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*Primary Research Paper*

# Environmental factors influencing the regional distribution and local density of a small benthic fish: the stoneloach (*Barbatula barbatula*)

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## Abstract

We investigated the relationships between different environmental variables and the spatial distribution patterns of the stoneloach (*Barbatula barbatula*) at the stream system, the stream site, and the mesohabitat (riffle/pool) scales in south-western France. Stoneloach occurred at 240 sites (out of 554 sampling sites), chiefly close to the source, in areas at low elevation and with weak slopes. Population density at a site was primarily influenced by physical conditions. Stream width was positively related to the probability of presence of stoneloach within the stream system, but negatively related to local density. These results indicate that stoneloaches can occur in a wide range of streams, but they are less abundant in wide rivers, probably because of lower habitat heterogeneity. Slope was negatively correlated to both fish presence at the regional scale and local density, suggesting that stoneloach's swimming performance were weak under greater erosive forces. These results suggested that the distribution of populations and the density of stoneloach were governed by the suitability of physical habitat. Multi-scale studies of factors influencing a species' distribution allow to integrate patterns observed at different scales, and enhance our understanding of interactions between animals and their environment. The use of few pertinent variables in successful final models could reduce the effort and cost of data collection for water management applications.

## Introduction

The regional occurrence patterns and the local population structure of aquatic species are influenced by a large number of environmental factors, such as the geological history of the area, environmental stability (Ward & Stanford, 1979), ecosystem productivity (Lavandier & Décamps, 1984), habitat heterogeneity and suitability (Gorman & Kar, 1978), food availability, and competition and predation (Pianka, 1978). 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 local habitats 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; Boyero & Bailey, 2001; Inoue & Nunokawa, 2002; Boyero, 2003). Such data help ecologists to bring out relatively constant features of preferred habitats (Lobb & 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 & Sers, 1993). Fish species were often studied as model organisms under this topic (Harris & Silveira, 1999). 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 could be relevant models for a broader understanding of the relationships between the distribution and structure of populations, and habitat features at various spatial scales.

The stoneloach, *Barbatula barbatula* (Linnaeus 1758) (formerly *Noemacheilus barbatula*, Wheeler, 1992) is a slender, bottom-dwelling fish, that inhabits a range of freshwater environments (Smyly, 1955). The species occurs across much of Europe, from the Pyrenees mountains to the Balkans and Russia, although it appears to be absent from northern areas including much of Scandinavia and northern Scotland (Maitland, 1972; Greenhalgh, 1999). Stoneloach generally inhabit shallow, depositional habitats (Prenda et al., 1997; MacKenzie & Greenberg, 1998), and often show a preference for macrophytes where available (Hyslop, 1982; Welton et al., 1983; Roussel et al., 1998).

The aim of this study was to assess the influence of a limited set of environmental variables on the spatial distribution patterns of the stoneloach at three perception scales: the stream system, the stream site and the mesohabitat. The use of simple variables in successful final models could reduce the effort and cost of data collection for basic investigations and/or water management applications. We sought to bring out explicit models which would allow to better understand the relationships between habitat features, fish occurrence, and population density. Habitats of the stoneloach were described using several environmental variables, and the influence of each variable on fish presence and density was assessed using general linear modelling. 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 integrate scale-dependent patterns that determine a species' distribution.

## 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 (see 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, where we recorded the presence or absence of stoneloach. Site-specific data for fish occurrence were collected between 1980 and 2000. All sites were sampled by electro fishing (while wading) during low-flow periods, and using standardized methods (De Lury, 1947; Seber & Le Cren, 1967). Each site was characterised with five typological variables. These variables were chosen to relate the location of sampling sites within the stream system, and had to be easy to describe: elevation a.s.l. (m), distance from the source (km), and drainage basin area ($km^2$) were obtained from a Geographic Information System, whereas slope (‰) and stream width (m) where measured in the field using surveyor's instruments.

#### *Stream site scale*

We focused on 48 sampling sites which supported a stoneloach population, and which were distributed over the various geographic areas of the drainage basin (Fig. 1). Fish were sampled by

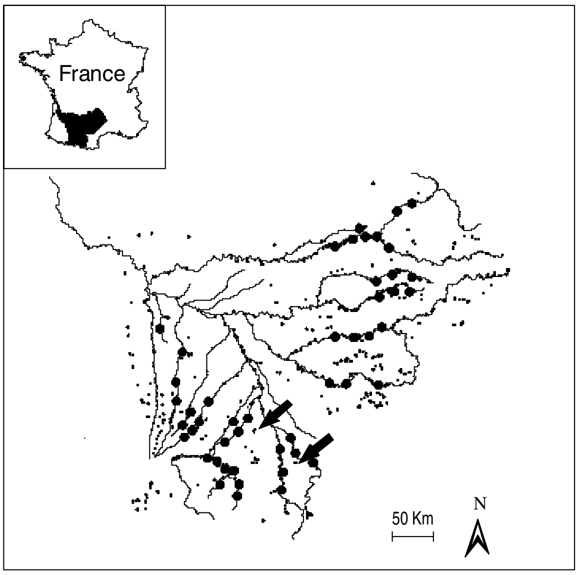


*Figure 1.* Map of the Garonne stream system, with location of the 554 sampling sites. Black circles showing the 48 sites which were selected for density models. The arrows show the location of the two sampling sites selected for the mesohabitat distribution model (River Douctouyre and River Leze).

