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Factors influencing the spatial distribution patterns of the bullhead (*Cottus gobio* L., Teleostei Cottidae): a multi-scale study

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Abstract. We used general linear modelling to assess the influence of environmental variables on the spatial distribution patterns of the bullhead (*Cottus gobio*) at stream system, site, and microhabitat scales in southwestern France. Bullheads occurred at 67 sites (out of 554 sampling sites), chiefly close to the source, in small and shallow streams. Population density at a site was primarily influenced by thermal conditions. Stream width was negatively related to the probability of presence of bullheads within the stream system, but positively related to local density, showing that bullhead density could increase within a range of stream width, but that wider rivers were unsuitable. Slope was negatively correlated to bullhead's occurrence and local density, and depth was negatively correlated to local density and microhabitat use, suggesting that bullhead's shimming performance was weak under greater erosive forces. Therefore, the most significant results suggested that the distribution of populations and individuals was first governed by the suitability of physical and hydraulic habitat, then population dynamics at a site was mainly governed by the thermal regime. Multi-scale studies of factors influencing a species' distribution thus allow to integrate patterns observed at different scales, and enhance our understanding of interactions between animals and their environment. Such models are essential in the exploratory phase of fundamental and applied investigations, because they help to target further research, and they should influence the measures to be taken in field surveys or conservation plans.

Introduction

The distribution of species is influenced by a large number of environmental factors, such as the geological history of the area, environmental stability (Ward and Stanford 1979), ecosystem productivity (Lavandier and Décamps 1984), habitat heterogeneity and suitability (Gorman and Kar 1978), and competition and predation (Pianka 1978). However, these factors operate at several spatial and temporal scales, e.g., geologic history affects the biogeography of species at a regional scale, whereas physical characteristics of microhabitats may influence local distributions and/or densities (Hastie et al. 2000). During the last decades, there have been many attempts to model the spatial distribution patterns of a number of species with the broader aim to bring out the influence of numerous biotic and abiotic factors, and the way they may act at various spatial scales (Morris 1987; Inoue and Nunokawa 2002). Moreover, detailed (quantitative) characterisations of preferential environments (from local to regional scales) are fundamental bases to the design of management and protection projects. Such data help ecologists to bring out relatively constant features of preferred habitats (Lobb and Orth 1991), to assess habitat suitability or alteration in a given area (Bain et al. 1988; Grossman et al. 1990), and/or to understand patterns of use and partition of space and resources in closely related species (Degerman and Sers 1993). Fish species were often studied as model organisms under this topic (Harris and Silveira 1999; Kruk and Penczak 2003). While great emphasis was laid on salmonids (Roussel et al. 1999), other freshwater species have received little or no attention, certainly because of their lack of halieutic and/or economic interest (Mastrorillo et al. 1997). Nevertheless, small benthic-dwelling fish, which are less mobile, should be more prone to exhibit important relationships with their habitat, and can be relevant models for a broader understanding of the relationships between the distribution of populations and individuals, and habitat features.

The bullhead (*Cottus gobio* L., Teleostei Cottidae) is one such species. Bullheads typically live in well oxygenated streams with rocky bottoms (Gaudin and Caillère 1990), and commonly co-occur with freshwater species associated to waters of good biological quality (see the fish database at http://www.fishbase.org/), e.g., salmonid fish and polluosensitive insects (Ephemeroptera, Plecoptera and Trichoptera). The species seems to occur throughout Europe (Koli 1969; Gaudin 1981; Pedroli et al. 1991; Englbrecht et al. 2000; Kontula and Väinölä 2001), with a patchy distribution from local to broad scales (Bomassi and Brugel 2000). Although abundant in some countries (e.g., southern England), the bullhead is rare at a European scale and is a listed species in Annex II of the EC Habitats Directive 92/43/EEC. Many factors, closely related to the destruction of physical and hydraulic stream habitats by man, have led to the decline of several populations. In France, the species is not globally threatened, but some populations were locally evicted by pollutions or channel calibration (Keith and Allardi 2001). In Switzerland, bullheads are now considered as rare to very rare into a third of the rivers, and a half of lakes (Pedroli et al. 1991). In Austria, the species has suffered a strong regression (Kainz and Gollmann 1989). Given the alterations in rivers which support bullhead populations, accurate quantitative descriptions of its preferential habitats are urgently required. However, there have been no previous multi-scale study of the influence of environmental conditions on bullhead's spatial distribution patterns and population structure.

The aim of this study was to assess the influence of several environmental variables on the spatial distribution patterns of the bullhead at three perception scales: the stream system, the stream section, and the microhabitat. Specifically, we sought to bring out explicit models which would allow to better understand the relationships between habitat features, and the distribution of populations and individuals. Habitats of the bullhead were described at the different spatial scales using several environmental variables, and the influence of each variable on fish distribution was assessed using general linear modelling (GLM). Congruent and contradictory results for variables considered at different scales are discussed, in order to assess their relevance from the regional to the local scale, and to better understand the patterns and processes that determine a species' distribution.

Materials and methods

Data collection

Stream system scale

The River Garonne has its source in the Maladetta Glacier (Spain), and it slopes from the southeast to the northwest, where it reaches the Atlantic ocean through the Gironde estuary. The River Garonne drains an area of about 57,000 km^2, and its total length is 525 km. Mean annual discharge amounts to about 545 $m^3\ s^{-1}$. Compared with other French rivers (e.g., the Seine and the Rhône rivers), the Garonne river is less disturbed by industrial pollution. However, its natural flow has been modified by the presence of several dams, promoting in that way animal and vegetal community fragmentation within the river channel and the alluvial floodplain (Décamps et al. 1988). From our laboratory database, we selected 554 sampling sites ranging from high mountain (2500 m a.s.l.) to plain or coastal (10 m a.s.l.) areas (Figure 1), where we recorded the presence or absence of bullheads. Site-specific data for fish species richness were collected between 1980 and 2000. All sites were sampled by electro fishing during low-flow periods, and using standardized methods (De Lury 1947; Seber and Le Cren 1967). Each site was characterised with six typological variables and one biological variable. The typological variables were chosen to relate the location of sampling sites within the stream system: elevation a.s.l. (m), stream order, distance from the source (km), drainage basin area (km^2), slope (‰), and stream width (m). The biological variable was fish species richness.

