

## Fish habitat preferences in large streams of southern France

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### SUMMARY

1. Relationships between fish and their habitat over whole geographic regions, which are evident from studies of many streams and species, can improve understanding of lotic communities and provide reliable management tools. Nevertheless, most habitat preference studies have been based on single sites, and confined to small streams and to game species.

2. Regional habitat preference models, based on local velocity, depth and roughness, were developed for twenty-four species and their size classes commonly found in large European streams. Fish surveys were conducted in six large streams in southern France over an 8-year period. To limit the influences of habitat variables other than those studied, we estimated fish preferences within each survey and averaged this information across surveys. Preferences were fitted with confidence intervals and their sensitivity to field uncertainty was evaluated.

3. Most species and size classes had significant preferences for local habitat conditions which were consistent across the region. Habitat preferences predominant in the region overall were not always observed at any one site, but habitat conditions preferred on average in the region were never actually avoided locally. These results support the use of regional preference models for fish and the development of similar models for other lotic groups whose sensitivity to local habitat conditions has been reported elsewhere.

*Keywords:* fish community, habitat model, microhabitat, preference curve, size class, transferability

### Introduction

Relating processes identified at the local-scale of organisms to variability in natural systems at larger scales is a major challenge of both basic and applied ecology (Levin, 1992; Peckarsky, Cooper & McIntosh, 1997). The management of multiple ecosystems (e.g. at a regional scale) requires predictive models based on mechanisms common to these systems. On the one hand, it is quite

natural to base such predictive models on local-scale processes because these are generally easier to identify and more mechanistic than large-scale ones. Identifying local processes, common to different sites, can provide management tools which are transferable across ecosystems and applicable over extensive areas. On the other hand, local processes are numerous, interact and are constrained by large-scale ones. These are generally identified for target species and rarely transferable across different systems. As a result, a prerequisite for the development of large-scale predictive models in population and community ecology is the identification of key local processes which are consistent over a large range of organisms and sites.

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Streams are well suited to tests of the effects of local-scale processes at larger scales because: (1) many stream organisms have strong preferences for local habitat variables such as velocity, water depth, roughness or shear stress (Gore & Judy, 1981; Bovee, 1982); and (2) stream managers need estimates of the impacts of habitat changes over large geographic scales (Petts *et al.*, 1989). The sound management of large streams (Petts *et al.*, 1989) and studies attempting to quantify impacts of large scale changes such as those related to climate (Poff, Tokar & Johnson, 1996), require knowledge of fish habitat preferences in different systems. Instream habitat models have been used widely to predict population/community patterns in stream reaches based on the preferences of individual organisms for their local habitat. These models link a hydraulic component, describing local physical conditions in stream reaches, with models of preference for these local conditions (e.g. the Instream Flow Incremental Methodology; Bovee, 1982). These have been frequently criticised or defended (Scott & Shirvell, 1987; Gore & Nestler, 1988; Lamouroux, Souchon & Hérouin, 1995; Castleberry *et al.*, 1996; Williams, 1996; Poff *et al.*, 1997).

As with other ecological models based on local-scale processes, instream habitat methods have been developed for target species and are often site-specific (Conklin *et al.*, 1995). These methods are usually confined to small streams and trout or other game species (Souchon *et al.*, 1989; Jowett, 1992; Capra, Breil & Souchon, 1995). There is little quantitative knowledge of the habitat preferences of fish species living in large, warmwater streams (Petts *et al.*, 1989; Bain, 1995). This is partly the result of several technical difficulties associated with fish sampling in deep and fast-flowing water (Persat & Copp, 1990). Among these problems, the complex behaviour of fish and the schooling of certain species prevent researchers from observing each individual to set up preference models, as is commonly achieved for salmonids (Bovee, 1986). Sampling techniques have been adapted to solve these problems by sampling habitat units rather than individual fish, with units of several square metres defined in various ways (Nelva, Persat & Chessel, 1979; Persat & Copp, 1990; Vadas & Orth, 1993; Pouilly & Souchon, 1994; Bain, 1995). Although few studies have used these techniques to date, these methods have provided valuable knowledge of the variation

in habitat preferences of different fish species (Aadland, 1993; Bain, 1995; Conklin *et al.*, 1995). In addition to the problems of sampling, preference models for each species should reflect relative differences in species' sensitivity to particular habitat variables. However, habitat preference is generally expressed on a scale from 0 to 1, depending on the values of local habitat variables. This practise prevents the comparison of species' sensitivity to habitat variables, and therefore, reduces the biological realism of the models (see also Scott & Shirvell, 1987; Poff *et al.*, 1997).

