



Juvenile fishes in macrophyte beds: influence of food resources, habitat structure and body size

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Mean juvenile fish abundance and fish frequency in a large lowland river during low discharge largely differed among the unvegetated and three morphologically contrasted macrophyte habitats. Single separate models revealed that juvenile fish distribution was largely influenced by trophic variables. With the exception of *Leuciscus cephalus*, which responded mainly to physical variables (depth and substratum), multiple regression models emphasized the importance of trophic variables for fish distribution. For *Blicca bjoerkna*, *L. cephalus* and *Lepomis gibbosus*, habitat shifts with respect to prey size were apparent; small juvenile fishes mainly responded to small zooplankton abundance, whereas large individuals were more influenced by the abundance of large zooplankton. Whatever the species, predictions from multiple regression models were always better for large individuals. Small juvenile fishes appeared to be less affected by the habitat variables measured, and exhibited more uniform spatial distribution. The relative importance of trophic resources and habitat physical structure among macrophyte types for fish-habitat relationships is discussed, and the necessity of quantifying habitat structural complexity is emphasized.

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Key words: juvenile fish; food resources; habitat structure; macrophytes; body size.

INTRODUCTION

For running waters, most of the fish-habitat models, predicting fish preferences at the local scale, generally support the view that hydraulics is a major determinant of fish community structure (Lamouroux *et al.*, 1999). In large rivers, hydraulic conditions are more uniform, and other factors can be involved in patterns of fish habitat use. Among these factors, aquatic vegetation contributes to an increase in habitat structural complexity (Hutchinson, 1975; Chambers, 1987; Chambers & Kalff, 1987; Sand-Jensen & Mebus, 1996), and thus is an important determinant of fish habitat selection (Werner *et al.*, 1977; Crowder & Cooper, 1982; Killgore *et al.*, 1989; Chick & McIvor, 1994).

The two main factors that generally are invoked to explain the high density of fishes in vegetated habitats are availability of food and shelter against predation (Rozas & Odum, 1988). High prey densities are typically associated with macrophytes (Cyr & Downing, 1988; Paterson, 1993). However, morphological characteristics (e.g. size, number, orientation of leaves and stems) can greatly differ among macrophyte types (Chick & McIvor, 1994) and plant architecture is likely to influence both invertebrate and fish distributions (Cyr & Downing,

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1988; Dionne & Folt, 1991). Nevertheless, few studies have compared the effects of different macrophyte types on fish habitat use (Chick & McIvor, 1997).

Many experimental studies suggest that fish foraging efficiency is reduced in complex habitats (Crowder & Cooper, 1982; Diehl, 1988; Dionne & Folt, 1991). Fishes should experience higher habitat profitability at intermediate macrophyte density (Crowder & Cooper, 1982), which could represent the best compromise between food availability and foraging efficiency.

Foraging profitability and risk of predation are related to fish body size and many studies stress the importance of body size on biological processes (Werner & Hall, 1988). Fishes vary dramatically in size during their ontogenetic development, and exhibit complex life cycles and habitat-use patterns (Schlosser, 1991). Ontogenetic changes in both resource and habitat use have been documented in a variety of species (Werner & Gilliam, 1984), and body size appears to be a crucial variable in fish-habitat relationships.

The present study focuses on the analysis of juvenile (0 year) fish-habitat relationships in a large lowland river. Juvenile fish distribution is influenced by aquatic vegetation. During their first year of life, many fish species generally use similar resources and feed on zooplankton (Mehner & Thiel, 1999), so food resources can be quantified using zooplankton abundance. Finally, only recently has significant attention been given to early life stages in freshwater fish ecology (Copp, 1992a, b; Garner, 1996a). These stages constitute critical periods in fish life cycles because mortality rate is highest in young fishes and these stages exhibit narrow and specific habitat requirements, which are critical for the recruitment of a species (Schiemer *et al.*, 1991). Thus, defining fish-habitat relationships during early ontogeny appears essential in understanding fish population and whole community functioning.

In an earlier study (Grenouillet *et al.*, 2000), trophic conditions (estimated by the density of periphyton) was found to largely influence juvenile fish distribution. Therefore, it was stressed that future studies must make better estimates of trophic resources, and the necessity of considering zooplankton abundance as a descriptor of juvenile fish habitat was emphasized. As far as is known, there is no fish-habitat study that simultaneously documents habitat structure and food resources among various macrophyte types, and that examines interactions with both fish and prey body sizes. Thus, a key feature of this study is that habitat structure and food resources are examined among unvegetated areas and three morphologically contrasted macrophyte types. The following questions were addressed: (1) Which factors explain the spatial distribution of juvenile fishes among the various habitat types studied? (2) How does body size affect juvenile fish-habitat relationships?

As smaller fishes are more vulnerable than larger fishes to predation risk (Werner & Gilliam, 1984), they were expected to use denser macrophyte beds. It was also expected that the smallest juvenile fishes would be more affected by small-sized zooplankton abundance, and it was hypothesized that growing individuals should exhibit habitat shifts with respect to prey size, in order to exploit larger zooplanktons. To verify these hypotheses, four fish species, *Alburnus alburnus* (L.), *Blicca bjoerkna* (L.), *Leuciscus cephalus* (L.) and *Lepomis gibbosus* (L.), were selected, which were likely to exhibit different responses. For each species, juvenile fish were grouped into two size classes (smaller and larger