Stream section scale

We focused on 32 sampling sites which supported a bullhead population, and which were distributed over the various geographic areas of the drainage basin (Figure 1). Fish were sampled by electrofishing using a two-pass removal method (De Lury 1947), which allowed calculation of their density (ind/ha). At each site, we recorded the following variables: bullhead density (individuals per ha), overall fish species richness, slope (‰), stream width (m), mean depth (m), mean current velocity ($cm\ s^{-1}$), pH, mean water conductivity ($\mu S\ cm^{-2}$),

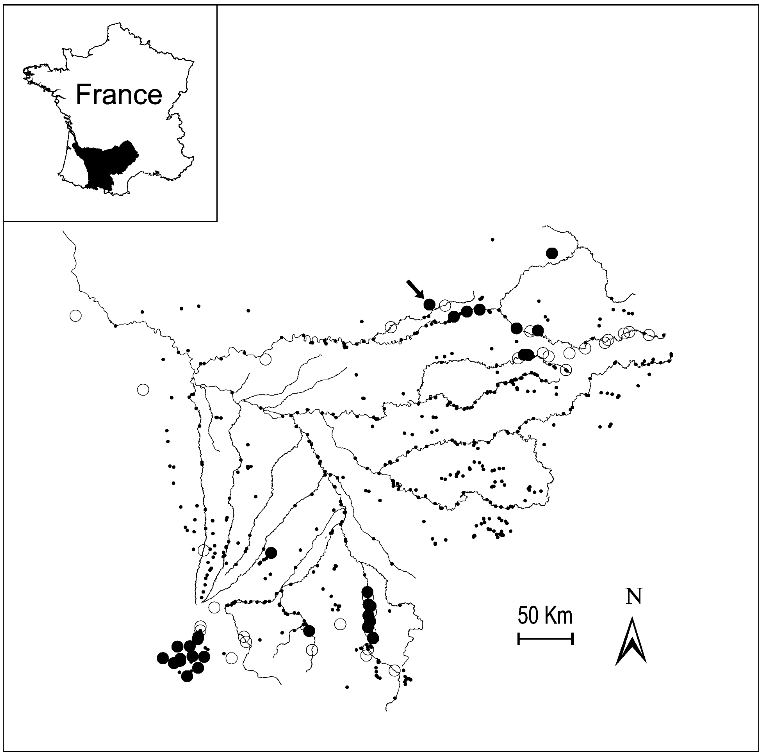


Figure 1. Map of the Garonne stream system, with location of the 554 sampling sites (dots and circles). Circles (black and open) indicate the 67 sites which carried a bullhead population, black circles showing the 32 sites which were selected for density models (see text). The arrow shows the location of the sampling site selected for the microhabitat distribution model (River Saint-Perdoux).

dissolved oxygen (mg l^{-1}), maximum water temperature (°C, recorded in summer).

Microhabitat scale

This part of the study was based on the River St Perdoux (S.W. France, elevation: 235 m a.s.l.), a second order stream in the north-eastern part of the Garonne stream system (see Figure 1). We investigated a 800 m stretch in the lower section of the river (i.e. 4800 m^2). Estimates of mean river width, water depth, and current velocity for this reach are 6 m, 0.16 m, and 27 cm s^{-1}, respectively. The mean annual flow was 0.33 m^3 s^{-1} (min–max: 0.01–2.33 m^3 s^{-1}), the mean annual water temperature was 10.9 °C (min–max: 0–18.8 °C).

Fish were sampled by electrofishing in 2002, during the low flow period (i.e. out of the spawning period), using a two-pass removal method (De Lury 1947). The total length of caught individuals ranged from 33 to 101 mm.

Fish microhabitat was described using 10 variables: % bedrocks, % boulders (> 200 mm), % cobbles (100–200 mm), % pebbles (20–100 mm), % gravel (2–20 mm), % sand (0.05–2 mm), % mud (< 50 μm), water depth (cm), bottom and mean current velocities (cm s^{-1}) (current velocities were measured at bottom-, mid- and surface-level using an OTT® portable flowmeter, thus allowing calculation of the mean current velocity). These 10 variables were measured in 0.1 m^2 quadrats centred on the points where fish were caught.

Data analysis

We used general linear modelling to analyse the distribution patterns of the bullhead at the various spatial scales. GLM allows a more versatile analysis of correlation than standard regression methods, because the error distribution of the dependent variable and the function linking predictors to it can be adjusted to the characteristics of the data. For these analyses we used a binomial distributed error and logit link to model the presence/absence data of bullhead at the stream system and microhabitat scales. Density of bullhead at the stream section scale was modelled as gamma distributed with an inverse link (see Crawley 1993). Differences between rivers in the density and presence of bullhead were controlled for by incorporating river as a random factor in the analyses at the stream system and stream section scales. Model selection started from a model including all the independent variables considered, and backwards removal of less significant variable one by one until all the variables remaining in the model contributed with a $p < 0.10$ to the fitting of the model using type III contrasts (SAS Institute 2000). Calculations were done with the GENMOD procedure of the SAS program (v. 8.2, SAS Institute 2000) or with the macro GLIMMIX (SAS Institute 1996) for the models including river as a random factor (stream system and stream section scale).

Results

Bullhead occurrence at the stream system scale

In the Garonne stream system, bullheads occurred at 67 sites out of 554 (Figure 1). Three typological variables were negatively correlated with the presence of bullhead populations (Table 1): distance from the source ($p < 0.0001$), slope ($p < 0.001$), and stream width ($p < 0.05$). Other factors under consideration (elevation, stream order, drainage basin area, local fish species richness) did not correlate significantly with the presence of the species. GLM thus provided an overview of the 'bullhead stream', through a limited number of pertinent variables. Whatever the elevation, the occurrence of bullheads at a broad spatial scale was more probable in lotic areas with shallow water, at a

Table 1. Model analysing the patterns of bullhead's distribution at the stream system scale.

