

Habitat occupancy patterns of juvenile fishes in a large lowland river: interactions with macrophytes

G. Grenouillet, D. Pont and J. M. Olivier¹

Laboratoire d'Ecologie des Hydrosystèmes Fluviaux, Université Lyon I

With 3 figures and 6 tables

Abstract: Juvenile fish were sampled by electric fishing using the point abundance sampling method in September 1998 in the Lower Saône River, during a very low discharge period when current velocity was not the structuring factor. Patterns exhibited by the four most abundant species were investigated at different spatial scales of habitat heterogeneity using logistic regression analysis. At the higher scale (distinction between side-arms and channel), significant responses were always characterized by higher probabilities of presence in side-arms. Three of the four species showed patterns at the mesohabitat scale (the different macrophytes beds). At the microhabitat scale (the sampling point), the role of aquatic macrophytes was investigated by distinguishing the main species. In order to investigate the relationship between juvenile fish abundance and food habitat characteristics, phyto- and zooplankton were sampled in each mesohabitat, in both channel and side-arms. The type of vegetation appeared to be crucial in the determination of plankton abundance, but plankton abundance was not sufficient to explain patterns of habitat use in the fishes. Morphological characteristics of the different macrophytes studied were contrasted. Then we hypothesized that such differences resulted in different habitat quality (i.e. protection against predators) and may have affected the habitat use of juvenile fishes.

Introduction

In running water systems, habitat presents a hierarchical structure and many studies have pointed out the usefulness of viewing environmental heterogeneity at different nested scales (FRISSELL et al. 1986, AMOROS et al. 1987, WARD 1998). In fish ecology, such an approach is all the more important because fish species are known to exhibit ontogenetic changes in habitat requirements over a wide range of spatial scales. Thus determining how species respond to habi-

¹ **Authors' address:** Laboratoire d'Ecologie des Hydrosystèmes Fluviaux, Université Lyon I, 43 Boulevard du 11 novembre 1918, F-69622 Villeurbanne cedex, France, e-mail: grenouil@cismisun.univ-lyon1.fr

tat heterogeneity and understanding how biological processes underlie these patterns require both multi-scale and hierarchical approaches.

Fish-habitat relationships have been considered from the biogeographical scale (e.g. BANARESCU 1990) to the microhabitat scale (e.g. BAYLEY & LI 1992). However, SCHLOSSER (1995) stressed our lack of knowledge about species-habitat relationships at a large scale, that is the role of landscape-level processes determined by the spatial heterogeneity at the floodplain level. Moreover, POIZAT & PONT (1996) emphasized the lack of an integrative approach that would give a multi-scale view of the response of organisms to habitat heterogeneity. Most available studies have been carried out at a fine spatial scale (microhabitat scale), and mainly focused on headwater streams where physical habitat structure (depth, current velocity and substratum) was frequently found to determine fish species distribution (LOBB & ORTH 1991).

In contrast with rhytonic ecosystems, large slow-flowing rivers have been only lately examined. In these potamic systems, the transversal dimension is characterized by a diversity of floodplain habitats interconnected with the lotic environment of the river (AMOROS et al. 1987), and physical conditions are supposed to be less severe. Typical rhytonic fish-habitat relationships are thus no longer likely to occur, and other factors are involved in patterns of fish habitat use. Among these factors, the patterns of aquatic macrophyte distribution induce considerable structural variations in space (HUTCHINSON 1975, SAND-JENSEN & MEBUS 1996, CHAMBERS 1987, CHAMBERS & KALFF 1987). Macrophytes contribute to an increase in habitat structural complexity (CROWDER & COOPER 1982), and the presence of vegetation is thus an important determinant of fish habitat selection (WERNER et al. 1977, GUILLORY 1979, KEAST 1984, KILLGORE et al. 1989, CONROW et al. 1990, CHICK & McIVOR 1994).

Influence of vegetation on distribution, abundance or behaviour of fish has been well documented in standing water systems or in experimental studies (CROWDER & COOPER 1982, ROZAS & ODUM 1988, SAVINO & STEIN 1989, CHICK & McIVOR 1994). In large rivers, few similar studies on the importance of vegetated habitats for fish are available. Fish studies that distinguish different kinds of macrophytes (e.g. COPP 1992a) are rare, and the classical microhabitat approach generally views vegetation as a qualitative variable coded in density classes (i.e. absence, occasional, dense).

In this context, the aim of this study was to assess habitat use by juvenile fishes in selected habitats in a large river, emphasizing the effects of spatial scales and aquatic macrophyte occupancy. We applied a multi-scale analysis in the Lower Saône River. By contrast with most similar rivers in Europe, this temperate and typical lowland river is still weakly regulated, and presents favourable conditions for the development of macrophyte beds in both channel and side-arms. The patchy distribution of vegetation thus structures habitat and these macrophyte beds constitute an appropriate observational scale, ac-

ording to the postulate that habitat and community may scale in the same way (FRISSELL et al. 1986, POWELL 1989, WIENS 1989). The questions we addressed were as follows. First, at which scales do species respond to habitat heterogeneity? Second, does identification of macrophyte species at the microhabitat scale enhance our understanding of fish distribution? Third, can the patterns revealed be explained by abiotic or biotic factors?

Material and methods

Study sites

The River Saône (France), the major tributary of the River Rhône, is 475 km long. Its drainage area is 29,143 km² and average annual discharge is 430 m³/s. The study site (45.5° N, 4.45° E) is located in the lower part of the river, and is characterized by a slope of less than 0.8‰, a mean width of 200 m, and a mean depth of 6 m. Data were collected from two stations, near the cities of Trevoux and Belleville-sur-Saône, some 30 km and 50 km above the confluence with the Rhône, respectively. These two stations were similar in their hydrological and geomorphological characteristics, with an alluvial floodplain containing side-arms.