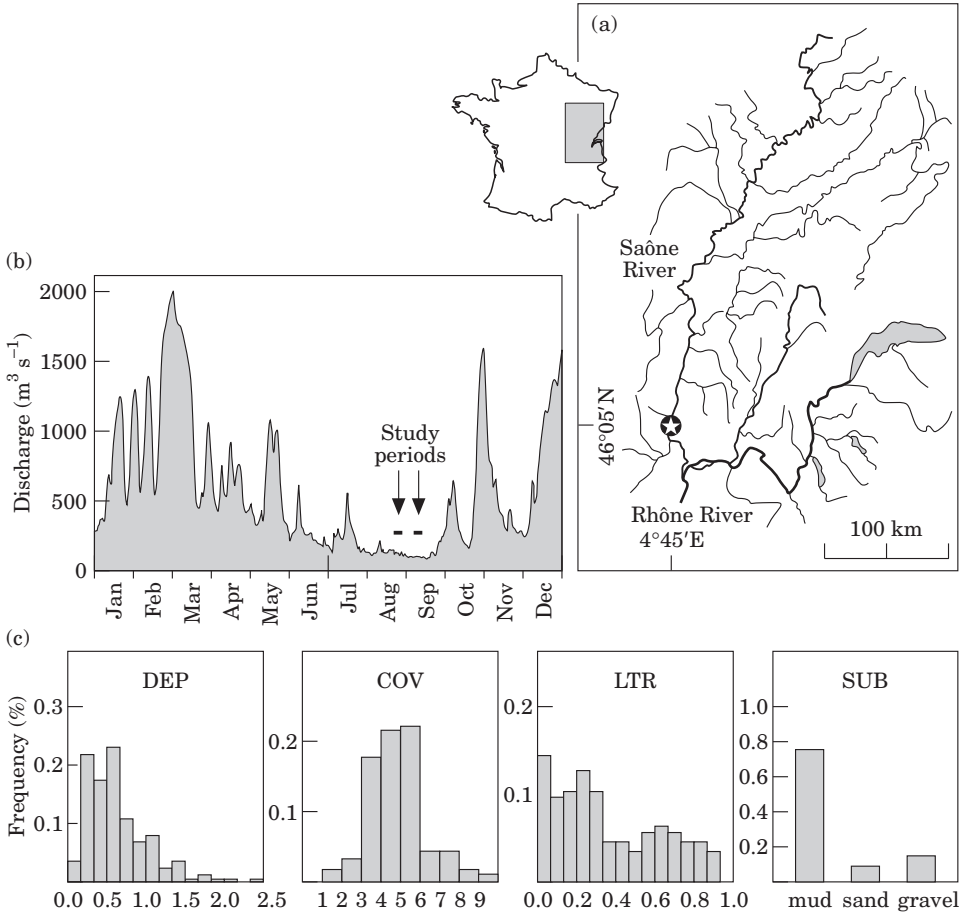


FIG. 1. Characteristics of the study site. (a) Location of the site (★) in the Saône River basin, France; (b) hydrological conditions during year 1998; (c) frequency distributions of habitat variables. DEP, depth (m); COV, total cover of vegetation (units explained in the text); LTR, % transmitted light; SUB, substratum.

than the median length of the species), and different patterns of habitat use between small and large juvenile fish were examined.

In this study, the occurrence of four species in relation to both physical and trophic variables were modelled using logistic regressions. First, relationships between each variable and the presence or absence of fish species were examined. Second, the probability of occurrence of fish species as a function of one or more independent variables using stepwise regression models was predicted. Thirdly, these results were compared with those obtained from linear models predicting juvenile fish abundance.

MATERIALS AND METHODS

STUDY AREA

The study site [Fig. 1(a)] was located near Belleville-sur-Saône in the lower part of the River Saône, France, 50 km above the confluence with the Rhône. This site was on a

tributary, with a length of 2 km, a slope of $<0.8 \text{ m km}^{-1}$, a mean width of 60 m, and a mean mid-section depth of 5 m.

The study period, 17–20 August and 6–9 September 1999, was chosen as (1) discharge was extremely low within the main channel ($90\text{--}100 \text{ m}^3 \text{ s}^{-1}$) [Fig. 1(b)], (2) all juvenile fishes had completed their larval development at the sampling time and attained a sufficient size to be caught by electrofishing, and (3) densities of juvenile fishes were known to stabilize after the end of the spawning season in late August and early September (Copp, 1989a).

MACROPHYTE BEDS AND SAMPLING DESIGN

Three morphologically contrasted species were selected: *Ceratophyllum demersum* (CER, with whorled leaves, entirely submerged and free-floating), *Nuphar lutea* (NUP, unarmed with mostly floating, but sometimes partly emergent, lead blades) and *Sagittaria sagittifolia* (SAG, with submerged or floating leaves; usually linear, mostly flat but sometimes inflated and spongy). In an earlier study, Grenouillet *et al.* (2000) showed that macrophyte development led to the presence of mainly (90%) monospecific macrophyte beds for these three species. In the present study, NOVEG was used to define sampling points where no plant species were present.

The sampling design consisted of a stratified random sampling programme, with sampling points randomly located within each type of habitat. In total, 175 samples were obtained, in NOVEG (37), CER (46), NUP (42) and SAG (50) habitats.

HABITAT DESCRIPTION

At each sampling point, where the current velocity was zero during the study period, qualitative and quantitative variables were used to evaluate microhabitat characteristics: Depth (DEP) was measured to the nearest cm. Total cover of vegetation (COV) was estimated by summing the cover of all plant species. Cover of each plant species was estimated using a 1 m^2 quadrat divided into 25 compartments. In each compartment, macrophyte cover was estimated for each species by visual observation of percentage cover; five scores were used: 0 (absent), 1 ($<5\%$), 2 (5–25%), 3 (25–50%), 4 (50–75%) and 5 ($>75\%$). For each plant species, the 25 scores recorded were then averaged to provide an index of cover, ranging from 0 to 5. Transmitted light (LTR) was measured using a LI-192SA Underwater Quantum Sensor ($\mu\text{mol s}^{-1} \text{ m}^{-2}$) and expressed as a percentage of light intensity at 0.3 m depth in the macrophyte bed compared to that just below the surface. Substratum (SUB) was defined using three qualitative variables: mud, sand and gravel.

ZOOPLANKTON SAMPLING

At each sampling point, water samples were collected in triplicate using an 8 cm diameter tube opened at both ends to determine zooplankton abundance. The tube was lowered vertically into the water and then closed at the bottom by a watertight sphere. This apparatus allowed the water column to be sampled where fishes were collected, i.e. the first 50 cm under the surface (or less at shallower points). Water samples (mean volume $5.1 \pm 2.1 \text{ l}$) were then filtered through a $40 \mu\text{m}$ mesh, and preserved in 5% formalin. At least 300 individuals in each subsample were counted and measured under a stereomicroscope at $\times 40$ magnification. Three size classes were defined: individuals $<0.5 \text{ mm}$ (Z1), individuals >0.5 and $<1 \text{ mm}$ (Z2) and individuals $>1 \text{ mm}$ (Z3). Zooplankton abundance was calculated for these three size classes.

JUVENILE FISH SAMPLING

Juvenile (0+ year) fishes were sampled by electrofishing using the point abundance sampling method (Nelva *et al.*, 1979; Persat & Copp, 1990). Following Copp (1989b, 1992a), a portable electrofishing apparatus with an anode diameter of 10 cm was used, and each point sample consisted of submersion of the activated anode to *c.* 50 m depth. Immobilized fishes were then collected using three vertical sweeps with a 25 cm diameter pond net, thus providing a quantitative sample (Copp & Garner, 1995). After capture,

the fishes were identified to species, measured to the nearest millimetre (total length, L_T , mm) and returned to the water. Only juvenile breams *B. bjoerkna* and *Abramis brama* (L.) were preserved in 4% formalin and identified in the laboratory. All other species were identified in the field. For each species, two size classes were defined: fish smaller (class 1) and fish larger (class 2) than the median length of the species.

DATA ANALYSIS

Juvenile fish presence or absence was modelled using logistic regression (Sokal & Rohlf, 1995) for four fish species and two size classes. The presence or absence response curve of a species (Ter Braak & Looman, 1986) describes the probability of the species being present, p , as a function of an environmental variable x . Three possible response types were expected: non-significant (model 1), $\log[p(1-p)^{-1}] = \beta_0$; logistic (model 2), $\log[p(1-p)^{-1}] = \beta_0 + \beta_1 x$; Gaussian (model 3), $\log[p(1-p)^{-1}] = \beta_0 + \beta_1 x + \beta_2 x^2$ where β_0 , β_1 and β_2 are regression parameters. To assess the significance of the estimated parameters β_1 and β_2 , each variable x was applied to the three models. Likelihood ratio tests were used to compare the predictive value of the models (Trexler & Travis, 1993; Sokal & Rolf, 1995). If the addition of a parameter significantly ($P < 0.05$) reduced the unexplained deviance, then the parameter was included in the logistic model. The reduction of deviance was used to assess the contribution of a model to the explanation of the variance in the data set (Peeters & Gardeniers, 1998).