Several factors limit the transferability of fish preference models between sites (Bergman, 1988; Bain, 1995). Firstly, few models have been developed using data pooled from several surveys and/or several reaches (e.g. Aadland, 1993; Groshens & Orth, 1994; Lamouroux, Capra & Pouilly, 1998). Pooling data from different field surveys creates several technical problems (Bovee, 1986), such as the difficulty of separating the effects of local physical conditions (e.g. flow velocity, water depth and substratum particle size) on fish density from the effects of parameters generally varying at larger scales (e.g. temperature, water quality and zoogeography). Unrecognized interactions between variables influencing fish density at different scales are expected to reduce the reliability of the models, and thereby, their transferability. It is often unclear whether such interactions are eliminated when analysing multi-survey data (for an interesting discussion on similar problems, see Dunham & Vinyard, 1997). A second factor limiting the possible transferability of preference models is that their level of uncertainty is generally not quantified. Given the high uncertainty around some hydraulic procedures used in habitat modelling (Williams, 1996), quantifying the confidence intervals for preference model predictions would reduce incorrect interpretations of habitat model outputs.

There is a need for models of fish habitat preference based on studies involving several species and streams. This is particularly true for species living in large European streams because little quantitative information concerning their local habitat preferences has been published. In this paper, we model the local-scale habitat preferences of twenty-four species and their size classes which are common to large European streams, and discuss the biological realism

of our models. To do this we: (1) analysed a data set of 1601 local observations made in six large streams in southern France; (2) developed regional preference models, limiting the possible bias caused by the effects of variables other than those studied (i.e. local velocity, water depth and roughness); (3) quantified the uncertainty associated with the preference models; and (4) estimated how the regional models applied at a particular site. We provide preference models in a simple form which can be used with current instream habitat models for fish. Then, we suggest extending our approach to other types of preference models and other lotic groups.

## Methods

### Sampling

Samples were taken in eight reaches of six streams in southern France, situated in the Rhône, the Loire and the Garonne River basins (orders 5–9, Fig. 1), with each reach including several pool-riffle units (New-

bury & Gaboury, 1993). Three reaches are in bypassed sections of the Rhône with severely reduced discharge (at Pierre-Bénite, Péage-de-Roussillon and Montélimar). Three others are tributaries of the Rhône with slightly regulated discharges (Ain River at Blye, Ardèche River at Saint Sernin and Drôme River at Saillans). The two other streams, situated in other major basins (the Loire at Grangent and the Garonne at Muret), are subject to only minor regulation. All reaches have a quasi-natural morphology and varying degrees of discharge regulation. Although the choice of these areas was influenced by financial constraints, the streams represent the range of reaches belonging to the 'barbel' zone in Western Europe (Huet, 1959).

More than 99% of sampled fish belonged to a total of twenty-four species, mainly cyprinids (Table 1). The fish were collected by electric fishing (towed Honda 5 kW/11 cv; Heron-Dream Electronic 180–1000 V/1–4 A direct current) in independent habitat units of several square metres using an open-sampling technique. These were subunits of reaches, with surface areas varying between 6 and 90 m<sup>2</sup> (95%

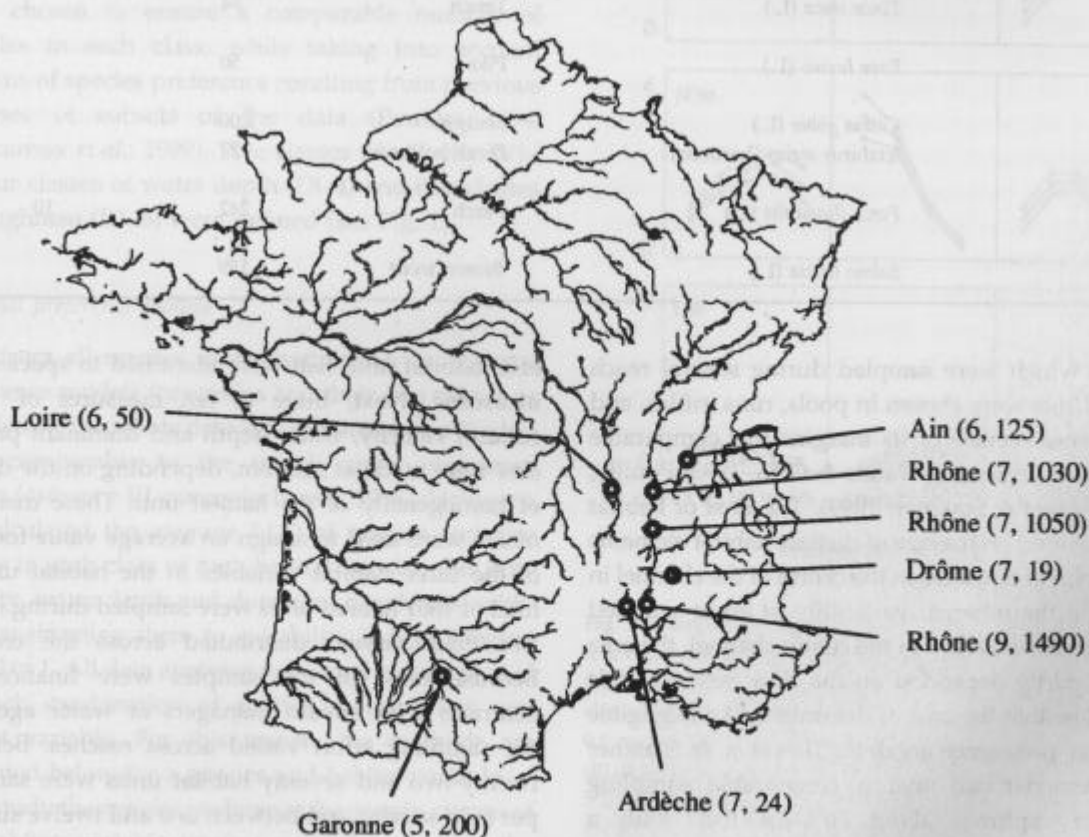


Fig. 1 Map of the sampled reaches. Each reach name is followed by the stream order and the average natural discharge (m<sup>3</sup> s<sup>-1</sup>).