In each station, three nested scales of habitat heterogeneity were defined. The highest scale (or macrohabitat) described the location in the alluvial floodplain, and was coded by "channel" or "side-arm". The intermediate scale (or mesohabitat) described the type of macrophyte beds. The finest scale (or microhabitat) corresponded to the sampling point where habitat description was performed.

Habitat description

Sampling was performed during the first week of September 1998. In total, 213 points were sampled at the stations of Trevoux and Belleville-sur-Saône (56 and 157 sampling points, respectively), both in channel and side-arms (74 and 139 sampling points, respectively). At each sampling point, qualitative and quantitative variables were used to evaluate microhabitat characteristics. During the study period, discharge was extremely low (about 95 m³/s) and current velocity was zero at each sampling point. Depth was measured to the nearest centimetre. Substratum was defined using four qualitative variables: mud, sand, gravel, and pebbles. Periphyton was measured semi-quantitatively and was noted as absent, scanty, medium, or dense. Following UEHLINGER (1991), the term periphyton was defined as the complex of algae, bacteria, fungi, protozoa, fine detritus and polysaccharides which covers the surfaces of submerged objects in water. This term refers to periphyton s.s. associated with inorganic and organic substratum. In sampling points with no vegetation, periphyton was visually evaluated by examining the bottom surface. In sampling points with vegetation, periphyton was evaluated by examining the aspect of stem and leaf surface.

Macrophyte sampling

At each sampling point with vegetation, the cover of each plant species was estimated using a 1 m² quadrat divided in 25 compartments. In each compartment, macrophyte cover was estimated for each species by visual observation of percent cover. According to this classification, 5 vegetation scores were noted: 0 (absence), 1 (<5%), 2 (5–25%), 3 (25–50%), 4 (50–75%) and 5 (>75%). For instance, one rod of *Scirpus* in one compartment was evaluated 1, and 20 rods were evaluated 5. For each plant species, the 25 values reported were then averaged to provide an index of cover, ranging from 0 (absence) to 10 (100% cover). We estimated the total cover of vegetation (VgCov) at each sampling point by the sum of the covers of all plant species.

Macrophyte development led to the presence of macrophyte beds, and among the different macrophytes reported, four species were frequently encountered: *Ceratophyllum demersum*, *Nuphar lutea*, *Sagittaria sagittifolia*, and *Scirpus lacustris*. *C. demersum* has whorled leaves and is entirely submerged, rootless, and free-floating. *N. lutea* is unarmed, with stout rhizomes, and mostly floating, but sometimes partly emergent, leaf blades. *S. sagittifolia* has submerged, floating, or emergent leaves; the blades of the submerged leaves are usually linear, sometimes lanceolate, mostly flat but sometimes inflated and spongy. *S. lacustris*, half-submerged, has erect stems, up to 3 m tall, and does not have leaves. Thus these four species are morphologically contrasted, and these contrasting growth forms are likely to provide different types of aquatic habitats.

By comparing the index of cover of each macrophyte species and VgCov, we calculated the proportion of each macrophyte species and thus identified the dominant plant species. Following the dominant plant species in each sampling point, macrophyte beds were defined by the following categorical variables (vegetation types): CER (*C. demersum*), NUP (*N. lutea*), SAG (*S. sagittifolia*) and SCI (*S. lacustris*). NOVEG was used to define sampling points where no plant species was present.

Although frequently composed by an assemblage of different plant species, the macrophyte beds were mainly dominated by one single species (Table 1). Over 90% of VgCov were due to the dominant plant species in CER, SAG and SCI beds. *N. lutea* represented over 70% in the NUP beds and was frequently associated with *C. demersum*.

Phyto- and zooplankton sampling

In each type of macrophyte bed, triplicate phyto- and zooplankton samples were collected from three different beds, in both channel and side-arms.

For phytoplankton, three 1-L samples were taken for measuring chlorophyll-a concentration. These samples were filtered through a Whatmann GF/C filter. After 24 hours extraction by 90% acetone and centrifugation, active chlorophyll-a concentrations were measured by spectrophotometry after acidification according to LORENZEN (1967).

For macrozooplankton (cladocerans and copepods), triplicate samples were collected by filtering 400 L of water through a 160- μ m mesh net, and preserved in a 5% formaldehyde solution. Zooplankton abundance was evaluated by counting at least 300 individuals in each subsample, or by enumerating individuals in the whole sample.

Table 1. Mean relative cover of the four main macrophyte species reported in each type of vegetation bed, and minimum and maximum values (in brackets). CER = *Ceratophyllum demersum* – dominated beds; NUP = *Nuphar lutea* – dominated beds; SAG = *Sagittaria sagittifolia* – dominated beds; SCI = *Scirpus lacustris* – dominated beds; NOVEG = no vegetation.

