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Comparative microhabitat use of cyprinid larvae and juveniles in a lotic floodplain channel

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Synopsis

The microhabitat of six cyprinids in a braided side-channel of the Upper Rhône River, France, was studied June to September 1985, using 'point abundance sampling' by electrofishing. Correspondence analysis of the samples-by-species data and Jacob's electivity index (calculated from the availability and exploitation of eight environmental variables) revealed three groups of species: (1) *Leuciscus cephalus* and *Alburnus alburnus*, which used relatively similar microhabitat during both larval and 0 + juvenile development; (2) *Rutilus rutilus*, *Leuciscus leuciscus* and *Chondrostoma nasus*, which used different microhabitats as larvae but whose microhabitat overlapped notably during 0 + juvenile development; (3) and *Gobio gobio*, whose juvenile microhabitat overlapped only marginally with that of other 0 + juveniles (no data were available on larvae). Overlap in microhabitat use by 0 + juveniles increased notably during a period of reduced discharge, when the amount of available vegetal and ligneous structures decreased; while most species exploited the increased area of shallow waters, juvenile *A. alburnus* appeared to be the only species that exploited the deeper waters off the channel's steeper banks. Although not quantified, numerous field observations of predation threat, particularly during the period of reduced discharge (which reduced the amount of cover), suggest that predation risk may influence the microhabitat use of young fishes. Compared with similar species in European lakes, the overlap in microhabitat use of these fluvial cyprinids appears to be more intensive.

> Individuals of different sizes in size-structured populations often differ greatly in the use of resources and/or space... The presence or absence of such diet or habitat segregation between different size classes can greatly affect population structure and dynamics.
>
> Gilliam & Fraser (1988)

Introduction

Microhabitat use is an important aspect in the life history of fluvial fishes, particularly during early ontogeny, when relatively small body size and restricted motility render young fishes susceptible to environmental hazards such as elevated water velocities (Lightfoot & Jones 1979, Heggenes 1988) and predation (Baltz et al. 1982, Cerri & Fraser 1983, Power & Matthews 1983, Scott 1987, Rozas & Odum 1988, Robinson 1989). It is therefore suprising that most accounts of microhabitat use by cyprinid larvae and early juveniles in European rivers have been incidental to studies of growth or diet (e.g. Stankovitch 1921, Brown 1979, Carrel 1986, Scott 1987, Haberlehner 1988). The few investigations directly concerned with the microhabitat use of fish larvae and juveniles in medium-to-large European rivers have either been limited to one species (Lightfoot & Jones 1979, Copp 1990a) or addressed but one or a few environmental variables (Schröder 1979, Schiemer & Spindler 1989).

In European lakes, the repartition of spatial resources by young cyprinids is facilitated by offshore migrations in 0 + juvenile roach *Rutilus rutilus* (L.), and the vertical segregation of other species, e.g. *Leuciscus cephalus* (L.) and *Scardinius erythrophthalmus* (L.), and their sub-cohorts (Hammer 1985, Mark et al. 1987, Rheinberger et al. 1987). In smaller rivers, *R. rutilus* and dace *Leuciscus leuciscus* (L.) of a few months age are reported to move from backwaters into lotic areas of the channel (Scott 1987), though Lightfoot & Jones (1979) found *R. rutilus* to be closely associated with macrophyte beds, which considerably reduced water velocities therein. By contrast, in a relatively wider side channel of a large river, *R. rutilus* larvae and juveniles were found to avoid water currents and preferred the shallow lentic waters of weakly sloped banks (Copp 1990a). To understand the dynamics of such differences in microhabitat use by different species of fish larvae and juveniles, comparative studies of habitat segregation/co-exploitation are essential. Thus, in the present study I compare the microhabitat use of cyprinid larvae and juveniles in a braided side-channel of the Upper Rhône River, a comparison that examines the temporal and spatial dynamics, as well as the preference for, or avoidance of, eight environmental variables by *R. rutilus, L. cephalus, L. leuciscus,* nase *Chondrostoma nasus* (L.), bleak *Alburnus alburnus* (L.) and gudgeon *Gobio gobio* (L.) during their larval and early juvenile (0+) development.

Methods and materials

The cyprinid larvae and juveniles were sampled once a week (in daylight) from early June to mid September 1985, then once again in late September (15 excursions in total), in a side-channel of the Brégnier-Brangues flood plain (Upper Rhône River, France) colloquially known as the 'Lône d'llon', henceforth referred to as 'llon' (Copp & Peňáz 1988). This side-channel, which is of braided geomorphological origin (see Petts & Foster 1985), has a surface area of about 6 ha and lies within a flood plain that was in the process of being by-passed by a hydroelectric development under construction during the study year. Just upstream of this flood plain, the Upper Rhône has a mean summer discharge of $\approx 700\,\mathrm{m^3\,s^{-1}}$, whereas the by-passed flood plain receives $\approx 150\,\mathrm{m^3\,s^{-1}}$ (Copp & Peňáz 1988). Ilon is approximately 40 m across at its downstream confluence with the main river and about 60 m across at its upstream end. The water temperature at Ilon fluctuated between 15 and 19° C in June 1985, remained at about 15° C through late June and early July, rose progressively to about 20° C through July until mid-August, then fluctuated between 15 and 21° C until the end of the study. The water conductivity generally fluctuated between 250 and 350 μS (Copp 1990a).