**Table 1** Twenty-four species considered in the present paper, their total abundance in samples and their size class definitions (if any)

Family/species code	Scientific name	Common name	Number of individuals	Size class limit(s) (cm)
<i>Anguillidae</i>				
Aan	<i>Anguilla anguilla</i> (L., 1758)	Eel	283	41
<i>Centrarchidae</i>				
Lgi	<i>Lepomis gibbosus</i> (L., 1758)	Pumpkinseed	967	8
<i>Cobitidae</i>				
Nba	<i>Barbatula barbatula</i> (L., 1758)	Stone loach	3331	6
<i>Cyprinidae</i>				
Aba	<i>Abramis brama</i> (L.)	Bream	58	
Abi	<i>Alburnoides bipunctatus</i> (Bloch)	Stream bleak	4154	7
Aal	<i>Alburnus alburnus</i> (L.)	Bleak	2800	8, 12
Bba	<i>Barbus barbus</i> (L.)	Barbel	3537	9, 22
Bbj	<i>Blicca bjoerkna</i> (L.)	White bream	340	9, 22
Cna	<i>Chondrostoma nasus</i> (L.)	Nase	632	8, 19
Cto	<i>Chondrostoma toxostoma</i> (Vallot)	French nase	976	7
Ggo	<i>Gobio gobio</i> (L.)	Gudgeon	5245	10
Lso	<i>Leuciscus (telestes) souffia</i> (Risso)	Blageon	2298	8
Lce	<i>Leuciscus cephalus</i> (L.)	Chub	6137	8, 17
Lle	<i>Leuciscus leuciscus</i> (L.)	Dace	420	8.5, 19
Pph	<i>Phoxinus phoxinus</i> (L.)	Minnow	5286	4
Ram	<i>Rhodeus amarus</i> (Bloch)	Bitterling	173	
Rru	<i>Rutilus rutilus</i> (L.)	Roach	3294	6, 11
Ser	<i>Scardinius erythrophthalmus</i> (L.)	Rudd	54	
Tti	<i>Tinca tinca</i> (L.)	Tench	94	
<i>Esocidae</i>				
Elu	<i>Exos lucius</i> (L.)	Pike	50	
<i>Ictaluridae</i>				
Cgo	<i>Cottus gobio</i> (L.)	Sculpin	200	
Ime	<i>Ictalurus melas</i> (Lesueur)	Black bullhead	27	
<i>Percidae</i>				
Pfl	<i>Perca fluviatilis</i> (L.)	Perch	242	10
<i>Salmonidae</i>				
Str	<i>Salmo trutta</i> (L.)	Brown trout	189	

of units), which were sampled during several reach surveys. Units were chosen in pools, runs, riffles, and at the channel centre or its margins (for comparable sampling strategies, see Vadas & Orth, 1993; Pouilly, 1994; Thévenet & Statzner, 1999). The area of habitat units depended on the size of distinct habitat elements (e.g. a group of boulders in the centre of the channel in a run) and the inherent variability of areas sampled without enclosures (e.g. in the centre channel, the area sampled partly depended on the flow velocity). We show below that the area of the units had a negligible impact on preference models. Thévenet & Statzner (1999) demonstrated that a comparable sampling procedure captured about 70% of fish, with a comparable efficiency among species and habitat conditions, and with a negligible fright bias. Within

each habitat unit, fish were identified to species and measured. Next, three to ten measures of water column velocity, water depth and dominant particle size were made at random, depending on the degree of homogeneity of the habitat unit. These measurements were used to assign an average value for each of the three habitat variables in the habitat unit. A total of 1601 habitat units were sampled during thirty-five field surveys distributed across the reaches. Because most of the samples were financed by contracts with stream managers or water agencies, the sampling effort varied across reaches. Between twenty-two and seventy habitat units were sampled per field survey, and between one and twelve surveys were carried out in each reach. Surveys took place between 1989 and 1997. These were made during the

day, at flows generally below the annual average, and surveys at each site were distributed similarly between seasons. For the more common species, size classes were defined from total length frequency distributions using the method of Persat & Chessel (1989) (Table 1).

In each habitat unit, we calculated a local Log-density (LLD) for each of the species and their size

$$LLD = \ln(1 + 1000d)$$

classes as:

where  $d$  is the areal density of the species, i.e. the abundance divided by the plan area of the unit ( $\text{individuals m}^{-2}$ ). Such a logarithmic transformation smoothed very high local densities, commonly observed for young-of-the-year or juveniles. Thus, it provided a compromise between presence/absence and density information (species LLD values varied between one and ten across habitat units where the species was present).