Effect	Estimate ± error	DF	F	P
Intercept	-2.0971 ± 0.3889			
Elevation		1.411	1.46	0.23
Stream order		1.411	0.03	0.86
Distance from source	-0.0162 ± 0.0032	1.412	26.46	< 0.0001
Drainage basin area		1.411	1.25	0.26
Slope	-0.0265 ± 0.0081	1.412	10.80	0.001
Stream width	-0.0183 ± 0.0085	1.412	4.61	0.03
Fish species richness		1.411	0.00	0.96

The final model explains 69% of the original deviance (404.6) and incorporates a random factor controlling for river effects on fish distribution. Estimates are provided for variables in the final model and correspond to the slopes obtained from the GLM model with binomial error and logit link. For variables not included in the model the significance when incorporated into the final model is given.

rather short distance from the source, in streams with weak slopes and width (see Figure 2).

Bullhead density at the stream section scale

Depending on the considered site, bullhead density ranged from 8 to 1112 ind. ha^{-1}. Maximum water temperature had the highest contribution to density at a site ($p < 0.01$, Table 2) through the negative effect of higher values (Figure 3), and areas with summer temperatures ranging from 12 to 17 °C where thus likely to support largest populations. Other factors influencing bullhead density through the negative effect of higher values were water conductivity, depth, and slope ($p \leq 0.05$; see Table 2). Conductivity, depth, and slope were around 120–200 $\mu S\ cm^{-2}$, 20–40 cm, and $< 0.4\%$, respectively in areas with the highest density. Conversely, stream width had a positive effect on bullhead density in areas were fish occurred. As for the analysis of bullhead presence at the stream scale, the overall fish species richness had no significant influence on bullhead's population density.

Microhabitat preferences

Bullhead density in the study section of the River St Perdoux was 362.5 ind. ha^{-1}, i.e., the third highest value that we recorded in the Garonne stream system. With the exception of bottom current velocity, % gravel, and % bedrocks, all microhabitat variables under consideration had a significant contribution to fish distribution ($p \leq 0.01$–0.0001; Table 3). The distribution of residuals of the GLM showed negative correlations between these variables and habitat use (Figure 4): bullheads used non-cohesive substrates which

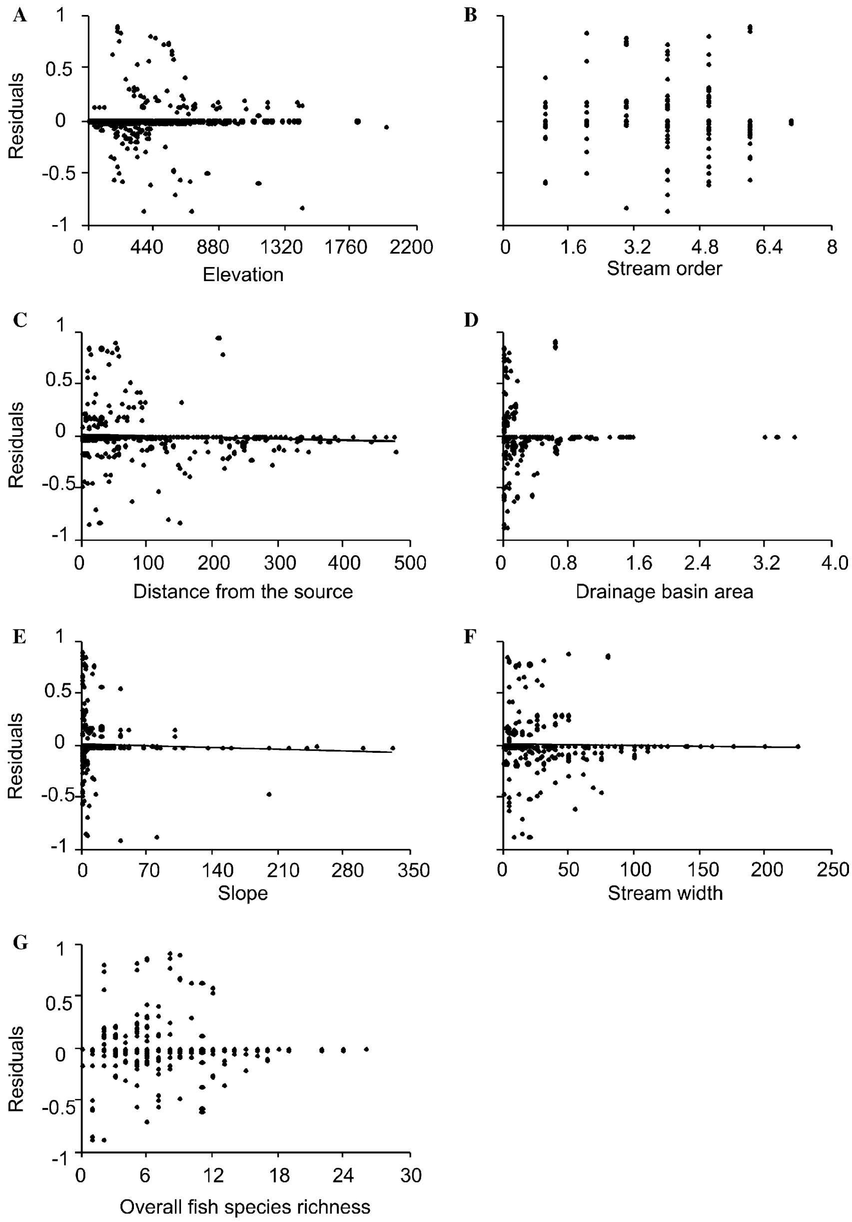


Figure 2. Relationship between different macroscale habitat variables and the presence of bullhead. (A) Elevation (m); (B) stream order; (C) distance from the source (km); (D) drainage basin area (10^4 km^2); (E) slope (‰); (F) stream width (m); (G) overall fish species richness. For variables retained in the final model residuals correspond to presence of bullhead expressed as the residuals of the GLM model with binomial error including all the variables in the final model out of the variable of interest. For these variables a linear regression line is provided. For variables not retained in the final model, residuals corresponds to the residuals of the final model.