Finally, stepwise logistic procedures were used to select significant variables which explained most of the deviance in fish occurrence. Except for vegetation type (VGTYPE), all habitat variables were used to build the models and each quantitative variable (x) was tested as a second order polynomial (x and x^2). At each step, a new variable was added to the model if it significantly ($P < 0.05$) reduced the unexplained deviance using the Akaike criterion. When models were selected, the variable VGTYPE was added to other selected variables, and likelihood ratio tests were applied to compare the predictive value of model including VGTYPE with those not including it. By this way, the effect of VGTYPE was tested after having removed the effects of variables added previously in the model.

The same procedure was used to model juvenile fish abundance (number of individuals per sampling point). Prior to the analysis, juvenile fish abundance was $\ln(x+1)$ -transformed, to reduce the over-emphasis of large samples and to spread the distribution more evenly through its range. Stepwise linear models were performed and only significant ($P < 0.05$) variables were included in the models. Then likelihood ratio tests were used to test the effect of VGTYPE on unexplained variance.

The multiple logistic models were validated as follows. First, one sample was removed. Second, the model was applied to the remaining samples and model coefficients were computed. Thirdly, the model was used to predict probability of fish presence in the sample previously removed. This procedure was repeated after removing another sample, and probability of fish presence was predicted in all samples this way. Then expected probability P was rounded off to 0 (if $P < 0.5$) or 1 (if $P \geq 0.5$). The similarity between observed and predicted distributions was then assessed by the proportion of correct predictions (Leftwich *et al.*, 1997).

For linear model validations, expected fish abundance was calculated in each sample from models built on the other samples. Then, models were tested by performing linear regression analysis to compare observed and expected fish abundance with perfect agreement (slope=1 and constant=0) using t -tests (Sokal & Rohlf, 1995). S-PLUS (MathSoft, 1998) was used for data analyses.

RESULTS

No significant difference was apparent among the two sampling dates for both habitat and zooplankton variables (date effect in random effect ANOVA, $P > 0.05$ for each variable). Therefore, the two sampling periods were pooled to investigate fish habitat use.

HABITAT AND ZOOPLANKTON CHARACTERISTICS AMONG THE DIFFERENT VEGETATION TYPES

Characteristics of habitat variables and zooplankton abundance measured in the 175 point samples are presented in Table I. Only substratum did not differ significantly among vegetation types, which were all frequently encountered on mud substratum. NOVEG and SAG habitats had the lowest mean water depth, whereas mean water depth was highest in CER and intermediate in NUP habitats. Mean cover of vegetation was highest in NUP habitats, with similar values in CER and SAG habitats. The percentage of transmitted light differed among vegetated and unvegetated habitats, with macrophyte beds characterized by lower transmitted light. Moreover, differences were also apparent among the three macrophyte types, with highest values in NUP, whereas similar values were observed in CER and SAG habitats.

For zooplankton abundance, the three size classes showed lowest values in NOVEG habitats. The smallest size class (Z1) showed highest values in SAG, whereas the other two (Z2 and Z3) showed highest values in CER and SAG, with intermediate values in NUP habitats. The three zooplankton variables were correlated among themselves, with $r^2=0.84$, 0.62 and 0.56 between Z1 and Z2, Z2 and Z3, and Z1 and Z3, respectively. The other correlations among habitat variables were all <0.4 .

JUVENILE FISH CHARACTERISTICS AMONG THE DIFFERENT VEGETATION TYPES

A total of 1005 juvenile fishes of fourteen species was caught in the 175 point samples. The four most abundant species accounted for 85% of the total caught: *A. alburnus* ($n=229$), *B. bjoerkna* ($n=59$), *L. cephalus* ($n=349$) and *L. gibbosus* ($n=216$).

L_T ranged from 10 to 50 mm for *A. alburnus* (median length=32 mm), from 17 to 48 mm for *B. bjoerkna* (median length=35 mm), from 10 to 85 mm for *L. cephalus* (median length=32 mm) and from 10 to 49 mm for *L. gibbosus* (median length=23 mm). The four species differed in body length (species effect in random effect ANOVA, $n=853$, $F_{1,3}=54.43$, $P<0.001$). *Lepomis gibbosus* was characterized by a smaller mean L_T ($P<0.001$ for all pairwise comparisons in Tukey–Kramer tests), and the three other species did not differ in their mean L_T ($P>0.05$ for all pairwise comparisons).

L_T differed significantly among the two sampling dates for *B. bjoerkna*, *L. cephalus* and *L. gibbosus* (date effect in random effect ANOVA, $P<0.001$ for the three species) but no significant difference was apparent for *A. alburnus* ($P=0.204$). However, length-frequency distributions of the four species overlapped broadly among the two sampling dates (Fig. 2).

When two size classes for each species were distinguished, significant differences in both frequency and mean fish abundance were apparent among the different habitats (Table II). Highest fish frequency and mean abundance values were observed in SAG habitats. For frequency values, only small *B. bjoerkna* and large *L. gibbosus* showed no significant differences among the three macrophyte types. Large *L. cephalus* and small *L. gibbosus* also showed high frequencies in NUP and CER, respectively. For juvenile fish abundance, only

TABLE I. Habitat conditions and zooplankton abundance among vegetation types

	Codes	Range (min-max)	Vegetation type			P
			NOVEG (n=37)	CER (n=46)	NUP (n=42)	
Habitat variables	DEP	(0.12-2.50)	0.43 ^a	0.95 ^b	0.65 ^c	0.47 ^a
	COV	(0.00-9.50)	—	4.29 ^a	5.15 ^b	4.36 ^a
	LTR	(0.01-0.92)	0.70 ^a	0.22 ^b	0.34 ^c	0.27 ^b
	SUB mud sand gravel		81.08 10.81 8.11	78.26 6.52 15.22	78.57 7.14 14.29	68.00 12.00 20.00
Zooplankton abundance	Z1 (<0.5 mm)	(2.26-8.39)	3.38 ^a	5.72 ^b	4.54 ^c	6.36 ^d
	Z2 (0.5-1.0 mm)	(0.00-6.55)	1.07 ^a	3.95 ^b	2.34 ^c	3.90 ^b
	Z3 (>1.0 mm)	(0.00-4.97)	0.23 ^a	2.50 ^b	0.85 ^c	2.22 ^b

Proportions (%) are presented for categorical variables, minimum, maximum and mean values are presented for continuous variables.

Codes for habitat variables as in Fig. 1. Zooplankton abundance (number l⁻¹) is ln-transformed. NOVEG, No vegetation; CER, *Ceratophyllum demersum* dominated beds; NUP, *Nuphar lutea* dominated beds; SAG, *Sagittaria sagittifolia* dominated beds.