We defined different classes of velocity, water depth and dominant roughness size in order to compare LLD values across these classes. Class limits were chosen to ensure a comparable number of samples in each class, while taking into account patterns of species preference resulting from previous analyses of subsets of the data (Pouilly, 1994; Lamouroux *et al.*, 1999). Five classes of velocity (V1–5), four classes of water depth (D1–4) and five classes of roughness (R1–5) were defined (see Fig. 2).

#### Regional preference models

Data from all reaches were used to derive regional preference models for species and their size classes as revealed by the whole data set. The preference models were comparable to the widely used preference curves (category III curves in Bovee, 1986). However, we calculated the average LLD of species and size classes in each class of each habitat variable (i.e. flow velocity, water depth and dominant roughness) without transforming them to suitability indices ranging from 0 to 1. All data analyses presented were repeated for each combination of species or size class and habitat variable. For this reason, the methods are presented below for a species and habitat variable.

To study the species preference for certain classes of the habitat variable, it is essential to reflect the differences in LLD across the habitat units of the

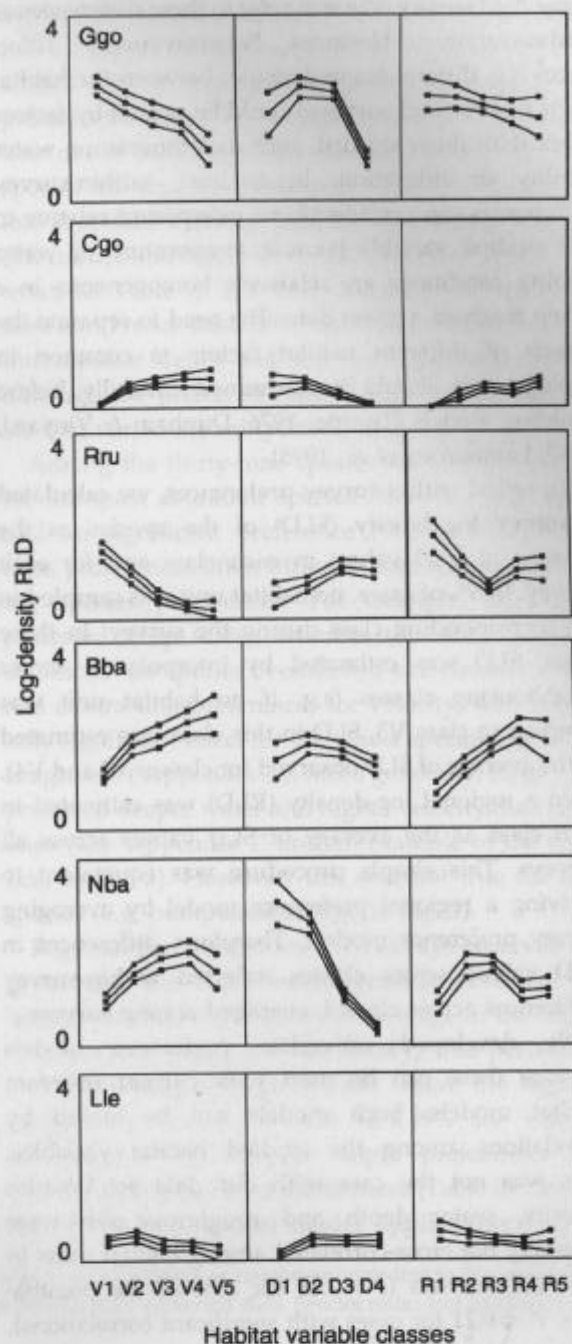


Fig. 2 Examples of regional log-densities (RLDs) observed in five classes of velocity (V1, 0–0.05  $\text{m s}^{-1}$ ; V2, 0.05–0.2  $\text{m s}^{-1}$ ; V3, 0.2–0.4  $\text{m s}^{-1}$ ; V4, 0.4–0.8  $\text{m s}^{-1}$ ; and V5, > 0.8  $\text{m s}^{-1}$ ), four classes of water depth (D1, 0–0.2 m; D2, 0.2–0.4 m; D3, 0.4–0.8 m; and D4, > 0.8 m) and five classes of dominant roughness (R1, 0–0.016 m; R2, 0.016–0.064 m; R3, 0.064–0.256 m; R4, > 0.256 m; and R5, large bedrocks). The RLD curves are given for six species (see codes in Table 1). The observed RLDs correspond to the middle curves. The upper and lower curves indicate the 90% confidence interval for RLD.

same field survey. We will refer to these differences as within-survey differences. Between-survey differences (i.e. differences in densities between the habitat units of two field surveys) could be caused by factors other than those studied, such as temperature, water quality or migration. In contrast, within-survey differences can confidently be interpreted relative to the studied variable because temperature or water quality conditions are relatively homogeneous in a given reach on a given date. The need to separate the effects of different habitat factors is common in ecology and should be examined carefully before building models (Thorpe, 1976; Dunham & Vinyard, 1997; Lamouroux *et al.*, 1998).