A wing dam had been constructed at Ilon's upstream end to deflect the main river's flow. This structure accentuated aggradation of Ilon's upstream end, forming an alluvial plug that in turn created a range of conditions, depending upon river discharge. Colonisation of the alluvial plug by pioneer vegetation had helped establish an island a few metres behind the wing dam. This island was separated from the channel's right (convex) bank by a 20 to 30 m wide riffle bed and a small, slightly deeper gully (≈ 0.75 m) through which water could pass during slightly reduced discharge (overall river $\approx 500\,\mathrm{m^3\,s^{-1}}$). The island was separated from the wing dam and the left (concave) bank by a relatively deep gully (≈ 1.5 m), through which water passed continuously except during extremely reduced river discharge (overall river $\approx 350\,m^3\,s^{-1}$, by-passed flood plain minimum $\approx 120\,m^3\,s^{-1}$). Downstream of the alluvial plug, the weakly-sloped convex right bank was composed of gravel changing progressively downstream to sand and silt deposits, the bank became muddier and steeper as the channel approached its downstream confluence with the river's main channel. In contrast, because of scour action, the concave left bank remained steep throughout its length, was composed of mud/silt and exposed rock embankment, and possessed a number of dead and living branches/trees lying at, or submerged below, water level.

During elevated discharge ($>700\,m^3\,s^{-1}$), the right bank of alluvial plug became a riffle bed, with some lentic zones behind the island, behind the wing dam where it joins the left bank, and along the periphery of the convex right bank. During mean discharge, weak-to-moderate current velocities were limited to the gullies on either side of the mid-channel island. As scouring action and alluvial deposition still occurred during elevated discharge, aquatic vegetation was generally confined to the margin of the right bank and almost entirely around the mid-channel island. During extremely reduced discharge, such as occurred for about three weeks between mid-August and early September 1985, the upstream end was almost completely isolated from the main river, rendering the channel almost entirely lentic and exposing vast shallows along the right bank, opposite the long, deep gully of the concave left bank. During this period of extremely reduced discharge, the available aquatic vegetation and ligneous debris was limited to some areas on the island's periphery and to the more downstream sections of either bank of the channel.

Sampling by a two-person crew from a rubber boat was undertaken using a battery-powered, portable electrofisher equipped with a 10 cm anode for greater efficiency with fish larvae and juveniles (Copp 1989b). The samples were collected according to the 'point abundance sampling' strategy, originally described by Blondel et al. (1970) for nesting birds, adapted for adult fishes by H. Persat (Nelva et al. 1979) and for fish larvae and juveniles by Copp & Peňáz (1988). Similar sampling approaches have been applied to microhabitat studies elsewhere (Baltz et al. 1982, Bain et al. 1985, Moyle & Baltz 1985). Selection of the 25 weekly sampling points was made with a random point of the index finger (eyes closed), a valid alternative to computer-generated coordinates (D. Chessel personal communication), which would be virtually impossible to locate in the field. The anode's effective field, i.e. the sample area, was measured as $\approx 0.07\,m^2$ (Copp 1989b). Although 25 point samples were anticipated for each week, the number of samples on 12 June was limited to 15 because of equipment failure, thus a total of 365 point samples were collected over the study period (i.e. 14 × 25, plus 15).

At each sampling point, the fishes collected were preserved in 4% formaldehyde, after which microhabitat availability and use were evaluated via qualitative and quantitative measurements of eight environmental variables: situation (channel, weak bank, steeper bank), water depth (<0.2, 0.2–0.5, 0.5–1.0, >1.0 m), water current (absent, weak, strong), substratum (mineral/silty mud [<0.06 cm], silty sand [0.06–0.2 cm], silted gravel [0.2–2.0 cm], silted rocks [2–20 cm], indeterminable), water surface illumination (sun, mixed, shade, overcast), ligneous debris (absent, some, dense), macrophytes (absent, some, dense) and periphyton (absent, attached, detached). Water depth was measured with a graduated dip-net pole. Water current was evaluated using a small dip net with flexible 0.5 mm mesh netting; upon immersion of the hand net, no ballooning of the dip net was noted as current absent, gentle ballooning indicated a weak water velocity and rapid ballooning of the net represented a strong current. Because rapid water velocities were rarely encountered (less than 10 points from 365 points), water current is considered here as either absent or present. Similarly, dense vegetation rarely occurred and therefore macrophytes are also considered as either present or absent. Water surface illumination was evaluated as indicated above to test the common assumption that freshwater fish larvae prefer sunny locations to shaded areas.

In the laboratory, the cyprinids were identified according to Koblickaya (1981), measured using an observation microscope fitted with a calibrated micrometer lens, and categorised in three intervals with respect to crucial events in their larval and 0 + juvenile development (E.K. Balon personal communication): young larvae, first feeding to differentiation of the finfold; older larvae, differentiation of the finfold to transition to the juvenile period; and the juvenile period (as defined by Balon 1985).