For each quantitative variable, values among vegetation types with a common letter are not significantly different at P=0.05 (Tukey-Kramer test). Probabilities P (NS, not significant) are given for testing the type of vegetation effect on each variable (ANOVA and χ^2 tests for continuous and categorical variables, respectively).

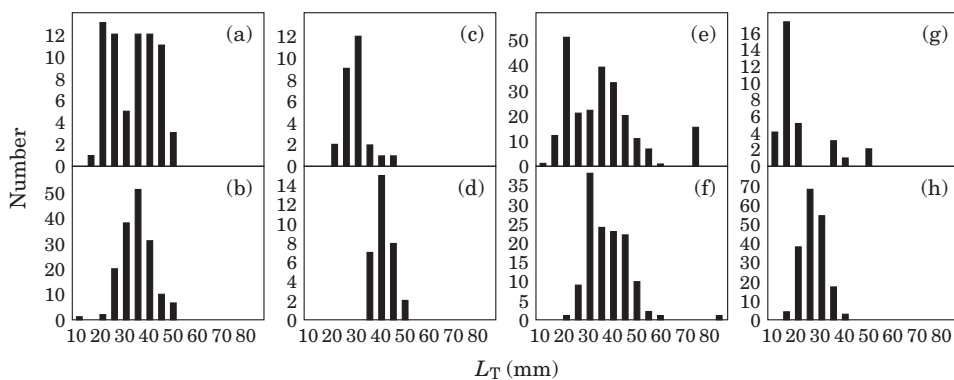


FIG. 2. Length distributions of (a), (b) *Alburnus alburnus*; (c), (d) *Blicca bjoerkna*; (e), (f) *Leuciscus cephalus*; (g), (h) *Lepomis gibbosus*. Upper plots, first sampling period; lower plots, second sampling period. (a) $n=69$, median=32 mm; (b) $n=160$, median=27 mm; (c) $n=27$, median=39 mm; (d) $n=32$, median=39 mm; (e) $n=218$, median=31 mm; (f) $n=31$, median=33 mm; (g) $n=32$, median=15 mm; (h) $n=184$, median=24 mm.

small *B. bjoerkna* did not exhibit significant response to the type of vegetation. Highest values of abundance were observed in SAG habitats. Large *L. cephalus* and small *L. gibbosus* also showed high abundance values in NUP and CER, respectively. A strong correlation between mean abundance and frequency was apparent ($r^2=0.93$; Fig. 3).

SINGLE VARIABLE SEPARATE ANALYSIS FOR FISH OCCURRENCE V. HABITAT VARIABLES

Depth (DEP) had no significant effect on the occurrence of small individuals, whereas large *B. bjoerkna* and *L. cephalus* exhibited the same logistic response, with marked preferences for shallow water (Table III; Fig. 4). For vegetation cover (COV), small *B. bjoerkna* and large *L. cephalus* showed maximum probabilities of occurrence for highest cover values, and small and large *L. gibbosus* showed Gaussian response curves with maximum probabilities of occurrence under intermediate vegetation cover. For transmitted light (LTR), a Gaussian response curve was apparent for large individuals of *A. alburnus*, *B. bjoerkna* and *L. gibbosus*, whereas small *L. gibbosus* exhibited a logistic response with maximum probabilities of occurrence for lowest transmitted light values.

For abundance of three zooplankton size classes, only large *L. cephalus* exhibited a Gaussian response for the abundance of the smallest zooplankton (Z1), with maximum probabilities of occurrence close to the highest values observed (Table III; Fig. 5). All other significant responses were characterized by a positive effect of zooplankton abundance on juvenile fish occurrence. Abundance of Z1 had a significant effect for all species, and for both small and large individuals. Occurrence of large *L. cephalus* was not influenced by the abundance of Z2. Z3 had a significant effect for large *A. alburnus*, small *B. bjoerkna*, and small and large *L. gibbosus*.

TABLE II. Frequency of occurrence and mean abundance for juvenile fishes among the different vegetation types

Fish variable	Fish species	Small fish				Large fish					
		NOVEG	Vegetation type CER	NUP	SAG	P	NOVEG	Vegetation type CER	NUP	SAG	P
Frequency	<i>Aal</i>	0.03 ^a	0.11 ^b	0.02 ^a	0.36 ^c	<0.001	0.00 ^a	0.06 ^a	0.02 ^a	0.38 ^b	<0.001
	<i>Bbj</i>	0.00 ^a	0.09 ^b	0.07 ^b	0.18 ^b	0.011	0.00 ^a	0.02 ^a	0.05 ^a	0.22 ^b	<0.001
	<i>Lee</i>	0.08 ^a	0.15 ^a	0.14 ^a	0.42 ^b	<0.001	0.13 ^a	0.13 ^a	0.31 ^b	0.48 ^b	<0.001
	<i>Lgi</i>	0.03 ^a	0.28 ^b	0.07 ^a	0.38 ^b	<0.001	0.00 ^a	0.15 ^b	0.21 ^b	0.26 ^b	<0.001
	<i>Aal</i>	0.06 ^a	0.13 ^a	0.04 ^a	0.49 ^b	<0.001	0.00 ^a	0.14 ^a	0.03 ^a	0.62 ^b	<0.001
Mean abundance	<i>Bbj</i>	(0.24)	(0.39)	(0.09)	(1.46)	NS	(0.00)	(0.61)	(0.05)	(1.90)	<0.001
		0.00 ^a	0.10 ^a	0.08 ^a	0.16 ^a		0.00 ^a	0.02 ^a	0.03 ^a	0.25 ^b	
		(0.00)	(0.20)	(0.17)	(0.26)		(0.00)	(0.02)	(0.05)	(0.54)	
	<i>Lee</i>	0.23 ^a	0.15 ^a	0.19 ^a	0.53 ^b	0.014	0.16 ^a	0.18 ^a	0.45 ^b	0.62 ^b	0.002
	<i>Lgi</i>	(1.54)	(0.28)	(0.43)	(1.58)		(0.38)	(0.46)	(1.43)	(1.74)	
	0.02 ^a	0.31 ^b	0.07 ^a	0.48 ^b	<0.001	0.00 ^a	0.14 ^a	0.20 ^a	0.50 ^b	<0.001	
	(0.03)	(0.72)	(0.14)	(1.26)		(0.00)	(0.30)	(0.36)	(1.68)		

Codes for vegetation types as in Table I. *Aal*, *Alburnus alburnus*; *Bbj*, *Blittec hjoerkna*; *Lee*, *Leuciscus cephalus*; *Lgi*, *Lepomis gibbosus*. For each species, small fish and large fish grouped: individuals smaller and individuals larger than the median length of the species respectively.

For mean fish abundance, given are ln(x+1)-transformed data, with mean number of individuals per sampling point in brackets.

For each variable, values among vegetation types with a common letter are not significantly different at $P=0.05$ (pairwise logistic comparison and Tukey–Kramer tests). Probabilities P (NS, not significant) are given for testing the type of vegetation effect on each fish variable.