To reflect within-survey preferences, we calculated a survey log-density (SLD) of the species as the average of LLD values in each class and for each survey. In 6% of cases, no habitat unit was sampled in the corresponding class during the survey. In these cases, SLD was estimated by interpolation across neighbouring classes (e.g. if no habitat unit was sampled in class V3, SLD in this class was estimated as the average of SLD observed for classes V2 and V4). Then a regional log-density (RLD) was estimated in each class as the average of SLD values across all surveys. This simple procedure was equivalent to deriving a regional preference model by averaging survey preference models. Therefore, differences in RLD values across classes reflected within-survey differences across classes, averaged among surveys.

We developed univariate preference models because these can be used with current instream habitat models. Such models can be biased by correlations among the studied habitat variables. This was not the case with our data set because velocity, water depth and roughness size were generally not cross-correlated among habitat units in our field surveys ( $P > 0.05$  for 85% of the possible tests,  $r^2 < 0.21$  for cases with significant correlations).

#### *Tests of the regional preference models*

Analyses of uncertainty for RLDs, as well as analyses of differences in RLD across classes, are complicated by three technical problems. Firstly, RLD values are weighted averages of local LLD values. Secondly, LLD values were not normally distributed despite the logarithmic transformation of densities (cf. Bain, 1995; Lamouroux *et al.*, 1998). Finally, LLD values had

different observed standard deviations across the classes and the reaches, and their real standard deviations were difficult to estimate. Therefore, we chose to use simple and conservative statistical analyses.

Firstly, the 90% confidence interval for RLD was calculated assuming RLD to be an average of 1601 LLD values for which standard deviation was estimated in each class as equal to that observed. This operation provided a visual approximation of the uncertainty for RLD values. Then we used a conservative analysis of variance to test the significance of RLD variation across classes. For this second analysis, we estimated the standard deviation of LLD values as equal, in each class, to its maximum value observed across classes. Thus, we chose to overestimate the standard deviation of log-densities, instead of using more complex and still not rigorous estimates of this standard deviation.

#### *Relevance of the regional preference models at a particular site*

We tested the applicability of the regional preference models at a particular site for each species and habitat variable combination with a significant regional model (according to the above analysis of variance). For each combination, we used the regional model to define a group of preferred habitat units (i.e. units with habitat conditions in the two preferred classes) and a group of habitat units avoided (the others). In each of the eight reaches where the species was present, we compared LLD values of the first group with those of the second group by analysis of variance (ANOVA). If observed LLDs were significantly higher in the preferred group ( $P < 0.05$ ), the regional model was confirmed at the site. If no significant difference was observed between the groups, the regional model was not confirmed at the site. If observed LLDs were significantly lower in the preferred group ( $P < 0.05$ ), the regional preference was 'reversed' at the site. We summarized these tests for species and sites to investigate potential deviations with the regional model. We calculated the percentage of confirmations and reversals of the regional preference among the tests for species and for sites. The reasons for the failure of a particular test were likely to vary between the numerous species and site combinations, and could not be inferred using the data available in this



study.

#### *Sensitivity of the preference models to field uncertainties*

In addition to these analyses, we tested the influence of the surface areas of the habitat units on species RLDs. For this test, we recalculated RLD values after a random permutation of habitat unit area. Randomly permuting area is equivalent to randomly modifying the observed fish density in habitat units. Thus, these simulations provided a test of the sensitivity of our results to various sampling uncertainties.

Another question was whether analysing fish data in terms of log-density provided different information from models based on the presence/absence of the species in the habitat units (e.g. Yu, Peters & Stroup, 1995). Preference models based on density analyses are potentially more precise than those using presence/absence, since these take into account fish abundance in habitat units. However, both approaches are used in instream habitat modelling. We repeated our analyses with fish data in habitat units transformed to presence/absence data. Consequently, instead of calculating RLDs, we calculated the observed frequency of occurrence of the species in the habitat units, grouped by habitat variable classes. These frequencies are estimates of the probability of occurrence of species.

#### **Results**

Confidence intervals for regional log-densities suggested that most species and size classes had strong preferences for velocity, water depth or roughness (see the examples in Fig. 2 and all results in 'Appendix 1'). The conservative analysis of variance

confirmed these results (see the summary in Table 2 and all results in 'Appendix 1'). It demonstrated that sixteen out of twenty-four species had significant preferences ( $P < 0.05$ ,  $P < 0.001$  in most cases) for at least one of the three habitat variables. Out of the eight species showing no preference, five were among the less abundant with less than 200 individuals sampled (i.e. rudd, bitterling, bream, black bullhead and brown trout, see Table 1). The three other species were dace, nase and French nase. Most species used low velocity, intermediate depth and extreme roughness classes, although the preferred class of each habitat variable studied varied across species (Table 2).

Among the thirty-nine species-size classes defined for the most abundant species (Table 1), only seven had no significant preference ('Appendix 1'). Size class preferences often differed from the corresponding species preferences. For example, large nase preferred deep water, whereas this effect was not significant for species overall; two size classes of bleak had contrasting preferences for velocity, whereas the only significant effect for the whole species concerned roughness ('Appendix 1'). More generally, longer fish preferred deeper water and higher velocity than small ones (see 'Appendix 1' and an example of the chub, Lce, in Fig. 3). However, this was not true for each species (e.g. pumpkinseed, Lgi, in Fig. 3).