Type of vegetation beds	n	Macrophyte species			
		<i>C. demersum</i>	<i>N. lutea</i>	<i>S. sagittifolia</i>	<i>S. lacustris</i>
CER	43	0.91 [0.51–1]	0.08 [0–0.49]	0.002 [0–0.13]	0.01 [0–0.44]
NUP	35	0.20 [0–0.5]	0.71 [0.41–1]	0.03 [0–0.48]	0.01 [0–0.37]
SAG	70	0.04 [0–0.33]	0.02 [0–0.28]	0.91 [0.49–1]	0
SCI	14	0.01 [0–0.18]	0.02 [0–0.25]	0.01 [0–0.15]	0.93 [0.63–1]
NOVEG	51				

Fish sampling

Juvenile (0+) fishes were sampled by electric fishing using the point abundance sampling method (NELVA et al. 1979, PERSAT & COPP 1990). At the sampling time, all juvenile fishes had completed their larval development and attained a sufficient size to be caught by electric fishing. Fishing was done during daylight, and the fishing point was approached by boat. Following COPP (1989, 1992a), a portable electric fishing apparatus with an anode diameter of 10 cm was used for sampling the juvenile (0+) fishes, and each point sample consisted of an approximate 5-s submersion of the activated anode at about 50 cm depth (less at shallower points). After capture, the fishes were identified to species, measured to the nearest millimetre and returned to the water. Only juvenile bream (*Blicca bjoerkna* and *Abramis brama*), which were not identifiable in the field, were preserved in 4% formalin and discriminated in the laboratory.

Data analysis

Prior to analyses, fish data were reduced to presence/absence. To investigate relationships between independent (continuous or categorical) habitat variables and this binary response, we first examined the effects of each single habitat variable. Then models were fitted to the data using all habitat variables as independent variables.

Ecological profiles

We related species occurrence to each habitat variable. All environmental variables were converted to categories in order to determine species-variables associations (χ^2), and to generate ecological profiles of habitat use by species. For one given species, the ecological profiles were calculated as the difference between the frequency of that spe-

cies in the samples of one category of variable and the frequency of that species in all samples. Deviations from expectations for species and variables were tested by χ^2 analysis and, if significant, they demonstrated preferences or avoidances.

Logistic regression analysis

The presence/absence response curve of a species (TER BRAAK & LOOMAN 1986) describes the probability of the species being present, $p(x)$, as a function of an environmental variable x . The Gaussian logit curve (JONGMAN et al. 1995) is a symmetric and bell-shaped response curve, in which the logit-transform of probability $g(x)$ is a quadratic function:

$$g(x) = \log\left(\frac{p(x)}{1-p(x)}\right) = \beta_0 + \beta_1 x + \beta_2 x^2 = a - \frac{1}{2} \frac{(x-u)^2}{t^2}$$

The parameters β_0 , β_1 and β_2 are regression coefficients. Estimates of the optimum u , the tolerance t and the maximum probability p_{max} can be obtained from the estimates of parameters β_0 , β_1 and β_2 :

$$u = \frac{-\beta_1}{2\beta_2}$$

$$t = \frac{1}{\sqrt{-2\beta_2}}$$

$$p_{max} = \frac{1}{1 + e^{(-\beta_0 - \beta_1 u - \beta_2 u^2)}}$$

The optimum u corresponds to the value of the environmental variable x for which probability of occurrence is highest (p_{max}), and the tolerance t is a measure of ecological amplitude. Logistic regression was first introduced in ecology by AUSTIN (1980) and AUSTIN et al. (1984). We used logistic regression (SOKAL & ROHLF 1995) to describe relationships between juvenile fish incidence (presence/absence) and habitat variables. Separate single analyses were performed for three quantitative habitat variables: depth, VgCov and periphyton, in order to investigate fish response curves. For each of the four fish species retained, we tested whether parameters β_1 and β_2 differed significantly from zero ($P < 0.05$). If β_1 was significant but not β_2 , then the response curve was logistic, with a maximum probability observed for one of the two extreme values (the lowest or the highest) of the variable tested. If β_2 was significantly negative, the response curve was gaussian (bell-shaped and symmetric), and then optimum and tolerance parameters, and p_{max} were calculated.

Finally, we carried out a logistic regression, using all quantitative and qualitative habitat variables jointly, to model occurrence of juvenile fish species. In these models, terms were added sequentially. By this way, the effect of a given variable was tested after having removed the effects of variables added previously to the model.

We used S-PLUS (MathSoft Inc. 1998) and ADE-4 software package (THIOULOISE et al. 1997) for data analyses.

Results

Habitat characteristics

Characteristics of habitat variables measured are presented in Table 2. At the macrohabitat scale, no differences between channel and side-arm sites were observed for depth and periphyton ($P = 0.490$ and $P = 0.230$, respectively; site effect in random effect ANOVA). Sites differed ($P < 0.001$) both in their substratum composition and their vegetation cover. Side-arms were characterized by a high component of mud substratum, and a high mean cover of vegetation.

At the mesohabitat scale, all habitat variables differed among vegetation types ($P < 0.001$ for substratum, depth and periphyton, and $P = 0.017$ for VgCov; vegetation type effect in random effect ANOVA). NOVEG habitats had the lowest mean water depth, associated with a poorly developed periphyton. CER and SAG were frequently encountered on mud substratum. Dense values of periphyton were frequently noted in SAG, whereas CER and NUP consti-

Table 2. Characteristics of habitat variables measured for different scales of habitat heterogeneity (see Material and methods). Proportions are presented for discrete variables, and mean, minimum and maximum values are presented for continuous variables. VgCov = total cover of vegetation; NOVEG, CER, NUP, SAG and SCI as in Table 1.