Table 2. Model analysing the factors related to the density of bullheads at the stream section scale.

Effect	Estimate ± error	DF	F	P
Intercept	−0.0913 ± 0.0209			
Fish species richness		1.11	0.56	0.47
Slope	0.0001 ± 0.0001	1.12	4.63	0.05
Stream width	−0.0006 ± 0.0002	1.12	7.97	0.02
Depth	0.0324 ± 0.0142	1.12	5.19	0.04
Velocity		1.11	0.50	0.49
pH	0.0056 ± 0.0027	1.12	4.21	0.06
Conductivity	0.0001 ± 0.0000	1.12	7.75	0.02
Oxygen		1.11	0.01	0.90
Temperature	0.0030 ± 0.0008	1.12	14.40	0.003

The final model explains 49.9% of the original deviance (924.6) and incorporates a random factor controlling for river effects on fish abundance. Estimates are provided for variables in the final model and correspond to the slopes obtained from the GLM model with gamma error and inverse link. Note that consequently, negative slopes indicate a positive association with bullhead density, and positive slopes indicate negative relationships (see Figure 3). For variables not included in the model the significance when incorporated into the final model is given.

associated a wide range of coarse mineral particulates, i.e., pebbles, cobbles and boulders deposited on sand (the later particulates usually representing 10–60% per suitable 0.1 m^2 habitat). Used habitats also associated low depths (5–20 cm) and mean current velocities (<40 cm s^{-1}). Conversely, individuals avoided muddy (i.e., clogged bottom) and homogeneous areas (e.g., sandy areas) (Figure 4). Such field data support the observation that bullheads usually take refuge under pebbles or cobbles, or immediately below the largest particulates, where current velocity is weakened and sand accumulates.

Discussion

Interactions between animals and their environment influence species' distribution patterns, and, subsequently, the composition of species assemblages (Begon et al. 1996). Modelling the spatial distribution patterns of organisms is therefore of obvious importance to understand the ecological functioning of both communities and ecosystems. While increasing interest has been taken in the study of habitat and spatial distribution of freshwater fish (e.g. Larsen et al. 1986; Newall and Magnuson 1999), most studies focused on one perception scale, i.e., a region, a stream, or the suitable microhabitats (Pusey et al. 1993; Rathert et al. 1999; Roussel and Bardonnet 2002). Beyond the quantitative information that it yielded (thus documenting the habitat preferences of the bullhead at various spatial scales), our work clearly emphasized the importance of examining species–habitat relationships at different spatial scales, e.g. because congruent or contradictory results among different scales may enhance our understanding of the patterns and processes that determine a species' distribution, and, subsequently, the organisation of species assemblages.

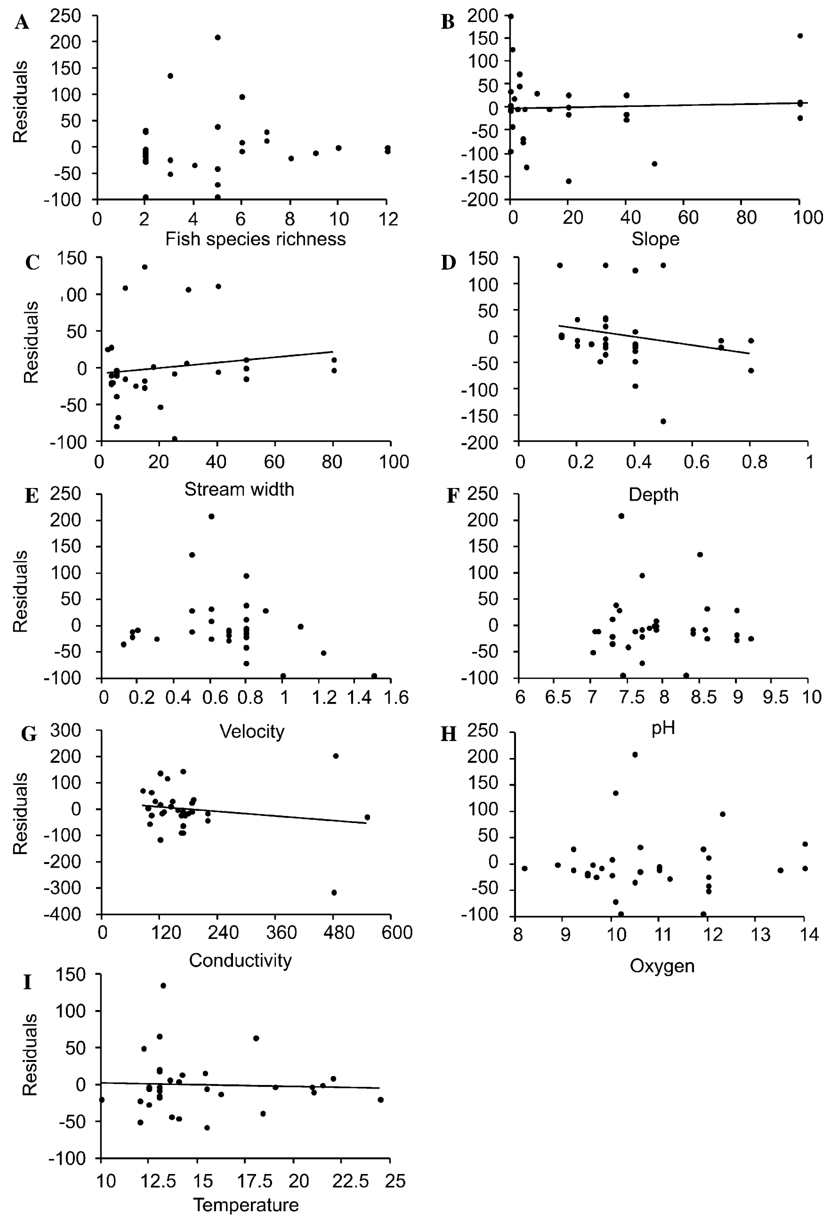


Figure 3. Relationship between different habitat characteristics and density of bullhead. (A) Fish species richness; (B) slope (‰); (C) stream width (m); (D) depth (m); (E) velocity (m s^{-1}); (F) pH; (G) conductivity (μS cm^{-2}); (H) oxygen (mg l^{-1}); (I) temperature (°C). For species retained in the final model residuals correspond to bullhead abundance expressed as the residuals of the GLM model with gamma error including all the variables in the final model out of the variables of interest. For these variables linear regression line is provided. For variables not retained in the final model, residuals corresponds to the residuals of the final model.