electrofishing using a two-pass removal method (De Lury, 1947), which allowed calculation of their density (individuals per ha). At each site, the following variables were recorded during summer time: stoneloach density (ind $ha^{-1}$), slope (‰), stream width (m), mean depth (m), mean current velocity (cm $s^{-1}$), dissolved oxygen (mg $l^{-1}$), maximum water temperature (°C).

*Mesohabitat scale*

This part of the study was based on two rivers: River Lèze and River Douctouyre (S.W. France), second-order streams in the south-eastern part of the Garonne stream system (see Fig. 1). Fish were sampled by electrofishing using a two-pass removal method (De Lury, 1947) on 11 hydromorphological units in each river. Electrofishing was carried out in 2002 during the low flow period of the streams (summer period: July–August), in order to maximize the efficiency of fish capture and counts. Each of the 22 hydromorphological unit (6 riffles and 5 pools in river Lèze, 5 riffles and 6 pools in river Douctouyre) was described using 10 variables: % paving stones, % boulders (> 500 mm), % cobbles (200–500), % pebbles (100–200 mm), % stones (20–100 mm), % gravel (2–20 mm), % sand (0.05–2 mm), % mud (< 50 $\mu$m), mean depth (m), mean current velocity (cm $s^{-1}$). Current velocities were measured using an OTT® portable flowmeter.

*Data analysis*

We used general linear modelling (GLM) to analyse the distribution patterns of the stoneloach. 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. Presence/absence data at the stream system scale was analysed as the dependent variable with binomial distributed errors and logit link function. River was included as a random factor to control for the potential correlation between points obtained from a same river (Littell et al., 1996). Densities of stoneloach at the stream site were modelled using a negative binomial distribution and a log link, while at the mesohabitat scale, stone loach fit to a normal distribution and the identity link was used (see Crawley, 1993). 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 GLIMMIX macro and the GENMOD procedure of the SAS program (v. 8.2, SAS Institute, 2000).

## Results

*Stoneloach occurrence at the stream system scale*

In the Garonne stream system, stoneloach occurred at 240 sites out of 554. The model explained 48.2% of the total variance in stoneloach occurrence, as estimated by the deviance of the final model (392.5) and that of the null model (758.1). Three typological variables were negatively correlated with the presence of stoneloach populations (Table 1): distance from the source ($p < 0.0001$), slope ($p = 0.002$), and elevation ($p = 0.004$). Conversely, stream width was positively correlated ($p = 0.03$) with the occurrence of stoneloach. Drainage basin area was not significantly correlated with the presence of the species. GLM thus provided an overview of the 'stoneloach stream', through a limited number of pertinent variables. Whatever the size of the catchment area, the occurrence of stoneloach at a broad spatial scale was more probable in piedmont streams (200–600 m a.s.l., stream width <50 m) at a rather short distance from the source (<100 km), in areas with weak slopes (<5‰) (see Fig. 2a).

*Stoneloach density at the stream site scale*

Depending on the considered site, stoneloach density ranged from 8 to 7566 ind $ha^{-1}$. The model explained 41% of the total variance in stoneloach density (see Table 2), as estimated by the deviance of the final model (57.6) and that of the null model (60.1). Only two of the considered variables (slope and stream width) significantly influenced the local density of the species. Fish density decreased with increasing river slope ($p < 0.01$) and with increasing stream width ($p < 0.001$). Areas with stream width ranging from 0 to 10 m and slopes ranging from 0 to 10 ‰ were thus likely to support largest populations (see Fig. 2b). Temperature, oxygen, depth and water velocity had no significant influence on population densities (Table 2).

*Table 1.* Model analysing the patterns of stoneloach's distribution at the stream system scale. Backwards model, with binomial distributed errors, logit link, and river included as a random factor. The model explained 48% of the original deviance

| Effect | Estimate ± standard error | $F$ | df | $p$ |
|---|---|---|---|---|
| Intercept | 1.1187 ± 0.3479 | | | |
| Slope | −0.0253 ± 0.0079 | 10.22 | 1.409 | 0.0021 |
| Width | 0.0122 ± 0.0056 | 4.75 | 1.409 | 0.0317 |
| Distance | −0.0124 ± 0.0022 | 29.98 | 1.409 | < 0.0001 |
| Elevation | −0.0015 $t$± 0.0005 | 8.64 | 1.409 | 0.0042 |
| Drain | | 0.72 | 1.408 | 0.4034 |

Only variables with $p < 0.05$ are interpreted as statistically significant. For variables not included in the model no parameter estimate is presented and the $F$ and $p$ values correspond to the values when added to the final model.