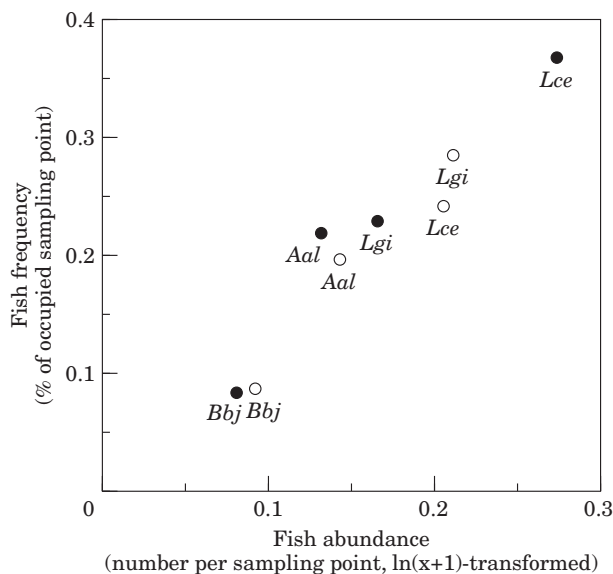


FIG. 3. Abundance-frequency relationship. For each fish species, abundance and frequency are calculated from two size-classes: individuals smaller (●) and individuals larger (○) than the median length of the species. Species codes as in Table II.

MULTIPLE REGRESSION MODELS FOR JUVENILE FISH PRESENCE OR ABSENCE AND ABUNDANCE

For each species, multiple logistic and linear regression models showed non-uniform distribution of juvenile fishes (Table IV). Clear differences appeared between species, and, for one species, between the two size-classes.

For small fish, both logistic and linear models showed that trophic variables were of first importance. In particular, the abundance of small zooplankton (Z1) was the only variable retained in linear models for *A. alburnus*, *B. bjoerkna* and *L. gibbosus*, whereas abundance of small *L. cephalus* was explained mainly by substratum and depth. For logistic models, Z1 was the most important variable for the four species. *Alburnus alburnus* also responded to depth, whereas *L. cephalus* and *L. gibbosus* responded to transmitted light (LTR).

For large fish, Z1 was always the most important variable explaining both occurrence and abundance for *A. alburnus*, *B. bjoerkna* and *L. gibbosus* (Table IV). Occurrence of large *A. alburnus* was also explained by vegetation cover (COV) and for both occurrence and abundance data, the type of vegetation (VGTYPE) was significant. Large *B. bjoerkna* also responded to the abundance of larger zooplankton in both logistic and linear models. For large *L. cephalus*, depth, substratum and the abundance of smallest zooplankton explained both occurrence and abundance. For large *L. gibbosus*, occurrence was also explained by vegetation cover and the type of vegetation, whereas abundance was influenced by all three zooplankton size classes, with a most important effect of smallest zooplankton.

Percentage of total deviance reduced by logistic regression models varied from 10.2% for small *B. bjoerkna* to 50.0% for large *B. bjoerkna*, and percentage of

TABLE III. Estimated values for parameters β_0 , β_1 and β_2 from simple logistic regression models

Habitat variable	Fish species	Small fish			Large fish				
		β_0	β_1	β_2	Reduction in deviance (%)	β_0	β_1	β_2	Reduction in deviance (%)
DEP	<i>Aal</i>	—	—	—	NS	—	—	—	NS
	<i>Bbj</i>	—	—	—	NS	-1.16	-2.51	—	6.67
	<i>Lce</i>	—	—	—	NS	0.11	-1.91	—	6.50
	<i>Lgi</i>	—	—	—	NS	—	—	—	NS
COV	<i>Aal</i>	—	—	—	NS	—	—	—	NS
	<i>Bbj</i>	-3.31	0.24	—	4.03	—	—	—	NS
	<i>Lce</i>	—	—	—	NS	-1.58	0.16	—	2.16
	<i>Lgi</i>	-4.30	1.49	-0.16	12.65	-8.48	2.94	-0.28	17.88
LTR	<i>Aal</i>	—	—	—	NS	-2.07	6.23	-12.75	9.23
	<i>Bbj</i>	—	—	—	NS	-2.77	8.86	-19.27	11.27
	<i>Lce</i>	—	—	—	NS	—	—	—	NS
	<i>Lgi</i>	-0.05	-4.67	—	16.70	-1.74	9.39	-23.69	19.16
Z1	<i>Aal</i>	-5.57	0.67	—	15.27	-6.56	0.81	—	21.60
	<i>Bbj</i>	-5.48	0.56	—	9.97	-11.47	1.44	—	49.61
	<i>Lce</i>	-3.66	0.44	—	7.03	-8.04	2.42	-0.19	6.29
	<i>Lgi</i>	-5.08	0.67	—	16.60	-6.17	0.80	—	22.18
Z2	<i>Aal</i>	-3.40	0.48	—	8.87	-4.37	0.70	—	18.17
	<i>Bbj</i>	-3.58	0.38	—	5.25	-4.82	0.66	—	14.53
	<i>Lce</i>	-2.30	0.31	—	4.08	—	—	—	NS
	<i>Lgi</i>	-3.24	0.57	—	13.25	-3.69	0.60	—	14.45
Z3	<i>Aal</i>	—	—	—	NS	-2.86	0.51	—	8.45
	<i>Bbj</i>	-3.02	0.39	—	4.57	—	—	—	NS
	<i>Lce</i>	—	—	—	NS	—	—	—	NS
	<i>Lgi</i>	-2.41	0.57	—	11.51	-2.40	0.43	—	6.20

Fish occurrence is expressed as a second order polynomial function of habitat variable x . Reduction in deviance (NS, not significant) is given. Abbreviations for habitat variables as in Table I and species codes as in Table II.