Table 3. Model analysing the patterns of distribution at a microhabitat scale.

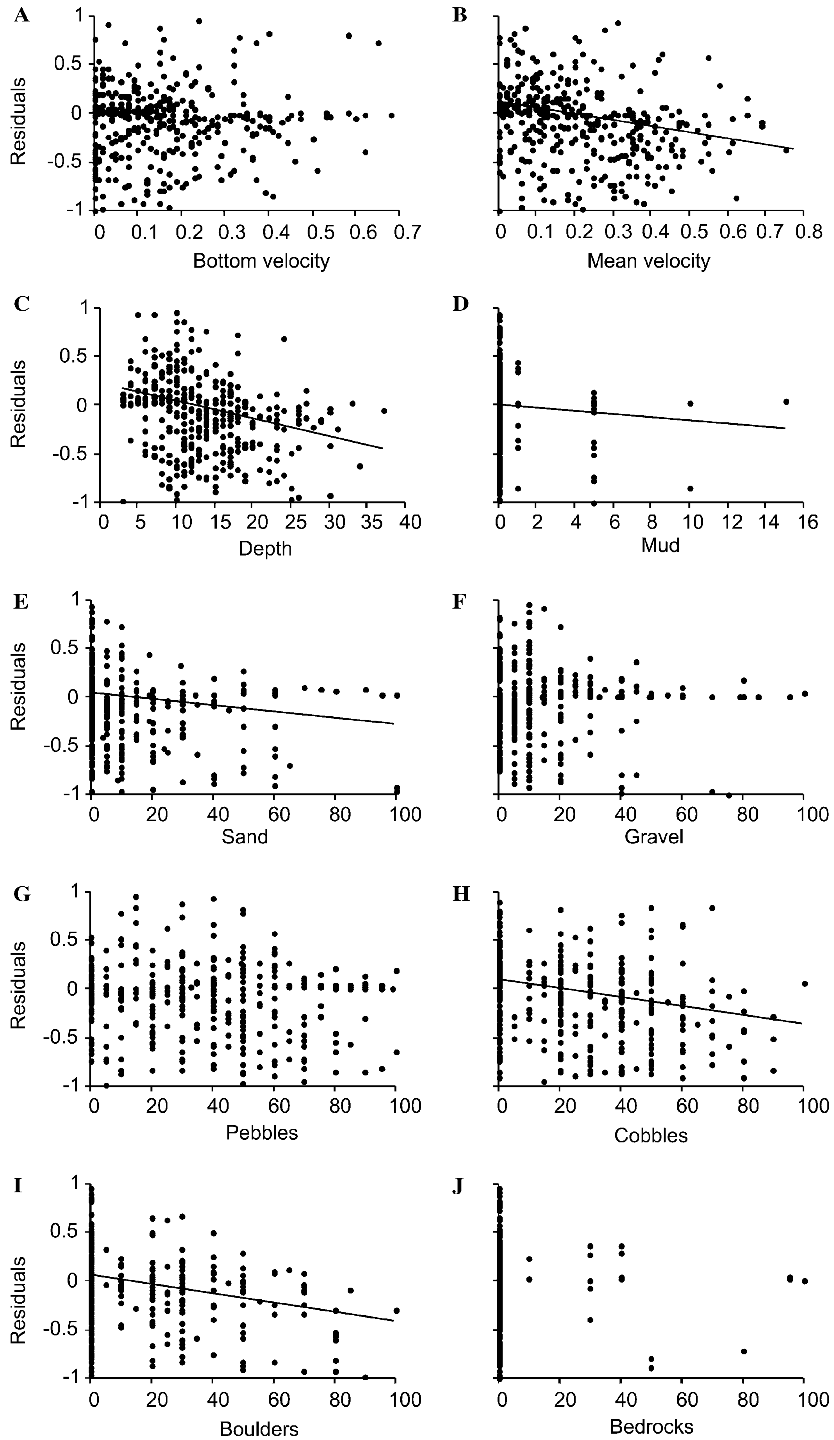
Effect	Estimate ± error	DF	F	P
Intercept	−8.6050 ± 0.8080			
Bottom velocity		1.541	0.40	0.53
Mean velocity	6.1657 ± 0.8382	1.542	64.74	< 0.0001
Depth	0.1960 ± 0.0231	1.542	91.40	< 0.0001
Mud	0.1841 ± 0.0649	1.542	6.66	0.01
Sand	0.0541 ± 0.0083	1.542	49.34	< 0.0001
Gravel		1.541	0.54	0.46
Pebbles	0.0329 ± 0.0077	1.542	21.91	< 0.0001
Cobbles	0.0729 ± 0.0081	1.542	121.39	< 0.0001
Boulders	0.0643 ± 0.0082	1.542	81.03	< 0.0001
Bedrocks		1.541	0.53	0.47

The final model explained 43% of the original deviance (740.31). Estimates are provided for variables in the final model and correspond to the slopes obtained from the GLM model with binomial error and logit link. For variables not included in the model the significance when incorporated into the final model is given.