Regional preferences were not always observed at a given site, but were never actually reversed (i.e. habitat conditions preferred on average in the region were never actually avoided locally). The percentage ( $\pm 1$  SD among species) of sites where the regional model was confirmed was  $62 \pm 19\%$  for velocity preferences,  $58 \pm 19\%$  for depth preferences and  $40 \pm 11\%$  for roughness preferences (Table 3). Species for which the regional model applied poorly at a

**Table 2** List of species with a significant preference ( $P < 0.05$ ) for classes of velocity, depth or roughness according to the conservative analysis of variance. For each of the three habitat variables, species are listed in their preferred class. Species codes and habitat variable classes are defined in Table 1 and in Fig. 2, respectively

V1	V2	V3	V4	V5	D1	D2	D3	D4	R1	R2	R3	R4	R5
Aan	Pph		Nba	Bba	Nba	Ggo	Lgi	Pfl	Lce		Nba	Bba	Lgi
Cgo	Lso			Cgo		Pph	Lce	Aan	Rru			Pfl	Cgo
Pfl	Abi					Cgo	Lso		Aan				
Elu							Rru		Bbj				
Lce									Aal				
Lgi													
Rru													
Tti													

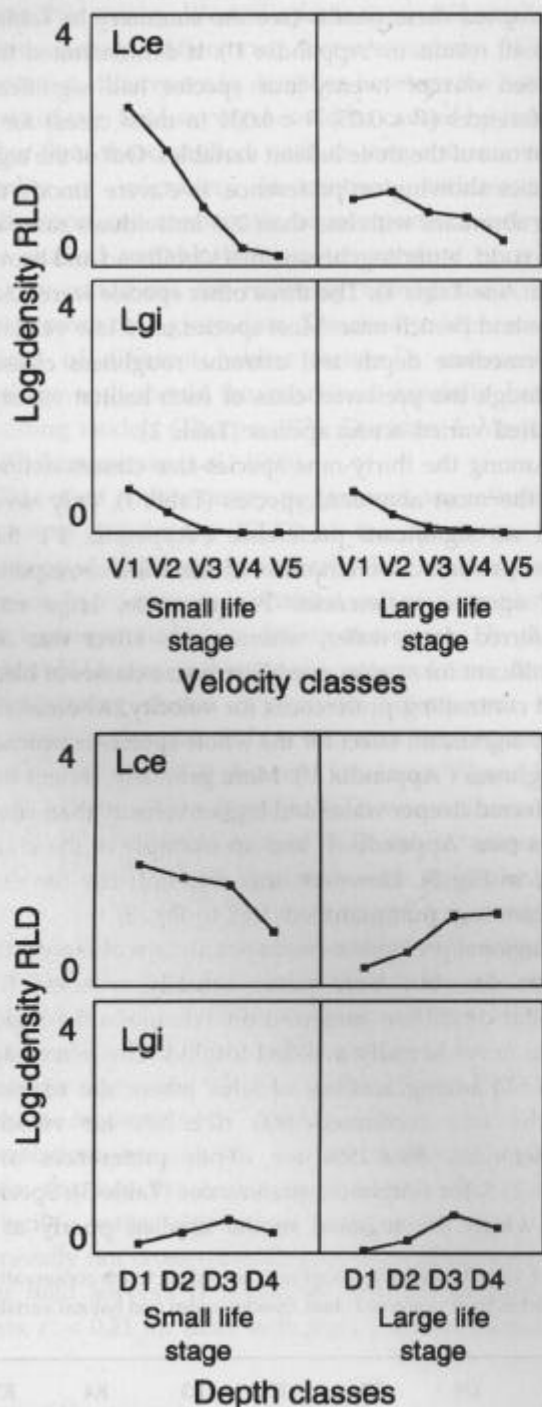


Fig. 3 Regional log-densities (RLDs) versus velocity and depth classes for the smallest and the largest size class of chub ('Lce') and pumpkinseed ('Lgi'). See Fig. 2 for class definitions.

given site were pike and minnow (velocity), perch and chub (depth), and barbel and perch (roughness). Sites where the regional models applied poorly were essentially in the Garonne (all variables), in the

Drôme (depth) and in the Loire (roughness).

Tests of the sensitivity of our models to field uncertainty indicated that random permutations of habitat unit area (or random modifications of species observed density) had a negligible impact on regional log-density estimates. For simplicity, only results concerning a few species (those of Fig. 2) and concerning velocity are provided here (Fig. 4). No statistics were given for these simulations because the curves corresponding to the two estimations of the log-density were barely distinguishable (Fig. 4). Hence, models were not sensitive to uncertainties in sampling methods, neither those associated with the area of habitat units nor those associated with the abundance of fish in inhabited units. In addition, analyses of presence/absence information in the habitat units revealed that the average frequency of species, or their size classes in a given class, was linearly related to the RLD ( $P < 0.01$ , see Fig. 5). Again, only results concerning velocity are shown, results for other variables being similar. These results imply that patterns observed in our data were driven by presence/absence in the habitat units rather than variation in density.