	Substratum				Depth (m)	Periphyton				VgCov
	mud (%)	sand (%)	gravel (%)	pebbles (%)	mean [min.-max.]	absent (%)	scanty (%)	medium (%)	dense (%)	mean [min.-max.]
Macrohabitat										
Channel ($n = 74$)	8.1	47.3	28.4	16.2	0.74 [0.15-2.5]	48.6	9.5	29.7	12.2	5.4 [0-16]
Side-arm ($n = 139$)	69.1	7.9	19.4	3.6	0.70 [0.15-2.5]	43.9	10.8	18.7	26.6	10.3 [0-26]
Mesohabitat										
NOVEG ($n = 51$)	37.7	18.9	20.8	22.6	0.38 [0.15-1.3]	67.9	11.3	15.1	5.7	
CER ($n = 43$)	74.4	15.4	10.3	0	0.83 [0.2-2.2]	59.0	25.6	15.4	0	13.6 [3.6-26]
NUP ($n = 35$)	41.2	17.6	35.3	5.9	1.19 [0.3-2.5]	73.5	5.9	11.8	8.8	10.7 [3.36-22]
SAG ($n = 70$)	55.7	24.3	17.1	2.9	0.56 [0.15-1.1]	8.6	5.7	31.4	54.3	11.0 [5.44-22]
SCI ($n = 14$)	0	41.2	52.9	5.9	1.13 [0.5-1.65]	41.2	0	47.1	11.8	8.0 [4.72-16]
Microhabitat										
($n = 213$)	47.9	21.6	22.5	8.0	0.72 [0.15-2.5]	45.5	10.3	22.5	21.6	8.6 [0-26]

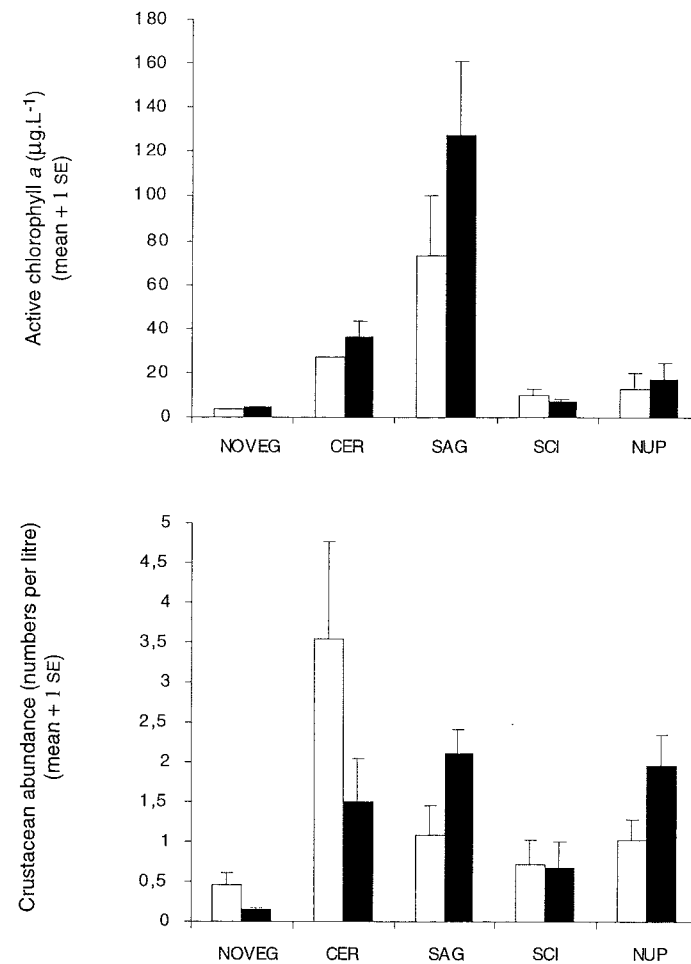


Fig. 1. Mean active phytoplankton chlorophyll-a concentration ($n = 3$) and mean zooplankton crustacean abundance ($n = 3$) in each of the five mesohabitats (NOVEG, CER, NUP, SAG, SCI as in Table 1), in both channel (open bars) and side-arm (solid bars) habitats.

tuted poor-periphyton habitats. Mean cover of vegetation was lowest in SCI and highest in CER, with intermediate values for SAG and NUP.

Distribution of phyto- and zooplankton showed clear differences among vegetation types (Fig. 1). For both chlorophyll-a concentration and crustacean abundance, lowest values were observed in unvegetated areas. SAG had the highest component of chlorophyll-a, whereas crustacean abundance was highest in CER, SAG and NUP habitats. Analysis of variance, using site and vegetation type as fixed factors, detected neither difference among sites nor significant in-

Table 3. Analyses of variance for the effects of site and vegetation type on phytoplankton chlorophyll-a (chl-a) concentration and zooplankton crustacean abundance. Degrees of freedom df , mean squares MS , F -ratio and probabilities P are given.

	Source of variation	df	MS	F -ratio	P
Chl-a concentration	Site	1	1239.5155	1.5196	0.2327
	Vegetation type	4	8018.6717	9.8304	0.0002
	Site \times Veg. type	4	815.7039	0.8470	0.5129
	Residual	20	815.7039		
Crustacean abundance	Site	1	0.0619	0.0564	0.8146
	Vegetation type	4	4.4820	4.0863	0.0140
	Site \times Veg. type	4	2.2696	2.0693	0.1230
	Residual	20	1.0968		