Bullhead's occurrence within the stream system was roughly influenced by river typology, with a marked preference for small and shallow streams, whatever their elevation. The corresponding range within a river system often extended close to the source. This pattern fits with the broad altitudinal and latitudinal distribution of the species. From Greenland and Arctic areas of Scandinavia to northern Italy, in the south and eastwards to the Black Sea and Russia, the bullhead may indeed occur from 0 to 2380 m a.s.l. (Pedroli et al. 1991). Within this range, our results suggest that population density at a site was primarily influenced by thermal conditions. Temperature is recognized as a major ecological factor affecting the development of freshwater species (e.g. Vannote and Sweeney 1980; Newbold et al. 1994) and chiefly influences the density of fish populations through growth and fecundity (Lobon-Cervia et al. 1996). Previous studies reported that water temperature in studied bullhead streams ranged from 2 to 16.5 °C (Andreasson 1971; Gaudin 1981), whereas Volckaert et al. (2002) specified that bullhead's current range fits between the maximum July isotherm of 20 °C, and the minimum January isotherm of −20 °C. The bullhead being a cold stenothermic species (Hänfling et al. 2002), it is likely that higher temperatures in lower areas of stream systems limited its broad-scale distribution.

►

Figure 4. Relationship of different microhabitat variables and the presence of bullhead. (A) Bottom velocity (m s^{-1}); (B) mean velocity (m s^{-1}); (C) depth (cm); (D) mud (%); (E) sand (%); (F) gravel (%); (G) pebbles (%); (H) cobbles (%); (I) boulders (%); (J) bedrocks (%). For species retained in the final model residuals correspond to the residuals of the GLM model with binomial error including all the variables in the final model out of the variables of interest. Ordinary least square regression lines are shown for variables in the final model. For variables not retained in the final model, residuals corresponds to the residuals of the final model.


A
B
C
D
E
F
G
H
I
J
Residuals
Bottom velocity
Mean velocity
Depth
Mud
Sand
Gravel
Pebbles
Cobbles
Boulders
Bedrocks

Physical habitat and channel morphology descriptors accounted for fish occurrence, local density, and microhabitat use. Stream width was negatively related to the probability of presence of bullheads at the stream system scale, whereas it was positively related with bullhead density at the stream section scale. This pattern can be clearly understood if we look at the range of measurements included in the analyses. Stream width ranged from 0 to more than 200 m in the presence/absence model (stream system scale), but only from 0 to 80 m in the local density model (stream scale). Despite this difference, the results are not that contradictory: bullhead density may increase within a determinate range of values (stream width = 0–80 m), but wider rivers are unsuitable for the species. Conversely, some variables showed congruent results at different scales, i.e., slope was negatively correlated to bullhead's regional distribution and local density, and depth was negatively correlated to local fish density and microhabitat use. Slope and depth are the two variables which determine the erosive force acting substrate and bed scour in a given area (Cobb and Flannagan 1990; Cobb et al. 1992), and subsequently on stream animals. The bullhead being an unskilled swimmer deprived of air-bladder (Keith and Allardi 2001), it is likely that it was not able to maintain position under greater erosive forces (Roussel and Bardonnet 1997), and/or that it could not found refuge habitats in areas with higher slopes and/or depth (Welton et al. 1983; Gaudin and Caillère 1990). Such an assumption is strengthened by the observation that mean current velocity showed a negative relationship with microhabitat use, and that individuals preferred large and stable substrate (see Figure 4).

Fish species richness had no significant influence on both the regional distribution and local density of the bullhead. Other fish species co-occurring with the bullhead in the Garonne stream system were chiefly trout, lamprey, minnow, and stone-loach. Bullheads commonly coexist with these species with no or little competitive interactions (Welton et al. 1983; Jørgensen et al. 1999). Coexistence is favoured by the behavioural and morphological characteristics of this benthic fish (small-bodied and benthic-dwelling fish, usually living under cobbles and rocks, sedentary and territorial behaviour) (Welton et al. 1983; Gaudin and Caillère 1990, 2000; Welton et al. 1991; Gabler et al. 2001). Nevertheless, bullhead's density and microdistribution at a site was reported to be significantly influenced by the presence of predators such as the pike or the burbot in Swedish rivers (Degerman and Sers 1994), or by the presence of competitors such as Signal crayfish in a British lowland river (Guan and Wiles 1997). At our study sites, such species did not co-occur with the bullhead. However, considering the results of GLM with fish species richness, we have no evidence that competition or predation influence bullhead's presence and/or density in the Garonne stream system, and further field studies would be needed to confirm this hypothesis which cannot be directly verified from our data. We must finally notice that the territorial behaviour of the species may influence the distribution of individuals over the river bed through intraspecific competition (Mills and Mann 1983).

Because of its low dispersal ability (< 1 km, Downhower et al. 1990), the bullhead should be strongly pledged to the influence of environmental conditions. Thus, it is likely to constitute a relevant model organism encouraging further collections of case studies. The results we obtained with this species suggested that the distribution of populations and individuals was first governed by the suitability of physical habitat and hydraulic conditions, then population dynamics in a given reach was mainly governed by the thermal regime. Such models are essential in the exploratory phase of both fundamental and applied ecological investigations, as they may suggest subtle relationships that deserve more detailed study in subsequent research (e.g. population dynamics versus temporal habitat dynamics), and/or because they should influence the design of measures to be taken in later phases of field surveys or conservation plans. As a result of river management practices, many fish species have often been forced into small and more or less isolated populations (e.g. Hellawell 1978; Schiemer and Spindler 1989; Poulet 2000; Holcík 2003). Most biomonitoring techniques for aquatic biota use extensive number of site-specific data to allow predictions of the distribution of species to be expected in a given area, using a set of environmental characteristics (see e.g. review in Wright et al. 2000). Detailed (quantitative) characterisations of preferential environments are therefore fundamental bases to the design of management and/or protection projects. Substrate-based models (microhabitat) were usually successful in predicting the distribution of individuals at the 1–10 m scale (Roussel et al. 1999; Hastie et al. 2000). However, large-scale (macrohabitat) descriptions remain important to provide context (Strayer and Ralley 1993), and to target further research on local populations (Gittings et al. 1998) or microhabitat use (Hastie et al. 2003). Thus, whatever the species under consideration, further efforts should be made to better integrate data from large- to small-scale contexts.

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References

Andreasson S. 1971. Feeding habits of a bullhead (*Cottus gobio* L. *Pisces*) population. Report Institute of Freshwater Research Drottningholm 51: 5–30.

Bain M.B., Finn J.T. and Booke H.E. 1988. Steamflow regulation and fish community structure. Ecology 69: 382–392.