## Discussion

Our analyses of fish-habitat relationships using long-term samples provides new quantitative information on the habitat preferences of twenty-four species commonly found in European streams ('Appendix 1'). The results confirm that most species and size classes of fish assemblages have strong preferences for local velocities, depths or dominant roughness (Aadland, 1993; Bain, 1995). The findings demonstrate that significant preference models for fish can be developed at the regional scale for a group of streams with various morphological and hydrological properties. Furthermore, some fish exhibit preferences for a narrow range of habitat conditions (Fig. 2), indicating that regional models do not necessarily reflect broad ranges of suitable conditions as sometimes suggested (Conklin *et al.*, 1995). Regional trends in fish preferences shown by our results are consistent with existing knowledge of the species. For example, the use of shallow and fast-flowing water by the stone loach, the rheophilic behaviour of the barbel or the use of coarse substratum in swift currents by the black bullhead (Fig. 2) have already been described (Spill-



**Table 3** Percentage of sites where the regional preference model was confirmed (given for each species) and the percentage of species for which the regional preference model was confirmed (given for each site). These statistics are given for each habitat variable studied and correspond to significant preference models (see 'Appendix 1'). The species codes are defined in Table 1. The sites are shown in Fig. 1

Species and sites	Confirmation percentage		
	Velocity model	Depth model	Roughness model
<i>Species</i>			
Aal	-	-	43
Aan	83	50	50
Abi	50	-	-
Bba	50	-	13
Bbj	-	-	33
Cgo	50	75	50
Elu	33	-	-
Ggo	63	75	-
Lce	100	38	38
Lgi	86	43	43
Lso	50	75	-
Nba	50	88	50
Pfl	67	33	33
Pph	40	60	-
Rru	71	43	43
Tti	80	-	-
<i>All species:</i>			
Mean	62	58	40
Standard deviation	19	19	11
<i>Sites</i>			
Ain	77	78	56
Ardèche	83	89	33
Drôme	63	17	50
Garonne	38	29	29
Loire	70	38	25
<i>Rhône:</i>			
Pierre Bénite	58	75	30
Péage-de-Roussillon	58	75	30
Montélimar	60	38	60

man, 1961). Similarly, differences between the preference of species and their size classes are consistent with other results (Moyle & Baltz, 1985). The general use of shallower and slower-flowing water by smaller fish is consistent with the use of bank habitats by juveniles (Bain, Finn & Booke, 1988) and a size refuge from predation offered by shallow water (Schlosser, 1987).

Regional patterns in habitat preferences occur, despite flexibility across sites (Bain, 1995; Conklin *et al.*, 1995; Leftwich, Angermeier & Dolloff, 1997). Such flexibility had already been observed in previous analyses of subsets of our data (Pouilly, 1994;

Lamouroux *et al.*, 1998). Here we demonstrated that the habitat conditions preferred on average in the region were never actually avoided locally, although preferences predominant in the region were not always observed at any one site. In addition, data for a given species/site could be insufficient to reflect preferences at any one site (e.g. for the pike, for the Drôme or the Garonne River). Therefore, the regional models are attractive tools for large scale, multi-site management. We did not investigate the other potential reasons for the absence of preference at a given site because of their number and possible variation across species and sites. For example, the

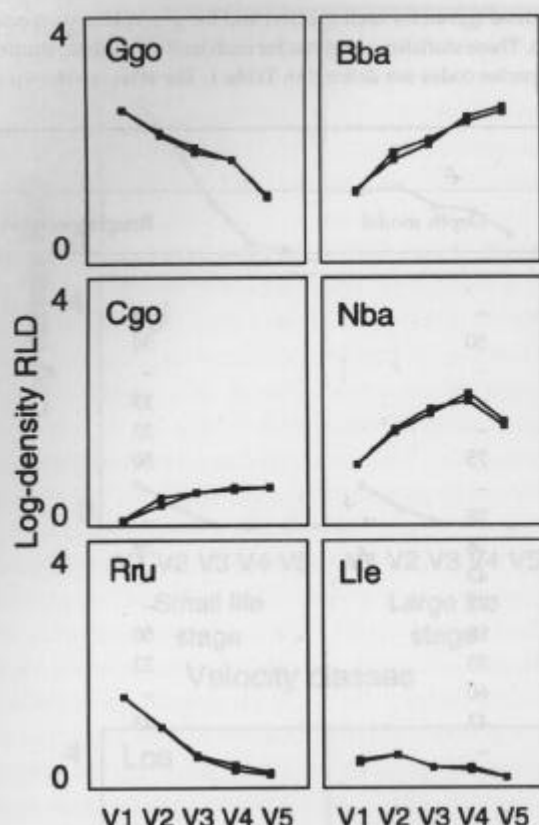


Fig. 4 Regional log-densities (RLDs) as a function of velocity classes for the species described in Fig. 2. For each species, the first curve is the observed RLD value of Fig. 2 and the second corresponds to RLD values obtained after a random permutation of habitat unit areas.

preference of chub for low velocity was observed at all sites, whereas their preference for deep water occurred at 38% of the sites. This could be a result of differences in size-class structure between sites (depth preferences vary with size classes of chub, see 'Appendix 1') or particular adaptations in sites where the frequency of preferred depth was low. More generally, biotic interactions, habitat availability, temperature and other habitat factors could be responsible for shifts in observed preferences (Leftwich *et al.*, 1997). As a consequence, interpretations of the flexibility in fish preferences between sites would require a detailed analysis for the preferences of each species and the knowledge of various habitat conditions at the sites.