The data were arranged in three matrices. Firstly, a 'fish-by-attribute' matrix (1365 × 3) contained the sample number, the developmental interval (young larvae, older larvae, juvenile) and standard length in mm of each specimen collected. From this matrix the mean standard length and associated statistics were calculated. Secondly, a 'samples-by-species' matrix (365 × 16) contained the number of young larvae, older larvae and 0+ juveniles of each species found at each sampling point. This matrix was reduced to non-null samples only (i.e. 115 × 16), used to calculate the index of dispersion (division of the variance by the mean), and then was submitted to 'correspondence analysis' (Benzecri 1969) using the multivariate package 'Macmul' (Thioulouse 1989). Correspondence analysis is particularly suitable for revealing patterns in fractional data sets, i.e. those comprised of partial or incomplete histograms (Persat & Chessel 1989), such as in the present case. Thirdly, a 'samples-by-variables' matrix (365 × 10) contained the various classes of the eight environmental variables recorded at each sampling point. Proper evaluation of microhabitat availability and use requires not only an unbiased, a priori sampling strategy (Bain & Finn 1990) but also a comprehensive interpretative tool. Thus, from the original 'samples-by-species' and the 'samples-by-variables' matrices, microhabitat preferences were calculated using Jacobs' (1974) improved version of Ivlev's electivity index:

$$D = \frac{r - p}{(r + p) - 2rp},$$

where r is the proportion of the resources used by each species (interval) and p is the proportion available in the environment. When calculating p, only weeks containing a given species interval (i.e. young larvae, older larvae, juveniles) were included. To evaluate the effect of reduced discharge on the microhabitat use of 0 + juveniles, electivities for this development interval were calculated separately for the period of mean discharge and for reduced flow. As in Bain et al. (1985), use of an *a priori* sampling strategy (e.g. 'point abundance sampling') incorporates microhabitat availability into the data through the collection of randomly-selected sampling points.

Results

Of the 365 point samples taken, 115 contained at least one of the six cyprinids addressed in the present study: *C. nasus, L. leuciscus, L. cephalus, A. alburnus, R. rutilus* and *G. gobio.* Of these, 686 were larvae and 679 were 0 + juveniles, of which the latter were generally found to be more dispersed among the samples than the former (Table 1). Only one *G. gobio* larva was collected, but the juvenile gudgeon demonstrated the highest degree of clumping. Two other cyprinids, common bream *Abramis brama* (L.) and silver bream *Blicca bjoerkna* (L.), were collected sporadically and in very low numbers. Throughout most of the summer of 1985, but particularly during the period of extremely reduced discharge, shoals of 0 + cyprinids were often observed rushing up into the shallow areas when threatened by a predator, usually observed to be perch *Perca fluviatilis* L.

Relevant axes from the 'correspondence analysis' of the reduced 'samples-by-species' matrix (115 × 16) were selected graphically (Fig. 1A), as described by Persat & Chessel (1989), who stated that 'in most cases we can graphically identify a rupture between two groups of values [dotted lines in Fig. 1A]. The first group of values corresponds to the structured part of the matrix [the initial four in the present case, Fig. 1A], and the second group, which constitutes the weakly decreasing values, indicates the ensemble of individual variations among the [species] and the samples' (my translation). Interpretation of the resulting ordinations from the 'correspondence analysis' (Figs. 1B, C) was facilitated using inertia analysis of the initial four axes (Table 2, programme by Thioulouse 1989), which cumulatively accounted for 43% of the variance, as well as the information on microhabitat electivites (Fig. 2, 3). Three groups of species were identified: (1) *L. cephalus* and *A. alburnus,* which used similar but apparently adjacent (i.e. overlapping) microhabitat during both larval and 0 + juvenile development; (2) *R. rutilus, L. leuciscus* and *C. nasus,* which used different microhabitats as larvae but whose microhabitats overlapped more notably during 0 + juvenile development, particularly during the three-week period of reduced river discharge; (3) and *G. gobio,* whose juvenile microhabitat overlapped only marginally with that of other 0 + juveniles (no data were available during larval development).

Despite the earlier appearance of the lithophilic (sensu Balon 1985) *L. leuciscus* and *C. nasus,* microhabitat co-exploitation by these species and the phyto-lithophilic *R. rutilus* was suggested by the proximity of the larvae in the ordination of axes one and two of the 'correspondence analysis' (Fig. 1B), overlap that could have been facilitated by the protracted spawning demonstrated in all three species (Table 1). However, spatial differences in microhabitat use of these three species were apparent from their respective electivities (white bars, Fig. 2), differences accounted for in the ordination of axes 3 and 4 (Fig. 1C). Although both young and older larvae of *R. rutilus* and *L. leuciscus* (Rr1 &

Table 1. Samples and specimen statistics for young larvae (exogenous feeding to finfold differentiation), older larvae (finfold differentiation to juvenile metamorphosis) and 0 + juvenile cyprinids (see Balon 1985) collected in the braided channel 'Ilon' during summer 1985, with the period of presence (dates) given in day/month. For samples, the number (n) of individuals from each species interval, the number of points (f) in which they occurred, the mean number and standard error (S.E.) of individuals in the 365 samples, and their index of dispersion (variance divided by mean) are given. For specimens, the mean standard length (mean SL) in mm, the standard error (S.E.) and range of lengths are given.