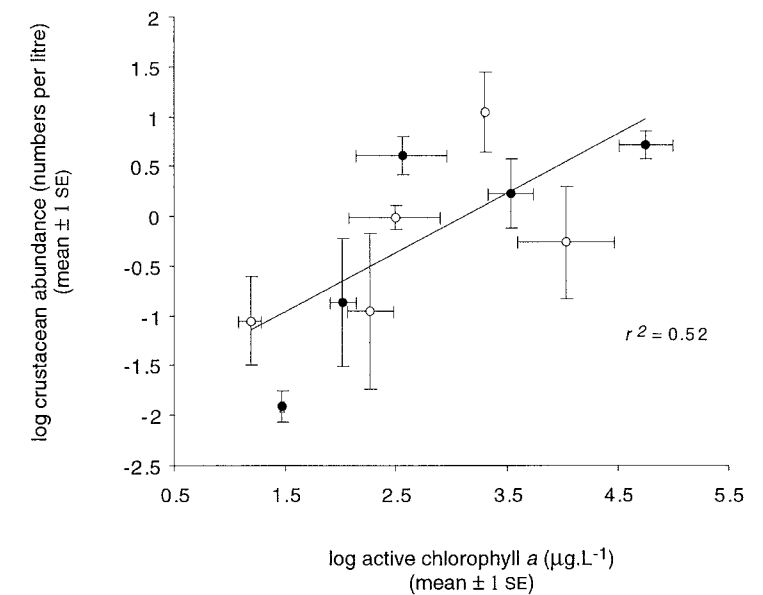


Fig. 2. Relationship between mean active phytoplankton chlorophyll-a concentration and mean zooplankton crustacean abundance in each of the five mesohabitats (NOVEG, CER, NUP, SAG, SCI as in Table 1), in both channel (open circles) and side-arm (solid circles) habitats.

teraction between site and vegetation type, but only a vegetation type effect (Table 3). Moreover, linear regression analysis of mean chlorophyll-a concentration versus mean crustacean abundance for each vegetation type revealed a significant positive correlation ($r^2 = 0.523$, $P = 0.018$): the patterns of distribution of phyto- and zooplankton were thus relatively consistent among vegetation types (Fig. 2).

We investigated the relationship between both phyto- and zooplankton abundance and mean periphyton abundance calculated for each vegetation type, in channel and side-arms. No significant relationship was observed between periphyton and crustacean abundance ($r^2 = 0.004$, $P = 0.870$). Although not significant, the relationship between periphyton and active chlorophyll-a was more marked ($r^2 = 0.356$, $P = 0.090$).

Patterns of habitat use by 0+ fishes

A total of 1443 juvenile fishes of eighteen species were caught in the 213 point samples. The number of 0+ fishes captured varied greatly between species and only four species occurred in more than 10% of the samples, ranging from 1.2 to 9.8-cm total length (Table 4). Two families (cyprinids and centrarchids) were represented among these four most abundant species, accounting for 92% of the total number of juvenile fishes caught: *Blicca bjoerkna* (L. 1758), *Leuciscus cephalus* (L. 1758), *Lepomis gibbosus* (L. 1758) and *Alburnus alburnus* (L. 1758). Due to the rarity of other species, only these four were considered for further analysis. *L. gibbosus* was the most frequently encountered species but *B. bjoerkna* had the highest average number of individuals per sample.

Ecological profiles

Among the different variables analyzed, the patterns obtained revealed that the covers of two macrophyte species, *Ceratophyllum demersum* and *Nuphar lutea*, produced no significant response (Fig. 3). The others had significant effect on the occurrence of at least one of the four fish species studied. *B. bjoerkna*, *L. cephalus*, and *L. gibbosus* showed a significant effect of the site, with higher abundances in the side-arms than in the channel sites. Only *L. gibbosus* showed a significant response to substratum, a marked preference for mud. *A. alburnus* was not influenced by depth, whereas *B. bjoerkna* and *L. gibbosus* preferred intermediate depth (0.5–1 m). Whereas *L. cephalus* avoided

Table 4. Mean number of specimens collected per sampling point, frequency of occurrence, and length data of the most abundant juvenile fishes. Only species occurring in more than 10% of the samples have been retained.

Fish species	Mean number	frequency	Total Length (cm)		
			Mean TL	minimum	maximum
<i>Alburnus alburnus</i>	0.56	0.13	4.6	2.8	6.6
<i>Blicca bjoerkna</i>	2.74	0.37	3.8	1.5	9.8
<i>Leuciscus cephalus</i>	1.63	0.34	4.0	1.9	7.8
<i>Lepomis gibbosus</i>	1.30	0.44	3.1	1.2	6.5