We looked at several controversial points associated with the development of preference models for fish at the local scale. Firstly, our results support current sampling approaches in large streams. Sampling

habitat units instead of surveying individuals enabled us to show fish preferences whether fish data were transformed to presence/absence (Bain, 1995; Yu *et al.*, 1995; Mastroiillo *et al.*, 1997; present study) or density indices (Aadland, 1993; present study). Analyses based on density are potentially more precise, but both types of data led to equivalent models in our study. Secondly, we emphasized limiting the effects of unrecognized interactions amongst habitat variables influencing fish. This problem is often neglected when analysing data originating from different surveys or sites (Dunham & Vinyard, 1997; Lamouroux *et al.*, 1998). However, if preference models are affected by differences in density across surveys as a result of temperature or water quality, using these to predict changes in community structure caused by modifications of velocity or depth has little chance of success. Thirdly, we provided confidence intervals for fish density in habitat variable classes. Preference models should always include estimates of their uncertainty because instream habitat models can easily lead to unreliable predictions (Williams, 1996). Finally, we deliberately avoided scaling our preference values between 0 and 1, as commonly practised (Bovee, 1982). This ensures that the models remain meaningful, estimating either log-densities or frequencies (see 'Appendix 1'). Resetting the models between fixed limits would smooth

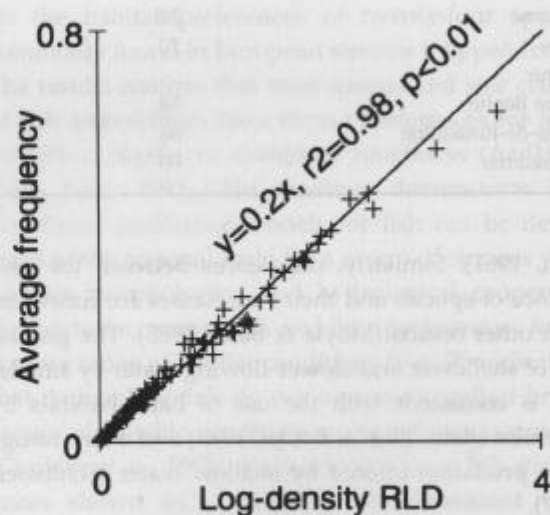


Fig. 5 Relationship between the average frequency of a species in a velocity class and its regional log-density (RLD). All possible combinations of the five velocity classes and the twenty-four species were included, unless the species was never present in the class (i.e. cases where  $x = y = 0$ ).

the strong variability in the sensitivity of species to the habitat variables. Such a practice is unsuitable for the study of multispecies assemblages because it would bias comparisons across species and predictions at the community level.

The results were presented as 'preference curves' because these reflect the biology of the species in a simple form and are compatible with models currently used in river management. However, other kinds of preference models may allow better predictions of the effects of local habitat conditions on stream organisms. These include models taking into account the local variability of fish habitat (Lamouroux *et al.*, 1998), multivariate approaches based on linear or logistic regressions (Yu *et al.*, 1990; Lamouroux *et al.*, 1999), non-linear techniques based on artificial intelligence (D'Angelo *et al.*, 1995; Mastrorillo *et al.*, 1997), models using species life-history traits instead of species themselves (Poff, 1997), or preference models for variables other than velocity, depth or roughness (Yu & Peters, 1997). Note that 'linear' models do not necessarily reflect linear preferences for the habitat variables, as confusingly suggested in studies involving non-linear models (D'Angelo *et al.*, 1995; Mastrorillo *et al.*, 1997). The term 'linear' refers to the mathematical structure of the model and a linear model can also reflect non-linear responses to habitat variables (Yu *et al.*, 1995; Lamouroux *et al.*, 1998). Integrating the methodological issues referred to in this paper (i.e. elimination of effects in multi-site studies, uncertainty quantification and sensitivity analysis) in all kinds of procedures used to derive preference models can improve the rigour of the biological component of instream habitat models.

The strong effect of local habitat variables, especially hydraulics, has also been demonstrated for other freshwater groups (Statzner, Gore & Resh, 1988), including plants (Biggs, 1996), invertebrates (Gore & Judy, 1981) and amphibians (Kupferberg, 1996). Together with our findings, these results suggest that tests of regional preference models could be extended to other lotic groups. More generally, biological models reflecting local processes observed in various sites are attractive for both basic and applied issues in ecology. Concerning basic issues, general models of local processes have great potential to provide insights into the mechanisms influencing community structure. In an applied context, transferable mechanistic models should provide robust

predictions of the ecological impacts of habitat modifications at regional or larger scales. These facilitate the wide application of impact studies while limiting their cost, a prerequisite of holistic management policies.

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