Begon M., Harper J.L. and Townsend C.R. 1996. Ecology: Individuals, Populations and Communities, 3rd edn. Blackwell Science, Oxford, UK.
Bomassi P. and Brugel C. 2000. L'état des connaissances sur les populations en Auvergne des espèces de l'ichtyofaune inscrites à l'annexe 2 de la directive 'habitats'. Rapport du Conseil Supérieur de la Pêche. Délégation Régionale Auvergne, Lempdes, France, pp. 5–11.
Cobb D.G. and Flannagan J.F. 1990. Trichoptera and substrate stability in the Ochre River, Manitoba. Hydrobiologia 206: 29–38.
Cobb D.G., Galloway T.D. and Flannagan J.F. 1992. Effects of discharge and substrate stability on density and species composition of stream insects. Canadian Journal of Fisheries and Aquatic Sciences 49: 1788–1795.
Crawley M.J. 1993. Glim for Ecologists. Blackwell Science, Oxford, UK.
Décamps H., Fortuné M., Gazelle F. and Pautou G. 1988. Historical influence of man in the riparian dynamics of a fluvial landscape. Landscape Ecology 1: 163–173.
Degerman E. and Sers B. 1993. A study of interactions between fish species in streams using survey data and the PCA-hyperspace technique. Nordic Journal of Freshwater Research 68: 5–13.
Degerman E. and Sers B. 1994. The effect of lakes on the stream fish fauna. Ecology of Freshwater Fish 3: 116–122.
De Lury D.B. 1947. On the estimation of biological populations. Biometrics 3: 145–167.
Downhower J.F., Lejeune P., Gaudin P. and Brown L. 1990. Movements of the chabot (*Cottus gobio*) in a small stream. Polskie Archiwum Hydrobiologii 37: 119–126.
Englbrecht C.C., Freyhof J., Nolte A., Rassmann K., Schliewen U. and Tautz D. 2000. Phylogeography of the bullhead *Cottus gobio* (Pisces: Teleostei: Cottidae) suggests a pre-Pleistocene origin of the major central European populations. Molecular Ecology 9: 709–722.
Gabler H.-M., Amundsen P.-A. and Herfindal T. 2001. Diet segregation between introduced bullhead (*Cottus gobio* L.) and Atlantic salmon parr (*Salmo salar* L.) in a sub-Arctic river. Archiv für Hydrobiologie 151: 609–625.
Gaudin P. 1981. Eco-éthologie d'un poisson benthique, le chabot, *Cottus gobio* L. (Cottidae): distribution, alimentation et rapports avec la truite, *Salmo trutta* L. Ph.D. Thesis, Université Claude-Bernard, Lyon, France.
Gaudin P. and Caillère L. 1990. Microdistribution of *Cottus gobio* L. and fry of *Salmo trutta* L. in a first order stream. Polskie Archiwum Hydrobiologii 37: 81–93.
Gaudin P. and Caillère L. 2000. Experimental study of the influence of presence and predation by sculpin, *Cottus gobio* L., on the drift of emergent brown trout, *Salmo trutta* L. Archiv für Hydrobiologie 147: 257–271.
Gittings T., O'Keefe D., Gallagher F., Finn J. and O'Mahony T. 1998. Longitudinal variation in abundance of a freshwater pearl mussel *Margaritifera margaritifera* population in relation to riverine habitats. Biol. Environ. Proc. R. Irish Acad. 98B: 171–178.
Gorman O.T. and Kar J.R. 1978. Habitat structure and stream fish communities. Ecology 59: 507–515.
Grossman G.D., Dowd J.F. and Crawford M. 1990. Assemblage stability in stream fishes: a review. Environmental Management 14: 661–671.
Guan R.Z. and Wiles P.R. 1997. Ecological impact of introduced crayfish on benthic fishes in a British lowland river. Conservation Biology 11: 641–647.
Hänfling B., Helleman B., Volckaert F.A.M. and Carvalho G.R. 2002. Late glacial history of the cold-adapted freshwater fish *Cottus gobio*, revealed by microsatellites. Molecular Ecology 11: 1717–1729.
Harris J.H. and Silveira R. 1999. Large-scale assessments of river health using an index of biotic integrity with low-diversity fish communities. Freshwater Biology 41: 235–252.
Hastie L.C., Boon P.J. and Young M.R. 2000. Physical microhabitat requirements of freshwater pearl mussels, *Margaritifera margaritifera* (L). Hydrobiologia 429: 59–71.
Hastie L.C., Cooksley S.L., Scougall F., Young M.R., Boon P.J. and Gaywood M.J. 2003. Characterization of freshwater pearl mussel (*Margaritifera margaritifera*) riverine habitat using River Habitat Survey data. Aquatic Conservation Marine Freshwater Ecosystems 13: 213–224.