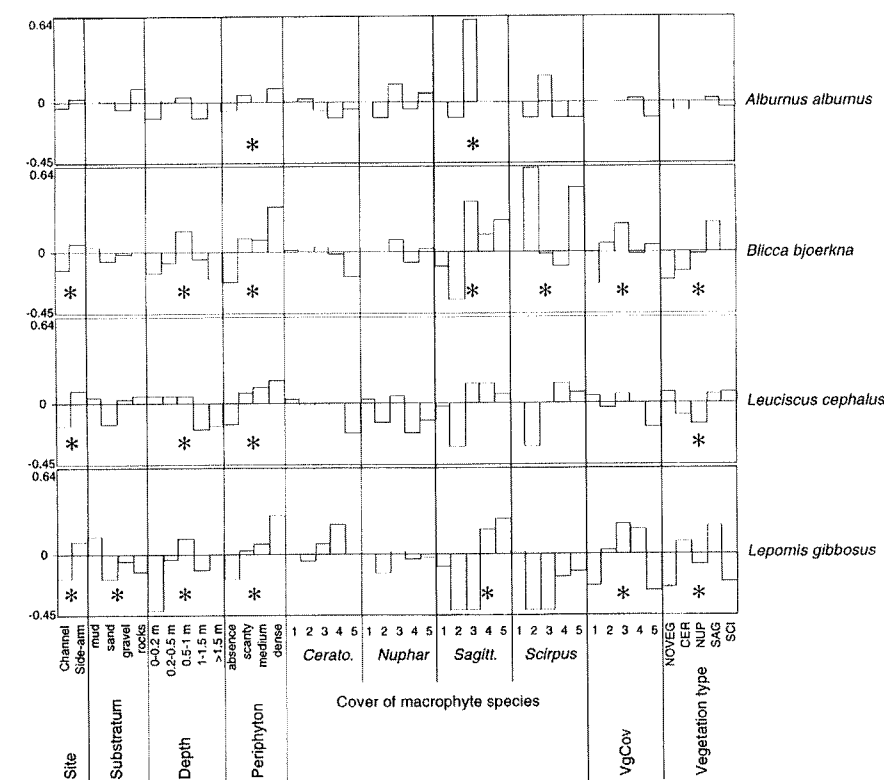


Fig. 3. Environmental profiles and χ^2 associations for 0+ fishes. Each histogram represents the difference between the frequency of that species in the group of samples having that category of environmental variables and the frequency of that species in all samples. Significant ($P < 0.05$) χ^2 associations between species and variables are indicated with an asterisk. VgCov = total cover of vegetation. NOVEG, CER, NUP, SAG, SCI as in Table 1.

the deeper water areas (depth >1 m) and occupied preferentially the shallow water areas, *B. bjoerkna* and *L. gibbosus* showed an avoidance reaction for these shallower water areas. These four species showed positive associations with high values of periphyton. Patterns obtained for the effects of the cover of macrophyte species revealed that *Sagittaria sagittifolia* influenced three of the four species studied, whereas *Scirpus lacustris* influenced only *B. bjoerkna*. The effect of total vegetation cover was significant for *B. bjoerkna* and *L. gibbosus*, with a marked preference for intermediate densities. Only *A. alburnus* did not exhibit any significant response for the type of vegetation.

Table 5. Estimated values for parameters β_0 , β_1 , β_2 , from the logistic regression model, and calculated optima, tolerance and maximum probabilities P_{\max} of occurrence of juvenile fish species. A Gaussian response is a bell-shaped curve. A logistic response is a sloping curve with the maximum at one end or the other. ns: not significant; l. v. o.: lowest value observed; h. v. o.: highest value observed.

Variable	Species	β_0	β_1	β_2	Type of response	Optimum	Tolerance	P_{\max}
Depth	<i>Alburnus alburnus</i>	-2.919	4.567	-3.730	Gaussian	0.61	0.37	0.18
	<i>Blicca bjoerkna</i>	-2.038	4.480	-2.450	Gaussian	0.91	0.45	0.50
	<i>Leuciscus cephalus</i>	-0.071	-0.715	-0.160	Logistic	<l. v. o.	-	-
	<i>Lepomis gibbosus</i>	-0.560	0.799	-0.354	ns	-	-	-
VgCov	<i>Alburnus alburnus</i>	-1.697	-0.024	-0.0004	ns	-	-	-
	<i>Blicca bjoerkna</i>	-2.062	0.301	-0.011	Gaussian	14.19	6.87	0.52
	<i>Leuciscus cephalus</i>	-0.445	-0.028	0.0003	ns	-	-	-
	<i>Lepomis gibbosus</i>	-1.880	0.342	-0.013	Gaussian	13.58	6.30	0.61
Periph	<i>Alburnus alburnus</i>	-2.802	0.839	-0.104	Logistic	>h. v. o.	-	-
	<i>Blicca bjoerkna</i>	-1.858	1.219	-0.109	Logistic	>h. v. o.	-	-
	<i>Leuciscus cephalus</i>	-1.519	1.205	-0.227	Logistic	>h. v. o.	-	-
	<i>Lepomis gibbosus</i>	-1.136	0.696	0.002	Logistic	>h. v. o.	-	-

Logistic regression analysis

The parameters of regression equations obtained for the three habitat variables, depth, VgCov and periphyton, are shown in Table 5. Versus depth, only *L. gibbosus* did not show a significant response curve. Two species (*A. alburnus* and *B. bjoerkna*) showed a Gaussian response curve and *L. cephalus* showed a logistic response curve. VgCov had no significant effect on the occurrence of *A. alburnus* and *L. cephalus*, whereas a Gaussian response curve was apparent for *B. bjoerkna* and *L. gibbosus*.

The four fish species exhibited the same logistic response to periphyton, suggesting that fish occurrence was positively related to periphyton density.

Optimum, tolerance, and maximum probabilities were calculated for Gaussian response curves. *A. alburnus* showed marked preferences for low depth (around 0.6 m), whereas *B. bjoerkna* showed maximum probabilities of occurrence in deeper areas (near 1 m). For vegetation cover (which varied between 0 and 26), *B. bjoerkna* and *L. gibbosus* showed the same significant Gaussian responses, with maximum probabilities of occurrence under intermediate vegetation covers (close to 14). Optima, tolerance values, and maximum probabilities of occurrence were very similar for both species.

Results of logistic multiple regression models for each juvenile fish species are shown in Table 6. According to these models, all species showed significant responses both to the station and the site. Only the probability of occurrence of *A. alburnus* was related to substratum. For depth, only *L. gibbosus*

Table 6. Logistic multiple regression for juvenile fish species. *df*: degrees of freedom; *Aa*: *Alburnus alburnus*; *Bb*: *Blicca bjoerkna*; *Lc*: *Leuciscus cephalus*; *Lg*: *Lepomis gibbosus*. VgCov: total cover of vegetation; Periph: periphyton. Note that the three quantitative variables (Depth, VgCov and Periph) are included in the model under a second order polynomial form. Asterisks denote parameters that are significantly different from zero at * $P < 0.05$, ** $P < 0.01$, or *** $P < 0.001$.