Species/interval	Dates	Samples					Specimens		
		n	f	mean	S.E.	I.D.	mean SL	S.E.	range(mm)
C. nasus									
young larvae	5/6–18/6	16	4	0.14	0.11	10.71	12.9	0.2	11.8–14.8
older larvae	12/6–16/7	13	6	0.11	0.05	2.29	16.4	0.4	14.6–18.8
juveniles	from 16/7	68	20	0.59	0.22	9.70	27.7	0.7	19.6–45.3
L. leuciscus									
young larvae	12/6–24.6	40	8	0.35	0.15	6.91	12.1	0.3	7.6–15.6
older larvae	12/6–16.7	74	8	0.63	0.38	25.83	15.0	0.2	10.5–18.3
juveniles	from 16/7	24	11	0.17	0.06	2.04	40.1	2.9	16.5–75.2
A. alburnus									
young larvae	22/7– 5/8	16	3	0.14	0.11	10.84	8.4	0.2	6.6–10.0
older larvae	22/7–27/8	58	5	0.51	0.34	25.52	10.4	0.1	9.4–14.0
juveniles	from 16/7	31	8	0.28	0.14	8.30	22.5	1.1	14.8–36.1
L. cephalus									
young larvae	5/6– 5/8	38	12	0.37	0.17	9.24	11.5	0.3	8.1–14.7
older larvae	5/6–27/8	60	15	0.52	0.18	7.20	12.2	0.2	9.9–17.1
juveniles	from 5/8	30	12	0.26	0.11	4.85	25.7	2.0	14.6–56.1
Rutilus rutilus									
young larvae	24/6–12/8	82	18	0.68	0.29	13.91	9.9	0.2	6.9–13.8
older larvea	18/6– 5/8	275	27	2.53	0.88	35.22	14.3	0.1	10.4–20.3
juveniles	from 16/7	342	53	3.09	0.49	8.90	25.3	0.3	13.7–39.1
Gobio gobio									
juveniles	from 5/8	184	12	1.61	0.91	59.03	23.8	0.3	16.0–40.2

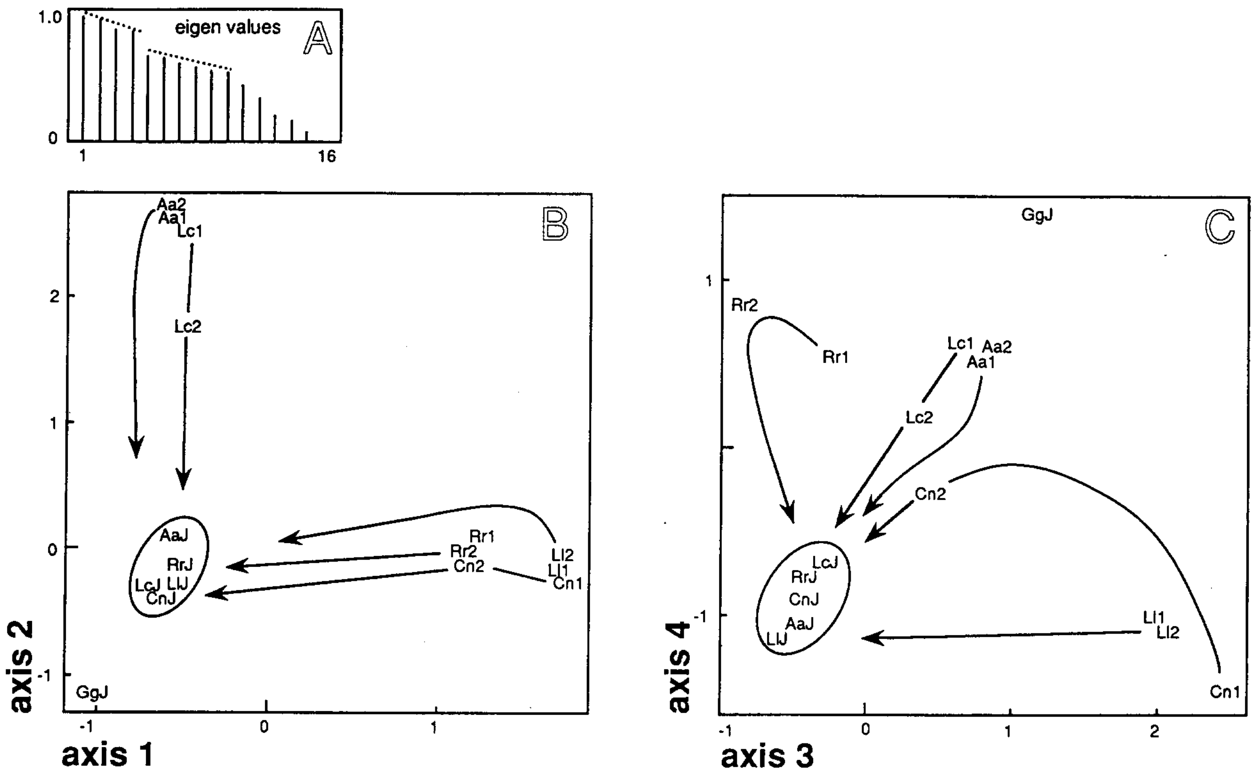

Fig. 1. 'Correspondence analysis' of the 'samples-by-species' matrix (115 × 16). A - Graphical selection of relevant eigen values, four in this case, by identification of the rupture in decreasing values as described by Persat & Chessel (1989). B - Ordination of axes one and two, C - ordination of axes two and three, revealing three groups of species: (1) *R. rutilus* (Rr), *C. nasus* (Cn) and *L. leuciscus* (Ll), which have little larval co-exploitation of spatial resources (suffixes: 1 = young larvae, 2 = older larvae), but more as juveniles (suffix: J = 0 + juveniles); (2) *A. alburnus* (Aa) and *L. cephalus* (Lc), which demonstrate overlap during both larval and juvenile development; (3) *G. gobio* (Gg.), which maintained some spatial distinction from other juveniles but for which no data on larvae were available.