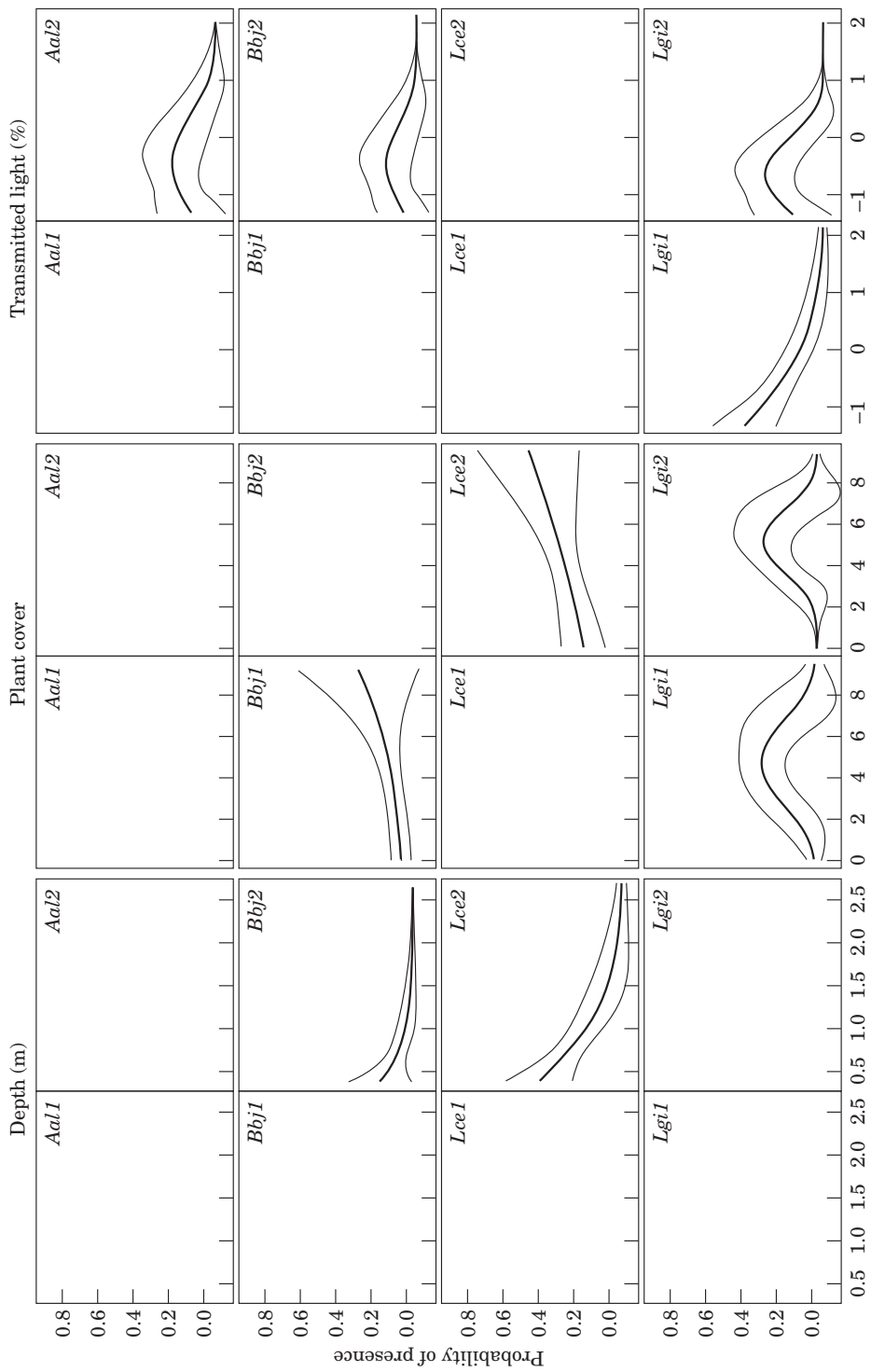


FIG. 4. Probability of presence of fish species *v.* physical variables. —, Expected frequency from logistic models (see Table III for parameter values) $\pm 95\%$ CI (---). Abbreviations for habitat variables as in Table I and species codes as in Table II. For each species, significant models are shown for individuals smaller (1) and individuals larger (2) than the median length of the species. Blank spaces indicate that species and size-classes were not significant.

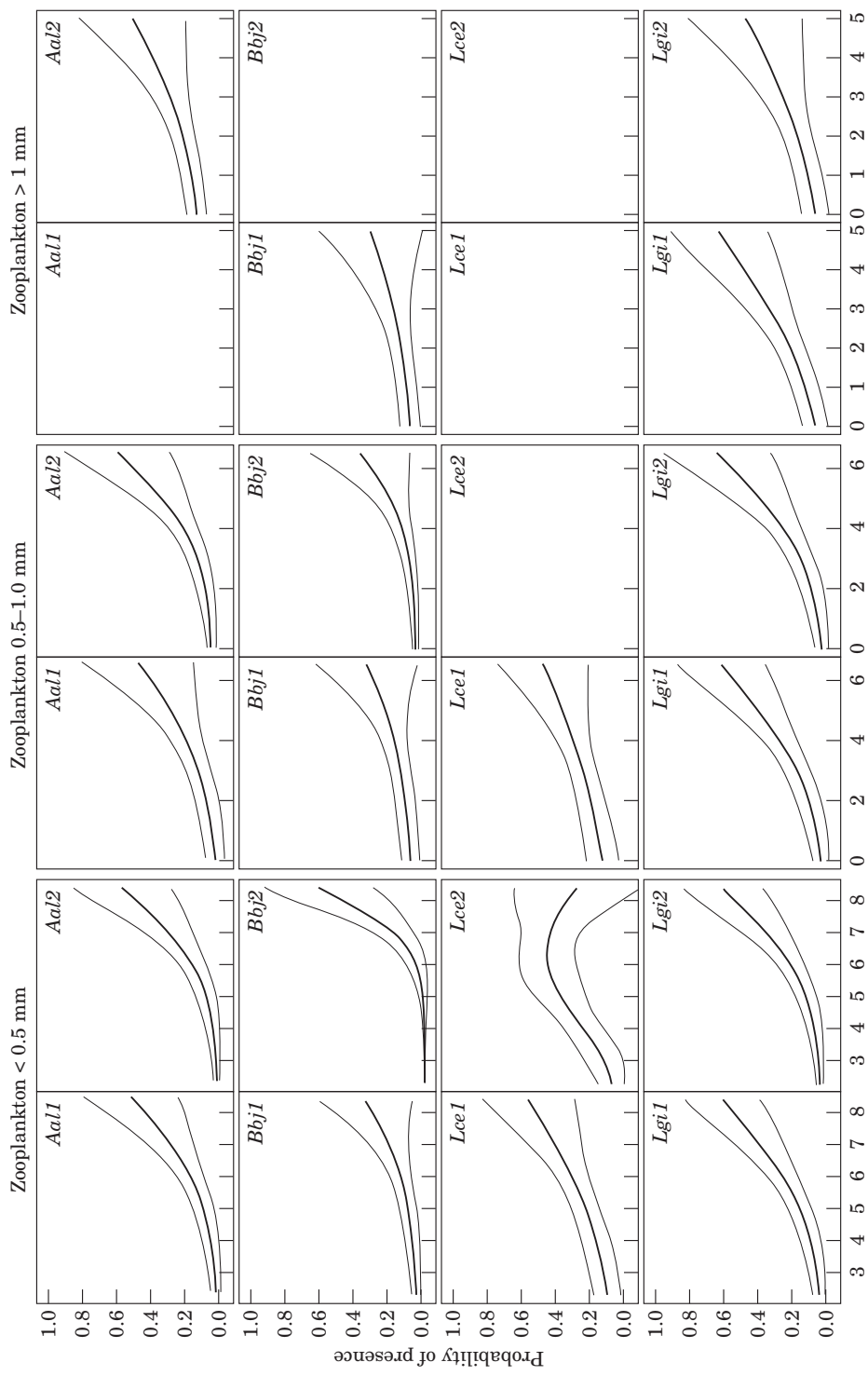


FIG. 5. Probability of presence of fish species v. trophic (zooplankton) variables. See FIG. 4 for further details.