Habitat variables and statistical values	<i>df</i>	Fish species			
		<i>Aa</i>	<i>Bb</i>	<i>Lc</i>	<i>Lg</i>
Station	1	***	*	***	***
Site	1	*	***	***	***
Substratum	3	**			
Depth	2	*	**	**	
VgCov	2		***		***
Periph	2	**	***	***	***
Vegetation type	4				
Depth × VgCov	1	*			*
Depth × Periph	1				
VgCov × Periph	1				
Total deviance		161.96	279.84	273.84	291.85
Residual deviance		90.70	189.62	165.23	177.74
Deviance explained (%)		44.0	32.2	39.7	39.2

did not exhibit a significant response. *B. bjoerkna* and *L. gibbosus* exhibited significant responses to VgCov. Then periphyton influence was significant for all species. Finally, after allowing for the effects of above cited variables, the type of vegetation bed was never significant. The depth × VgCov interaction was significant for *A. alburnus* and *L. cephalus*, whereas the depth × periph and VgCov × depth interactions were not significant. Percentage of total deviance explained by logistic multiple regression models varied from 32.2 % for *B. bjoerkna* to 44 % for *A. alburnus*.

Discussion

The present study was designed to investigate habitat occupancy patterns of juvenile fishes in a large lowland river, and three questions were addressed concerning (1) the role of spatial scales, (2) the role of the type of vegetation, and (3) the biotic and abiotic factors responsible for the patterns observed.

Concerning the role of spatial scales, our study reveals clear differences in juvenile responses to environmental heterogeneity. Among the four most abundant species, significant responses were always characterized by higher probabilities of presence in side-arms. At large scale, only *A. alburnus* did not exhibit significant response to site. At the microhabitat scale, ecological profiles re-

vealed the importance of periphyton for all species, whereas vegetation cover and water depth were significant for three and two species, respectively. After removing between-station and between-site variability, the influence of these four microhabitat variables remained similar for the two biotic variables (Periph and VgCov), but with slight differences for the two physical variables (water depth and substratum). The main information obtained by using such a multi-scale approach is the absence of vegetation type effect, although this variable appeared significant when examined separately.

From a methodological standpoint, periphyton can be considered as an easy-to-measure variable for estimating trophic conditions. Therefore it is an interesting descriptor of fish habitat. Mean zooplankton abundance and mean chlorophyll-a concentration were not significantly correlated with mean periphyton values for each vegetation type. However, zooplankton and chlorophyll-a concentration were not measured at each sampling point, and possible interactions between these and other habitat variables (e.g. depth or VgCov) were not considered. Therefore, more precise investigations on relationships between periphyton and planktonic communities are needed, and integrating descriptors of planktonic communities potentially remains of great interest in modelling fish-habitat relationships.

The two methods used to analyze the effect of vegetation on habitat occupancy patterns of juvenile fishes (ecological profiles and logistic regression models) are complementary and need to be interpreted jointly. On one hand, ecological profiles showed that three of the four species studied responded to the type of vegetation bed, and that macrophyte cover was significant for two plant species: *S. sagittaria* and *S. lacustris*. On the other hand, logistic multiple regression showed that the type of vegetation bed was no longer significant when added last, that is after having removed the effects of other habitat variables.

Three interactions were tested in our logistic multiple regression model, and only the depth \times VgCov interaction was significant for *A. alburnus* and *L. gibbosus*. Therefore, we can reliably consider the relationships revealed in this model.

For species which exhibited significant patterns at large scale, our study reveals that highest abundances were always observed in side-arms. Differences between main river channel and floodplain units have been well illustrated (e.g. PENCZAK & ZALEWSKI 1974, COPP 1989). It is now largely recognized that floodplain units are important nursery areas for young fishes (TURNER et al. 1994), providing both refuge (e.g. from low temperature and rapid currents (HOLLAND 1986)) and food resources (HOLLAND & HUSTON 1985).

Recent works based on similar themes have been conducted, and our results can thus be discussed in the light of previous studies that defined ecological profiles of the same juvenile fish species.

In this study, *A. alburnus* was not influenced by depth and the type of vegetation. Similar results were found in the Garonne River (GOZLAN et al. 1998), but GARNER (1996 a) showed that *A. alburnus* preferred moderate depth (1.5–2 m) and avoided macrophytes.

As observed in the Upper Rhône (COPP 1992 b), the Lower Rhône (POIZAT & PONT 1996), the Great Ouse (GARNER 1996 a, 1996 b) and the Garonne (GOZLAN et al. 1998), juvenile *L. cephalus* were strongly associated with shallow water. *L. cephalus* was shown to avoid *Nuphar* and to be associated with emergent macrophytes (GARNER 1996 b). Our results reveal a very similar ecological profile, with an avoidance for *Nuphar lutea*, and a preference for emergent macrophytes (in our study *Scirpus lacustris*).

This study indicates that *B. bjoerkna* and *L. gibbosus* preferred intermediate water depths and were associated with vegetation, and these results go hand in hand with other studies (COPP 1997, GOZLAN et al. 1998). However, in contrast with those of the Great Ouse (COPP 1997) who preferred dense macrophyte beds, the juvenile *B. bjoerkna* of our study selected intermediate macrophyte densities. We found the same preference for *L. gibbosus*, and our results are consistent with the results of KILLGORE et al. (1989), who showed fish abundance to be highest in areas of intermediate plant densities.