Rr2, Ll1 & Ll2 respectively in Fig. 1) preferred lentic waters over weakly sloped banks of mineral/silty mud or silty sand (Fig. 2), the young *L. leuciscus* larvae inhabited a range of water depths, as did the young *C. nasus* (Cn1), and demonstrated a preference for macrophytes and attached periphyton (D = + 0.8), but avoided ligneous debris (e.g. branches and areas without periphyton (D = − 1.0). In contrast, young *R. rutilus* larvae preferred waters of 0.5–1.0 m deep with dense debris and/or macrophytes. The young *C. nasus* larvae also preferred dense debris but differed from both *R. rutilus* and *L. leuciscus* in its avoidance of macrophytes and periphyton (D = − 1.0 for presence, D = + 0.6 in absence) as well as its preference for the silted gravel bottoms of the channel (Fig. 2). Young larvae of all three species demonstrated little preference for directly illuminated (i.e. sunny) waters (D = 0 to + 0.3).

As older larvae (black bars, Fig. 2), *R. rutilus* (Rr2 in Fig. 1) moved into the moderate deep waters (0.2–0.5 m) preferred by *L. leuciscus* larvae (both Ll1 & Ll2), but *R. rutilus* exploited areas of mineral/silty mud with detached periphyton (D = + 0.6 in presence, D = − 1.0 in absence) and macrophytes, whereas *L. leuciscus* preferred silted gravel with attached periphyton (D = + 0.8 in presence, D = − 1.0 in absence) and no aquatic vegetation. The older *C. nasus* larvae (Cn2) also moved to shallower waters (< 0.2 m) but rather than over weak banks they preferred the steeper banks of mineral/silty mud without periphyton (D = − 1.0 for presence, D = + 0.5 in absence) though with some ligneous debris and macrophytes

(Fig. 2). Preference in all three species for sun illuminated areas increased only marginally (D values of + 0.3 to + 0.6), with only older *R. rutilus* larvae avoiding shaded waters (D = − 1.0).

Despite a seven-week difference (Table 1) in the appearance of *L. cephalus* larvae (Lc1, Lc2) and *A. alburnus* larvae (Aa1, Aa2), protracted spawning in *L. cephalus* resulted in similar microhabitat use by these two phyto-lithophilic species during larval development, which is evident in both ordinations of the 'correspondence analysis' (Fig. 1). The microhabitat electivities of *A. alburnus* and *L. cephalus* larvae (both young and older) were essentially the same: lentic waters of 0.2–0.5 m depth over silted gravel with macrophytes and some ligneous debris (Fig. 2). Both species avoided waters shaded from the sun (D = 1.0), but only *A. alburnus* demonstrated a preference for directly illuminated waters (D = 0.6 and 0.7). Because the sixteen specimens of young *A. alburnus* larvae occurred in only three samples (Table 1), but concurrently with *L. cephalus*, their apparent preference for steeper banks and sunny areas should be considered tentative.

After completion of juvenile metamorphosis, the cyprinids demonstrated notable spatial overlap (Fig. 1), with only the immigrating *G. gobio* (GgJ in Figs. 1B & 1C) showing notable segregation. With the near absence of *G. gobio* larvae during the entire summer, I assume that they migrated in from upstream, a phenomen observed elsewhere on the Upper Rhône (Copp & Cellot 1988). With respect to microhabitat electivities of juveniles during normal discharge (white bars, Fig. 3), most species preferred lentic, shallow waters (< 0.2 m in all but *R. rutilus*, which preferred 0.2–0.5 m deep) over miniral/silty mud or silted gravel. However, while *C. nasus* and *L. leuciscus* demonstrated some preference for areas with macrophytes, both *L. cephalus* and *R. rutilus* avoided these and showed some preference for ligneous debris, which was avoided by *C. nasus*, *L. leuciscus* and *A. alburnus*

Table 2. Inertia analysis (programme by Thioulouse 1989) establishing the absolute and relative inertia (from 10 000), i.e. contribution, of each species interval to the first four axes of the 'correspondence analysis' (Fig. 1). Major contributors for each axis are underlined.

Species	axis 1		axis 2		axis 3		axis 4	
	absolute	relative	absolute	relative	absolute	relative	absolute	relative
C. nasus								
young larvae	344	560	11	17	763	1104	318	451
older larvae	121	289	4	9	13	27	12	25
juveniles	263	481	115	202	152	248	539	860
L. leuciscus								
young larvae	838	2067	18	42	1233	2709	388	835
older larvae	1504	2481	37	58	2442	3587	832	1198
juveniles	77	289	21	77	66	223	228	753
A. alburnus								
young larvae	53	261	859	4045	62	272	38	165
older larvae	199	334	3293	5280	243	362	151	220
juveniles	100	159	0	1	89	126	356	494
L. cephalus								
young larvae	97	156	1990	3053	112	159	121	169
older larvae	141	278	1347	2542	38	67	9	16
juveniles	139	245	32	55	36	56	175	271
R. rutilus								
young larvae	836	1293	0	0	55	76	167	226
older larvae	2557	3721	16	23	2148	2782	1639	2081
juveniles	962	1706	108	184	776	1224	2099	3247
G. gobio								
juveniles	1769	2216	2148	2579	1773	1977	2926	3199