TABLE IV. Stepwise regression models for juvenile fish species

Fish variables	Habitat variables and statistical values		d.f.	Small fish			Large fish		
	<i>Aal</i>	<i>Bbj</i>		<i>Lce</i>	<i>Lgi</i>	<i>Aal</i>	<i>Bbj</i>	<i>Lce</i>	<i>Lgi</i>
Juvenile fish occurrence									
DEP	41.6**	NS	NS	NS	NS	NS	NS	NS	NS
SUB	NS	NS	NS	NS	NS	NS	NS	31.9**	NS
COV	NS	NS	NS	NS	NS	20.5**	NS	32.4***	NS
LTR	NS	NS	37.7*	26.5*	NS	NS	NS	NS	23.1***
Z1	58.4***	100**	62.3**	73.5***	47.1***	NS	66.4***	NS	NS
Z2	NS	NS	NS	NS	NS	NS	21.0**	35.8***	NS
Z3	NS	NS	NS	NS	NS	NS	12.7*	NS	NS
VGTYPE	NS	NS	NS	NS	NS	32.4**	NS	NS	20.1*
Total deviance	143.54	107.04	180.55	177.88	136.18	97.57	205.62	157.16	32.5
Reduction in deviance (%)	18.8	10.2	11.8	19.4	37.3	50.0	19.9	19.9	32.5
Juvenile fish abundance									
DEP	NS	NS	NS	NS	NS	NS	NS	NS	NS
SUB	NS	NS	NS	NS	NS	NS	NS	18.2***	NS
COV	NS	NS	62.2***	NS	NS	NS	NS	54.4***	NS
LTR	NS	NS	NS	NS	NS	NS	NS	NS	NS
Z1	100***	100**	NS	NS	NS	NS	NS	NS	NS
Z2	NS	NS	NS	NS	NS	NS	NS	NS	NS
Z3	NS	NS	NS	NS	NS	NS	NS	NS	NS
VGTYPE	NS	NS	NS	NS	NS	NS	NS	NS	NS
Total variance	52.57	15.52	73.63	50.13	64.70	16.67	81.30	57.60	41.6
Variance explained (%)	10.7	5.3	8.2	18.2	20.7	33.1	29.5	29.5	41.6

Stepwise multiple logistic regressions were performed for juvenile fish occurrence, and stepwise linear regressions were performed for juvenile fish abundance ($\ln(x+1)$ -transformed). Abbreviations and species codes as in Table I and Table II, respectively. VGTYPE, Type of vegetation. Note that the quantitative variables (DEP, COV, LTR, Z1, Z2 and Z3) are included in the model as a second order polynomial form. Given are degrees of freedom d.f., percentage of reduced deviance for each habitat variable in logistic models, and percentage of explained variance for each habitat variable in linear models. Asterisks denote parameters that are significantly different from zero at $P < 0.05^*$, $P < 0.01^{**}$, or $P < 0.001^{***}$ (NS, not significant).

variance explained by linear multiple regression models varied from 5.3% for small *B. bjoerkna* to 41.6% for large *L. gibbosus* (Table IV). For each species, a larger part of variability was explained for largest individuals than for the smallest ones, in both logistic and linear regression models.

VALIDATION OF THE MODELS

Relationships between expected and observed values of juvenile fish occurrence indicate the ability of logistic models to correctly predict (1) the presence or absence of juvenile fishes from all samples, (2) the presence of juvenile fishes from samples where fishes were present, and (3) absence of juvenile fishes from samples where fishes were absent (Table V). For abundance data, the ability of linear regression models to correctly predict the abundance of juvenile fishes by testing the linear relationship between expected and observed fish abundance is indicated (Table V). For juvenile fish occurrence, models correctly predicted presence and absence of species for 76–91.4% of samples. However, when examining only samples where fishes were present, models did not predict correctly the presence of small individuals of two species: *A. alburnus* and *B. bjoerkna*. For other species, models correctly predicted the presence of juvenile fishes for 8.11–37.9% of samples. The models predicted absence more accurately than presence (for 92.8–100% of samples). For juvenile fish abundance, validation of the models on independent samples showed that models correctly predicted juvenile fish abundance for all fish species. Regression lines for expected *v.* observed abundance did not differ from the perfect agreement (constant did not differ from zero and slope did not differ from one).

DISCUSSION

The aim of this study was to investigate juvenile fish-habitat relationships and to examine fish spatial distribution among unvegetated areas and three morphologically contrasted macrophyte types. Four species were selected, each divided into two size classes. Two questions were addressed concerning (1) the factors which explain the spatial distribution of juvenile fishes among the various habitats studied, and (2) the influence of body size on relationships between juvenile fishes and both physical and trophic variables.

Results indicated that for each fish species, mean abundance and frequency differed among the various habitat types studied. As all habitat variables, except substratum, differed among habitat types, the three vegetation types offered contrasting conditions, both physical (depth, cover and transmitted light) and trophic (zooplankton abundance). The findings are thus in accordance with previous studies suggesting that differences in morphological characteristics among macrophyte types can result in different habitat quality and thus are likely to affect fish habitat use (Dionne & Folt, 1991). Trophic variables appeared to be the most important. In particular, the abundance of small zooplankton largely influenced juvenile fish distribution, except for *L. cephalus* which was more related to physical variables.

The study indicated that great differences in zooplankton abundance occur not only among vegetated and unvegetated areas, but also among the different types of vegetation. The macrophytes studied greatly differed in their morphological

TABLE V. Validation of regression models for occurrence and abundance of juvenile fishes

Fish species	Expected <i>v.</i> observed juvenile fish occurrence (% correct predictions)			Expected <i>v.</i> observed juvenile fish abundance		r^2
	All samples	Fishes present	Fishes absent	Slope		
				Constant Coefficient (\pm s.e.)	Coefficient (\pm s.e.)	
Small fish						
<i>Aal</i>	84.57	0.00	98.67	0.039(\pm 0.060)	0.801(\pm 0.226)	NS
<i>Bbj</i>	90.86	0.00	100.00	0.029(\pm 0.036)	0.674(\pm 0.323)	NS
<i>Lce</i>	76.00	8.11	94.20	0.097(\pm 0.086)	0.660(\pm 0.252)	NS
<i>Lgi</i>	78.29	22.22	92.81	0.026(\pm 0.055)	0.892(\pm 0.165)	NS
Large fish						
<i>Aal</i>	88.00	34.78	96.05	0.032(\pm 0.054)	0.852(\pm 0.154)	NS
<i>Bbj</i>	91.43	28.57	96.89	0.008(\pm 0.022)	0.909(\pm 0.116)	NS
<i>Lce</i>	77.14	35.42	92.91	0.029(\pm 0.064)	0.915(\pm 0.121)	NS
<i>Lgi</i>	85.71	37.93	95.21	0.027(\pm 0.042)	0.881(\pm 0.095)	NS

Abbreviations and models retained for each fish species as in Table IV. For expected *v.* observed juvenile fish occurrence, given is the proportion (%) of correct predictions. Results are presented for all samples ($n=175$), samples where fish were present and samples where fish were absent. Expected *v.* observed juvenile fish abundance is tested by linear regression analysis. Probabilities P (NS, not significant) for regression statistics are given for testing whether constants and slopes are significantly different from zero and one, respectively (t -tests).

characteristics. Previous studies focused on the relationship between plant architecture and invertebrate distribution. For example, Krecker's (1939) model is based on the concept that plant surface area increases with leaf dissection and states that the most dissected plant species support the highest abundance of invertebrates. In the present study, *C. demersum* and *S. sagittifolia* supported the highest values of zooplankton abundance. According to their morphology, these two plant species can be described as more complex than *N. lutea*, and, therefore, the present data support the hypothesis of Krecker (1939). Moreover, small zooplankton was more abundant in *S. sagittifolia* than in *C. demersum*. This result suggests that the distribution of zooplankton among vegetation types is not only influenced by plant architecture but can also be size-dependent. Therefore, relationships between structural complexity of macrophytes and zooplankton body size, although poorly investigated, could be useful for the understanding of vegetation use by fishes.