Hellawell J.M. 1978. Biological Surveillance of Rivers. Water Research Center, Stevenage Laboratory, UK, 332 pp.
Holcík J. 2003. Changes in the fish fauna and fisheries in the Slovak section of the Danube River: a review. Annals of Limnology 39: 177–195.
Inoue M. and Nunokawa M. 2002. Effects of longitudinal variations in stream habitat structure on fish abundance: an analysis based on subunit-scale classification. Freshwater Biology 47: 1594–1607.
Jørgensen L., Amundsen P.A., Gabler H.M., Halvorsen M., Erkinaro J. and Niemelä E. 1999. Spatial distribution of Atlantic salmon parr (*Salmo salar* L.) and bullhead (*Cottus gobio* L.) in lotic and lentic habitats of a diversified watercourse in northern Fennoscandia. Fish. Res. 41: 201–211.
Kainz E. and Gollmann H.P. 1989. Beiträge zur Verbreitung einiger Kleinfischarten in ö sterreichischen Fließgewässern. Oesterreichs Fischerei 42: 204–207.
Keith P. and Allardi J. 2001. Atlas des poissons d'eau douce de France, Vol. 47. Patrimoines Naturels, Paris, 387 pp.
Koli L. 1969. Geographical variation of *Cottus gobio* L. (Pisces, Cottidae) in Northern Europe. Annales Zoologici Fennici 6: 353–390.
Kontula T. and Väinölä R. 2001. Postglacial colonization of Northern Europe by distinct phylogeographic lineages of the bullhead, *Cottus gobio*. Molecular Ecology 10: 1983–2002.
Kruk A. and Penczak T. 2003. Impoundment impact on populations of facultative riverine fish. Annals of Limnology 39: 197–210.
Larsen D.P., Omernik J.M., Hugues R.M., Rohm C.M., Whittier T.R., Kinney A.J., Gallant A.L. and Dudley D.R. 1986. Correspondence between spatial patterns in fish assemblages in Ohio streams and aquatic ecoregions. Environmental Management 10: 815–828.
Lavandier P. and Décamps H. 1984. Estaragne. In: Whitton B.A. (ed) Ecology of European Rivers. Blackwell Scientific Publications, Oxford, UK, pp. 237–264.
Lobb M.D. and Orth D.J. 1991. Habitat use by an assemblage of fish in a large warmwater stream. Transactions of the American Fishery Society 120: 65–78.
Lobon-Cervia J., Dgebuadze Y., Utrilla C.G., Rincon P.A. and Granado-Lorencio C. 1996. The reproductive tactic of dace in central Siberia: evidence for temperature regulation of the spatio-temporal variability of its life history. Journal of Fish Biology 48: 1074–1087.
Mastrorillo S., Lek S., Dauba F. and Belaud A. 1997. The use of artificial neural networks to predict the presence of small-bodied fish in a river. Freshwater Biology 38: 237–246.
Mills C.A. and Mann R.H.K. 1983. The bullhead *Cottus gobio* a versatile and successful fish. Annual Report of the Freshwater Biology Association 51: 76–88.
Morris D.W. 1987. Ecological scale and habitat use. Ecology 68: 362–369.
Newall P.R. and Magnuson J.J. 1999. The importance of ecoregion versus drainage area on fish distributions in the St. Croix River and its Wisconsin tributaries. Environ. Biol. Fish. 55: 245–254.
Newbold J.D., Sweeney B.W. and Vannote R.L. 1994. A model for seasonal synchrony in stream mayflies. Journal of the North American Benthological Society 13: 3–18.
Pedroli J.-C., Zaugg B. and Kirchhofer A. 1991. Atlas de distribution des poissons et cyclostomes de Suisse. Centre Suisse de cartographie de la faune, Neuchâtel, Switzerland, p. 155.
Pianka E.R. 1978. Evolutionary Ecology, 2nd ed. Harper and Row, New York.
Poulet N. 2000. Impact de la fragmentation des cours d'eau sur la morphologie des poissons. Cas de la vandoise rostrée (*Leuciscus leuciscus burdigalensis*) du Viaur. D.E.A report, Université Toulouse III, France.
Pusey B.J., Arthington A.H. and Read M.G. 1993. Spatial and temporal variation in fish assemblage structure in the Mary River, south-eastern Queensland: the influence of habitat structure. Environ. Biol. Fish. 37: 355–380.
Rathert D., White D., Sifneos J.C. and Hughes R.M. 1999. Environmental correlates of species richness for native freshwater fish in Oregon, USA Journal of Biogeography 26: 257–273.

Roussel J.M. and Bardonnet A. 1997. Diel and seasonal patterns of habitat use by fish in a natural salmonid brook: an approach to the functional role of the riffle-pool sequence. Bulletin Français de la Pêche et de la Pisciculture 346: 573–588.
Roussel J.M. and Bardonnet A. 2002. The habitat of juvenile brown trout (Salmo trutta L.) in small streams: preferences, movements, diel and seasonal variations. Bulletin Français de la Pêche et de la Pisciculture 365–366: 435–454.
Roussel J.M., Bardonnet A. and Claude A. 1999. Microhabitat of brown trout when feeding on drift and when resting in a lowland salmonid brook: effects on Weighted Usable Area. Archiv für Hydrobiologic 146: 413–429.
SAS Institute Inc. 1996. SAS System for Mixed Models. SAS Institute Inc., Cary, North Carolina.
SAS Institute Inc. 2000. SAS/STAT® Software: User's Guide. SAS Institute Inc., Cary, North Carolina.
Schiemer F. and Spindler T. 1989. Endangered fish species of the Danube river in Austria. Regul. River. Res. Manage. 4: 397–407.
Seber G.A.F. and Le Cren E.D. 1967. Estimating populations parameters from catches large to relative populations. Journal of Animal Ecology 36: 631–643.
Strayer D.L. and Ralley J. 1993. Microhabitat use by an assemblage of stream-dwelling unionaceans (Bivalvia), including two rare species of Alismodonta. Journal of the North American Benthological Society 12: 247–258.
Vannote R.L. and Sweeney B.W. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. American Naturalist 115: 667–695.
Volckaert F.A.M., Hänfling B., Hellemans B. and Carvalho G.R. 2002. Timing of the population dynamics of bullhead *Cottus gobio* (Teleostei: Cottidae) during the pleistocene. Journal of Evolutionary Biology 15: 930–944.
Ward J.V. and Stanford J.A. 1979. Ecological factors controlling stream zoobenthos with emphasis on thermal modification of regulated streams. In: Ward J.V. and Stanford J.A. (eds) The Ecology of Regulated Streams. Plenum Press, New York, pp. 35–55.
Welton J.S., Mills C.A. and Pygott J.R. 1991. The effect of interaction between the stone loach *Noemacheilus barbatulus* (L.) and the bullhead *Cottus gobio* (L.) on prey and habitat selection. Hydrobiologia 220: 1–7.
Welton J.S., Mills C.A. and Rendle E.L. 1983. Food and habitat partitioning in two small benthic fishes, *Noemacheilus barbatulus* (L.) and *Cottus gobio* L. Archiv für Hydrobiologie 97: 434–454.
Wright J.F., Sutcliffe D.W. and Furse M.T.(eds), 2000. Assessing the Biological Quality of Fresh Waters: RIVPACS and Other Techniques. Freshwater Biological Association, Ambleside, UK.