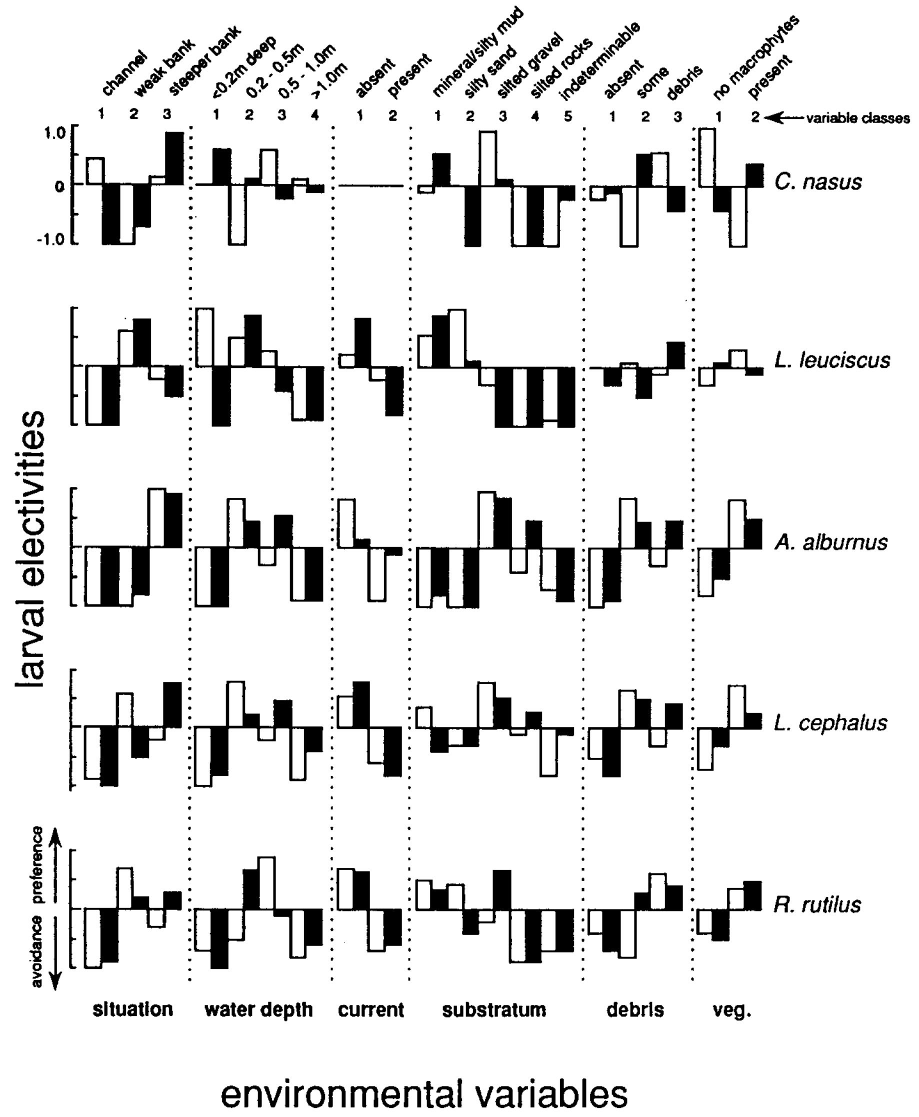

Fig. 2. Electivity index D from Jacob's (1974) formula for cyprinid young larvae and older lavae in Ilon during 1985. The white bars correspond to young larvae (suffix '1' in Fig. 1B, C), and black bars to older larvae (suffix '2' in Fig. 1B, C).

(Fig. 3). Only *A. alburnus* juveniles demonstrated any preference for directly illuminated waters (D = + 0.8), and little or no preference for attached or detached periphyton was evident (D values of − 1.0 to 0.4); in fact, both *L. cephalus* and *A. alburnus* juveniles demonstrated an avoidance of periphyton areas (D = 1.0 in absence, D = − 1.0 in presence).

During reduced discharge, most species modified their microhabitat to some extent (black bars, Fig. 3) except the *G. gobio*, whose continued inhabitation of shallow weak banks (Fig. 3) was reflected in a moderate preference for illuminated waters (D = + 0.7 in sun, D = − 1.0 in shade). Both *L. cephalus* and *R. rutilus* juveniles moved to either weak or steeper banks of silty sand (also silted gravel in *L. cephalus*) with a strong preference for macrophytes. Although *R. rutilus* moderately preferred dense ligneous debris and shaded or mixed (shade and sun) areas (D = + 0.4 and