The smallest juvenile fishes were expected to be more related to small zooplankton abundance, and this was verified for small fishes as only small zooplankton abundance was retained in both logistic and linear models. For large fishes, the abundance of small zooplankton was also the most important variable for *A. alburnus*, *B. bjoerkna* and *L. gibbosus*, but other zooplankton size classes were also significant for *B. bjoerkna*, *L. cephalus* and *L. gibbosus*.

Thus, the present results suggest that fish habitat use can vary according to resource availability, and the definition of different prey size classes appears to be useful in the understanding of fish-macrophyte relationships. Investigating relationships between juvenile fish distribution and zooplankton body size could reflect fish prey preferences. Habitat shifts with respect to prey size have been observed both in experimental and field studies (Mittelbach, 1981) and have been discussed in the light of optimal foraging theory. Some studies revealed species-specific dietary selection by juvenile fishes (Garner, 1996a), but other studies revealed large overlaps in the range of prey sizes eaten between fish size classes (Hall *et al.*, 1970; Keast, 1977; Werner *et al.*, 1977). Fish diet investigations should now be conducted to verify if observed habitat shifts, with respect to available prey size, also correspond to shifts in consumed prey.

Multiple regression models showed that depth influenced occurrence of small *A. alburnus* and large *L. cephalus* which preferred shallow water. Similar results were found in the Upper Rhône (Copp, 1992b), the Lower Rhône (Poizat & Pont, 1996), the Garonne (Gozlan *et al.*, 1998) and the Great Ouse (Garner, 1996a,b). However, these previous studies generally showed that depth was a crucial factor for fish habitat selection, with most juvenile fish species associated with shallow water (Copp, 1992b; Garner, 1996a). As a result, depth is frequently considered as a main factor resulting in inter-specific habitat segregation, and has been described as an anti-predator (Schlosser, 1988) or competitive (Clark & Levy, 1988) refuge.

In the present study, only two of the eight models revealed a significant effect of depth. This result is in accordance with other studies that examined macrophyte habitats of juvenile fishes, and that underlined the presence of vegetation as the most influential factor, with water depth being of lesser importance (Copp, 1993, 1997; Poizat & Pont, 1996). Similarly, weak relationships between depth and juvenile fish distribution were documented in lacustrine

systems (Bryan & Scarnecchia, 1992) and suggested that the effects of depth and vegetation cover could interact. Thus, the strong depth-related distribution of juvenile fishes observed in rhitronic systems is not a general pattern, and more complex fish-habitat relationships are likely to occur in large slow-flowing rivers.

Multiple regression models revealed that transmitted light was significant only for small individuals of *L. cephalus* and *L. gibbosus*, and that vegetation cover was significant only for large individuals of *A. alburnus* and *L. gibbosus*. Thus, the present results do not clearly support the hypothesis that juvenile fishes exhibit ontogenetic habitat shifts, from macrophyte to open-water. Such micro-habitat shifts were observed from temporal surveys in both lakes (Mittlebach, 1981) and rivers (Copp, 1990). However, sampling during fish development can reveal habitat shifts that, in reality, only reflect environmental changes. This was the case, for example, in Copp (1990) where fish appeared to move from vegetation to open-water habitats, while, at the same time, vegetation had become scarce. In the present study, despite significant differences in L_T for three of the four species, length distributions overlapped between the two sampling dates. Moreover, although *A. alburnus* did not exhibit differences in L_T among the sampling dates, habitat use differences were significant between the two size classes. Both small and large fish were sampled simultaneously at the two sampling dates, and habitat condition did not differ between the two periods. Therefore, observations of habitat use differences between the two size classes were reliable.

Both occurrence and abundance of juvenile fishes were modelled, so that variables which were significant in logistic and linear models could be compared. In both, small zooplankton abundance was the main determinant of juvenile fish distribution. However, some differences were apparent for the effect of other variables, and in particular, only logistic models revealed the influence of variables describing vegetation structure (vegetation cover and transmitted light). Surprisingly, prediction from multiple regression models were always better for large individuals, whatever the species. Moreover, mean abundance and occurrence of the two size classes of each fish species were similar, so this result was not a statistical phenomenon and juvenile fish-habitat relationships were definitely more pronounced for large individuals than for small individuals.

In defining eco-species on the basis of fish morphology, Garner (1996a) examined microhabitat use and diet of young and, old larvae and juveniles, and revealed that all eco-species were highly associated, with the early larval assemblage containing the greatest degree of overlap in both habitat and dietary selection. Using the same distinction between eco-species, Copp (1997) also revealed that ecological profiles were more pronounced for juveniles than for larvae. Finally, in tributaries of a natural section of a neotropical river, Mérigoux & Ponton (1999) examined spatial variations of young fishes grouped into two categories: early life stages and juvenile fishes. They showed that 17 fish taxa varied in space when examining juvenile fishes, whereas only seven showed spatial variations when examining early life stages. Comparing the F -values obtained by these authors when testing spatial effect, it was observed that for 14 taxa, spatial effect was more pronounced for juveniles than for early life stages, and that only five taxa showed opposite responses, with early life stages being more influenced than juvenile fishes. Early life stages are thus frequently more

uniformly distributed than older fishes, and this pattern appears to be largely widespread among various systems. In the present study, all fishes had completed their larval development and were all classed as juveniles. However, although belonging to the same ontogenetic development stage, differences in body size could have strong implications for juvenile fish. For example, body size mainly determines risk of predation, and small juvenile fish are likely to be more vulnerable to predation than large ones (Werner & Gilliam, 1984). As predator avoidance behaviour has been hypothesized to be responsible for habitat selection (Werner & Gilliam, 1984; Copp, 1992b; Bean & Winfield, 1995), it can be hypothesized that differences in predation risk could partially explain differences in habitat selection between the two size classes. Moreover, risk of predation is influenced by habitat structural complexity (Crowder & Cooper, 1982; Werner & Gilliam, 1984). In the present study, the different habitats studied largely differed in their structural complexity and for large individuals of two of the four species, the type of vegetation significantly influenced fish distribution. This finding suggests that the descriptors of physical conditions found in vegetation, that is the percent transmitted light and vegetation cover, are not sufficient to describe well the structural differences among the different habitat types. In particular, vegetation structural complexity remains hard to quantify, and the different methods used in previous studies make comparisons among various habitats difficult (McCoy & Bell, 1991). In the future, combining the two vegetation descriptors used in this study as a more synthetic variable may better reflect the structural complexity among various macrophyte habitats. Quantifying the structural complexity of macrophytes in this way might be useful for understanding vegetation use by juvenile fishes.

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