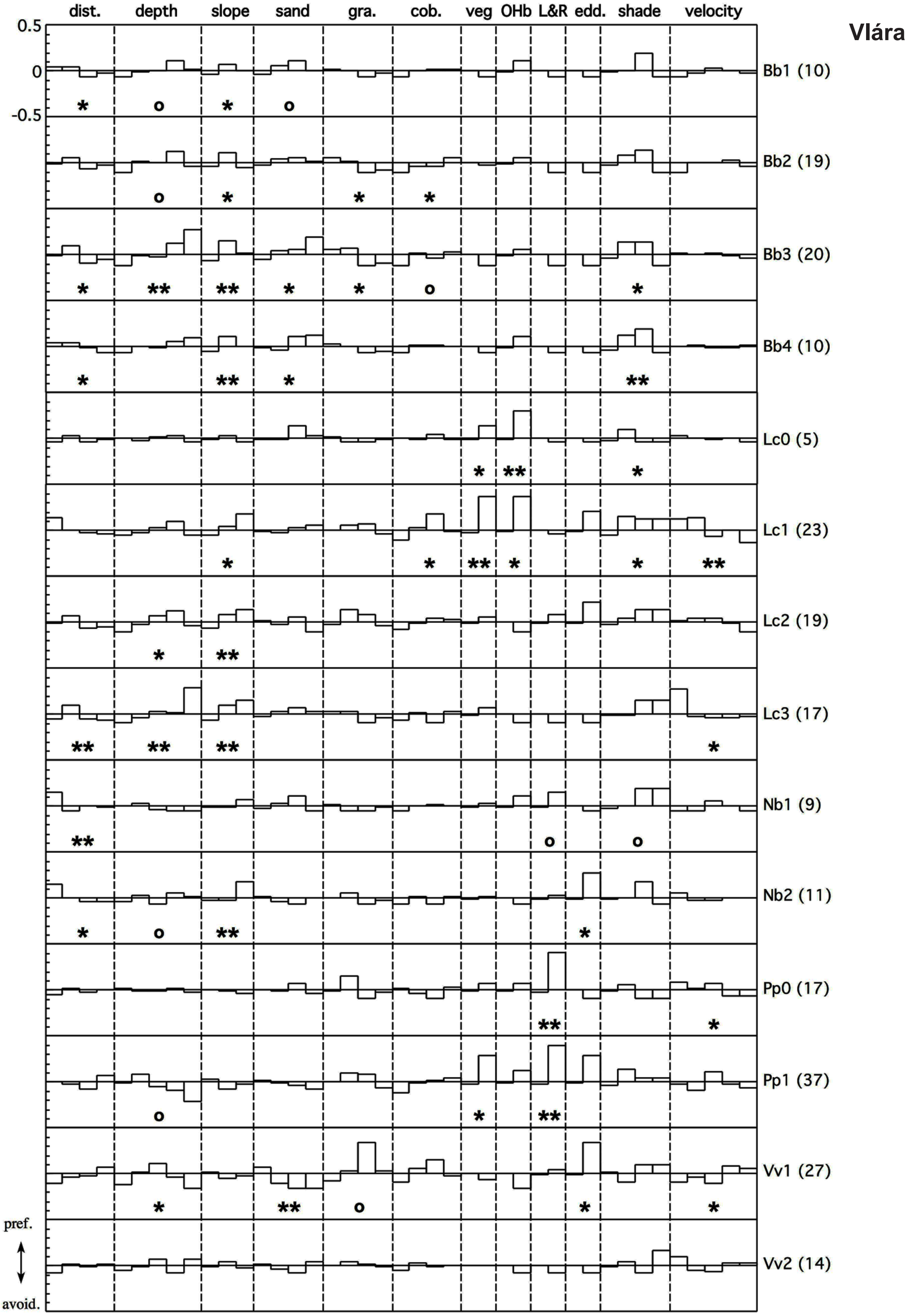

Fig. 7b. *Microhabitat electivity profiles of fish in the River Vlára (continued).*

(straightening, channelization, etc.). Keeping in mind that river rehabilitation initiatives are not necessarily guaranteed to result in enhanced fish species richness (Pretty et al. 2003), the potential benefits for spirlin and associated fish species should be investigated in areas of its current range, both in rivers where the species is threatened, and in those where the species' stocks appear to be doing well but could be enhanced (e.g. the rivers presented here). In light of the species' association with stream types that are inhabited by other fish species threatened at the European level (bullhead, spined loach, Ukrainian brook lamprey, burbot), the spirlin should be considered for inclusion in any future revision of Annex II of the European Commission's Habitats and Species Directive (92/43/EEC (1) of 21 May 1992).

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