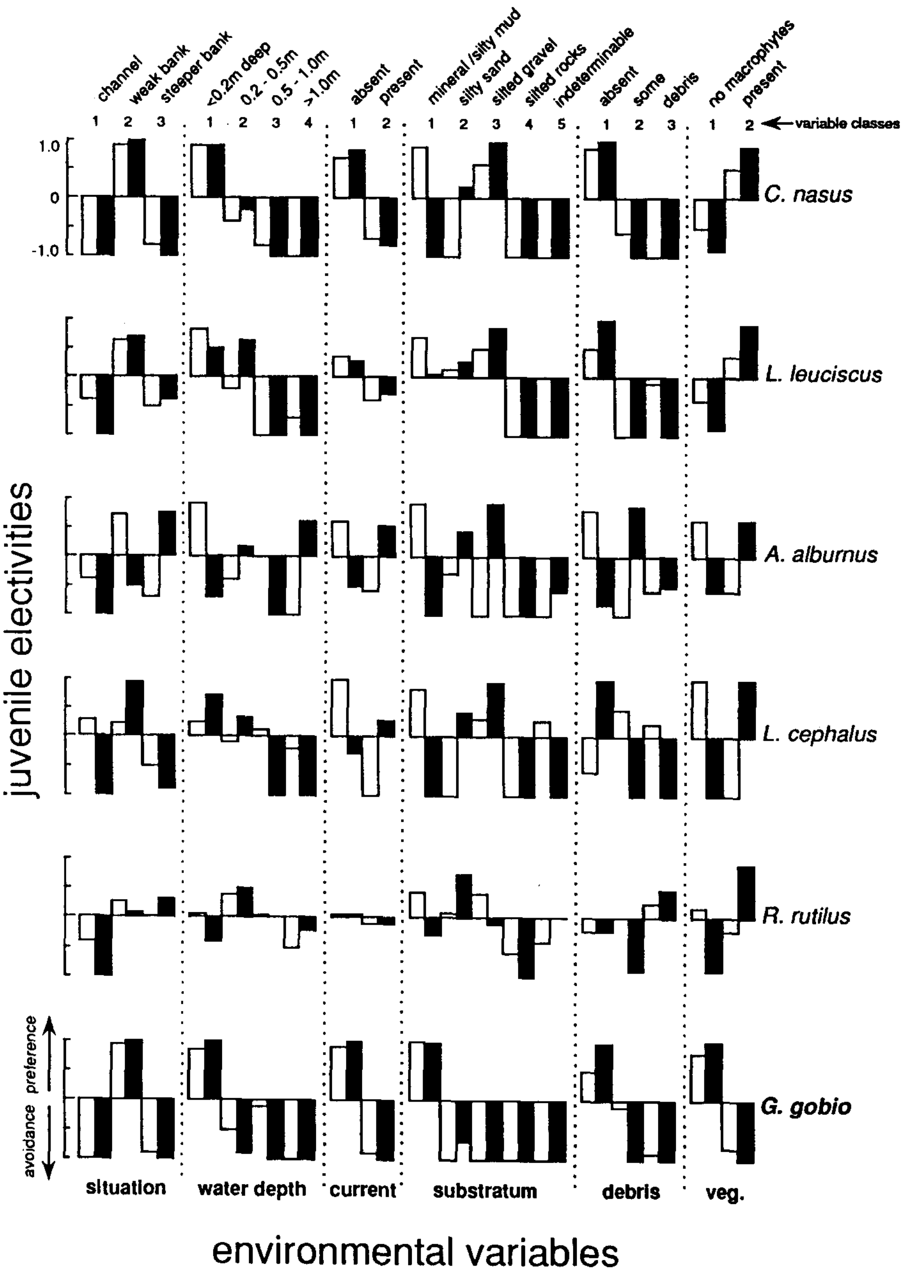

Fig. 3. Electivity index D from Jacob's (1974) formula for cyprinid 0 + juveniles (suffix 'J' in Fig. 1B, C) during mean discharge (white bars) and extremely reduced discharge (black bars) in Ilon during 1985.

+ 0.5), *L. cephalus* avoided debris and shade (D = − 1.0) as well as demonstrating a weak preference for water current. Juvenile *A. alburnus* also showed a mild preference for water current, but differed from the other species in its strong preference for steeper banks at > 1.0 m depth with macrophytes, some ligneous debris (Fig. 3) and mixed illumination (D = + 1.0). Juvenile *L. leuciscus* and *C. nasus* co-exploited a very similar microhabitat during low discharge, lentic waters of 0.2 m depth (also 0.2–0.5 m for *L. leuciscus*) over silted gravel with macrophytes but avoided ligneous debris. However, while juvenile *C. nasus* showed a preference for directly illuminated waters (D = + 0.9) and avoided attached periphyton (D = + 0.8 in absence, D = − 1.0 in presence), *L. leuciscus* were indifferent to both illumination (D = + 0.2 in sun, D = + 0.6 in shade) and periphyton (D ≈ 0 for all classes).

Discussion

> It would be interesting to know if the distribution differences apparent in the size classes of many species are indicative of a general trend in fishes or of sampling emphasis.
>
> G.S. Helfman (1978)

The young cyprinids of Ilon, a braided channel of the Upper Rhône River, exhibited considerable overlap in microhabitat use (Fig. 2, 3), particularly during a period of reduced river discharge. The drastic drop in water level experienced by the 0 + juveniles as a result of this decrease in flow severely limited the amount of littoral vegetation and branches, structures that small fishes (e.g. < 70 mm) use for feeding and as protective refuge against predation (Arnold 1974, Helfman 1978, Lightfoot & Jones 1979, Northcott 1979, Schröder 1979, Kriksunov et al. 1985, Haberlehner 1988, Rozas & Odum 1988). Similar associations between marine fishes and organic structures, principally reefs, are well known (Helfman 1978, Howard 1989).