Our study shows a diversity of response to water depth, which results in spatial segregation of juvenile fish species, and it seems very interesting that fish responses to water depth in our study are consistent with recent literature on juvenile fish ecology from other systems. Depth has been described as a competitive (CLARK & LEVY 1988) or anti-predator (SCHLOSSER 1988) refuge, and results in inter-specific habitat segregation.

However, most available studies on fish habitats in lotic systems mainly focused on physical habitat structure, that is water depth, current velocity and substratum. In contrast with rithronic systems, this study shows that more complex fish-habitat relationships can occur when hydrology is not the structuring factor, and effects of biotic factors can thus appear to be of first importance in juvenile fish distribution. In some measure, such large slow-flowing systems can be compared with lacustrine ecosystems where considerable research has examined the influence of biotic factors on fish distribution. In particular, fish and macrophyte interactions have received great attention (CHICK & MCIVOR 1994). Despite increased interest in microhabitat of juvenile fish during the last decade, few similar studies examined the role of biotic interactions in large river systems. However, feeding and predator avoidance behaviour have been hypothesized to be responsible for habitat selection (WERNER & GILLIAM 1984, COPP 1992 b, BEAN & WINFIELD 1995, GARNER 1996 a). As a result, more and more investigations emphasize the necessity of considering the role of biotic processes in the determination of fish habitat occupancy (GARNER 1996 a, 1996 b, DEWEY et al. 1997).

Possible mechanisms responsible for fish-habitat relationships

In accordance with the ecological classification based on reproductive strategies (BALON 1975), the two species influenced by VgCov belong to phytophilic nonguarder (*B. bjoerkna*) and nest-spawner guarder (*L. gibbosus*) guilds. The two species not influenced by VgCov belong to phytolithophils (*A. alburnus*) and lithophils (*L. cephalus*) guilds.

However, even when the actual habitat selection of the juveniles may be related to the reproductive strategies of the adults, this is certainly not the only possible explanation. Fish exhibit remarkable plasticity in their ecology, and habitat qualities partly determine fish habitat use (DILL 1983). Previous studies revealed that food availability and the presence of predators could dramatically modify the expected patterns of habitat use (WERNER & HALL 1988, ROZAS & ODUM 1988).

Both experimental and comparative studies showed that habitats with high densities of submersed macrophytes presented the greatest abundance and richness of macroinvertebrates (GERKING 1962, ORTH et al. 1984, GREGG & ROSE 1985). Relationships between macrophytes and invertebrates may thus influence fish (KEAST 1984): food profitability appears to be greater in vegetated areas where fish can eat bigger prey and can have a higher growth rate, a lower mortality rate, and a higher fecundity than in open habitats (ROZAS & ODUM 1988). This enhancement of the growth rate in vegetated areas was observed by RICHARDSON et al. (1998); it can result in a better first-year survival due to a greater resistance to winter conditions and to a reduced pressure of predation.

Our results confirm the hypothesis that aquatic vegetation offers favourable conditions for riverine plankton development, and thus constitutes food-rich habitats for fishes. Moreover, while plankton abundance was the same in both channel and side-arms, the type of macrophyte appears to be crucial for phyto- and zooplankton abundance.

The different macrophytes studied here differed as to their morphological characteristics (e.g. size, amount of branching and leaves, position of leaves). Such differences probably resulted in different habitat quality and have been hypothesized to affect the habitat use of juvenile fishes (DIONNE & FOLT 1991).

Three of the four fish species responded to the type of macrophyte bed, but our results show that the effect of macrophyte type can be explained by the habitat variables used to describe conditions in vegetation, that is substratum, depth, vegetation cover, and the amount of periphyton. This study suggests that not only the presence but also the cover of vegetation influence fish responses to habitat heterogeneity. Juvenile fishes responded to the cover of two of the four macrophyte species: *S. sagittifolia* and *S. lacustris*, that is the den-

ser submerged plants, whereas the mainly floating parts of *C. demersum* and *N. lutea* did not influence fish distribution.

Moreover, our results show the probability of presence of *B. bjoerkna* and *L. gibbosus* which responded to vegetation cover, to be highest in areas of intermediate plant densities. Fish abundance is known to be higher in areas of intermediate level of structural complexity (CROWDER & COOPER 1979, SAVINO & STEIN 1982); but few studies investigated the role of plant structure in the protection against predation (DIONNE & FOLT 1991). CROWDER & COOPER (1982) showed that low macrophyte densities (associated with low prey biomass) and high macrophyte densities (associated with low feeding rates) constitute weakly profitable fish habitats. Thus intermediate macrophyte densities appear to be the best habitat altogether in terms of feeding, growth, and stability of predator-prey interactions.

Conclusions

The results obtained in this study confirm that (1) habitat occupancy patterns of juvenile fish occur at different spatial scales, and suggest that (2) aquatic macrophytes affect fish habitat use, and (3) biotic variables can have strong implications in fish-habitat relationships. Therefore, this study emphasizes the necessity of considering the multi-scale structure of the river system, and biotic variables in fish-habitat studies.

In the future, our models should be tested on data from other systems to check which variables are useful in more general models on fish-habitat relationships. Integrating the estimation of macrophyte density would increase the predictive power of models that only use hydraulic variables at present. Other biotic variables (e.g. zooplankton abundance) should also be considered as habitat descriptors likely to influence juvenile fish distribution. As different macrophyte species offer different fish habitat qualities (e.g. trophic resources or refuge against predation), we may hypothesize that juvenile fish survival differs among vegetation types. As a result, we expect that inter-annual variability in macrophyte development could lead to differences in recruitment level, and affect fish population dynamics.

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