Commencement of shoaling behaviour and feeding migrations away from the littoral zone of lakes, particularly in turbid waters (Bohl 1980), often coincide with changes in morphology/physiology (Mark et al. 1989) and in diet (Hartmann 1983). In the present study (Fig. 2, 3), only juvenile *A. alburnus* demonstrated any appreciable movement away from the channel's littoral (i.e. banks), and this coincided with a preference for aquatic vegetation (previously avoided) in lotic waters along Ilon's steeper banks. The preference of most young cyprinids in Ilon for lentic, shallower waters at weakly sloped banks corroborates Schiemer & Spindler's (1989) observations of young rheophilic cyprinids in the Austrian Danube, suggesting that shallow littoral areas may provide safer daytime refuge from predation, as postulated by Bohl (1980). This contrasts Scott's (1987) observations in the River Frome, a small chalk stream of Southern England, where juvenile *L. leuciscus* moved into the elevated water velocities of the channel after inhabiting lentic areas for the first two months of life. The avoidance by *R. rutilus* larvae and juveniles of Ilon's deeper channel waters differs from their reported microhabitat dynamics in lakes (Rheinberger et al. 1987), where they apparently undergo a migration to deeper waters (≈ 1.0 m) a few weeks after hatching, whereas the microhabitat of *L. cephalus* larvae and juveniles appears to be the same under both lacustrine (Rheinberger et al. 1987) and fluvial conditions: near physical structures (vegetation or branches) in the relatively shallow littoral areas.

The preference demonstrated here for shallow waters and protective structures (Fig. 2, 3) is presumed to be an anti-predatory action (Manteifel et al. 1978) employed in response to the drop in discharge. Such predation was not empirically tested in the present study, but predator threat was frequently observed, particularly during the period of reduced discharge, when *P. fluviatilis* would chase shoals of 0 + cyprinids up into the shallows of Ilon's weakly-sloped banks. Young cyprinids such as *R. rutilus* and *Leucaspius delineatus* (L.) respond to predator threat and reduced light levels (< 0.1 lux) by moving to the substratum (Manteifel et al. 1978), a reaction also observed in *R. rutilus* of a Danubian backwater (Haberlehner 1988). This anti-predator response may well be employed by other small cyprinids (Fig. 3; Haberlehner 1988), which are generally more susceptible to predation because of their 'highly visible' shoaling behaviour and their lack of spines or barbs (Bohl 1980, Robinson 1989).

Littoral macrophytes in river channels reduce water velocities, thus creating lentic areas favourable to young fishes such as *R. rutilus* (Lightfoot & Jones 1979). In Ilon, macrophytes were rare in mid-channel and mainly restricted to the bank margins, however all of the cyprinids except *G. gobio* preferred areas with macrophytes during some if not most of their development in the first summer of life (Fig. 2, 3). In small North American cyprinids, a similar pattern of microhabitat selection has been observed; larvae also tend to frequent shallow, lentic areas with protective structures, whereas 0 + juveniles may exploit similar microhabitats but are known to venture out into deeper waters, particularly those in proximity to submerged vegetation (Keast 1978, Halyk & Balon 1983, Power 1987).

Contrary to the colloquial belief that cyprinid larvae and juveniles prefer sunny shallow waters (e.g. Stankovitch 1921), most cyprinids did not demonstrate a preference for sunny areas. Indeed, the weak preferences shown in some species for sunny areas, and the stronger preference in larvae of *A. alburnus* (see also Schröder 1979), are probably coincidental to their preferences for shallow (> 0.5 m), weakly-sloped banks. In Ilon, riparian cover generally stood well back from the weakly-sloped banks (i.e. the right bank and island), which were thus directly exposed to the sun throughout most of the day. Nonetheless, young fishes probably benefit from this coincidence, being that the illuminated shallows are often notably warmer than those of the adjacent deeper waters (Copp 1990b). Jacob's (1974) formula for electivities appeared to account well for such relations between available and exploited microhabitat. In a recent study limited to the growth and microhabitat of *R. rutilus* larvae and early juveniles in Ilon (Copp 1990a, b), chi-square analysis in general indicated the same microhabitat preferences but did not account for numerical differences in species (or interval) abundance between the point samples as does Jacob's electivity index D.

In conclusion, cyprinids of Ilon demonstrated notable spatial segregation during their early development in 1985, despite the co-occurrence of similar life-history intervals from different species caused by protracted spawning in *R. rutilus, C. nasus, L. cephalus* and *L. leuciscus*. Although the microhabitats of *L. cephalus* and *A. alburnus* larvae were very similar, those of *R. rutilus, L. leuciscus* and *C. nasus* larvae overlapped only partially (Fig. 1B, C, 2). After transformation to the juvenile period, the cyprinids continued to demonstrate some repartition of spatial resources (Fig. 3), despite the strong interspecific associations observed in Ilon (Fig. 1B, C) and elsewhere on the French Upper Rhône (Copp 1989a). The overlap in their microhabitat increased during a period of reduced discharge, which restricted the amount of available vegetal/ligneous structures and increased the amount of shallow waters around the island and the alluvial plug. While most species exploited some portion of these vast shallows, juvenile *A. alburnus* appeared to be the only species that exploited the deeper waters off the channel's steeper banks.

The numerous unquantified events of predation threat observed in the field, supported by the general preference of 0 + cyprinids for shallows and protective structures, suggest that predation risk may influence the microhabitat use of young fishes, contrary to conclusions derived elsewhere from studies of microhabitat use in adult fishes (e.g. Grossman & Freeman 1987). Although the present study provided considerable information on the spatial and temporal dynamics of microhabitat use in 0 + cyprinids, future investigations should address both the available and exploited nutritional resources, as well as the extent of predation risk, in order to clarify: the extent of resource partitioning or co-exploitation in fluvial fishes during their larval and juvenile development, the extent to which predation risk influences this repartition of resources, and the similarities or differences in resource repartitioning by 0 + cyprinids in lacustrine and fluvial conditions.

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