*Stoneloach density at the mesohabitat scale*

Stoneloach densities in the study reaches of Rivers Lèze and Douctouyre were 7566 and 7406 ind $ha^{-1}$, respectively, which corresponds to the highest abundance values we recorded in the Garonne stream system. The model explained 40% of the total variance in stoneloach density at the mesohabitat scale. The distribution of residuals of the GLM showed negative correlations between % mud (i.e., clogged bottom) and fish density (Fig. 2c, $p < 0.001$). Other variables under consideration (depth, current velocity, coarse mineral particulates) did not show significant relationship with fish density at the mesohabitat (hydromorphological unit) scale (Table 3). These results suggested that stoneloach used a wide range of non-cohesive substrates associating combinations of coarse mineral particulates.

## 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 & 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 & Bardonnet, 2002). Beyond the quantitative information that it yielded (thus documenting the local and broad scale habitat preferences of the stoneloach), 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.

At first sight, our models did show that a few pertinent variables could explain spatial variations in fish occurrence and local density, and that,

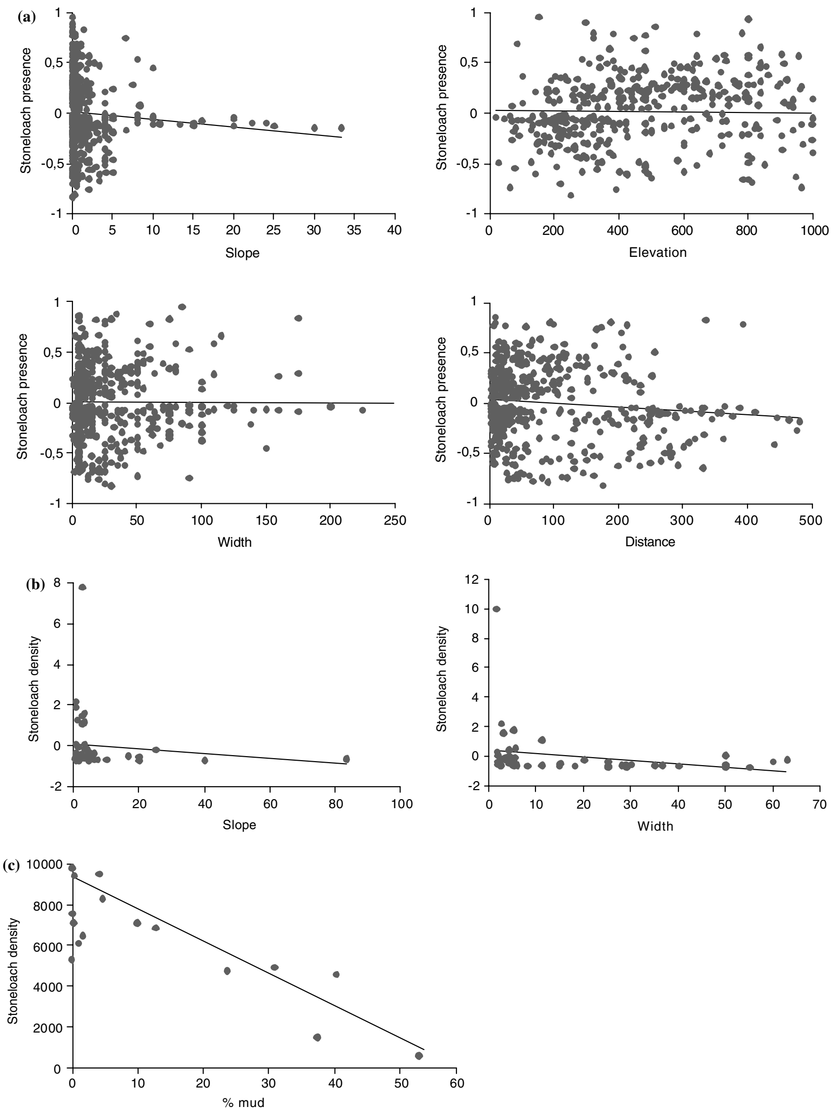


*Figure 2.* (a) Relationship between different stream system scale variables and the presence of stoneloach. For variables retained in the final model residuals correspond to presence of stoneloach expressed as the residuals of the GLM model with binomial error including all the variables in the final model out of the variable of interest. For these variables linear regression line is provided. (b) Relationship between different site scale variables and density of stoneloach. For variables retained in the final model residuals correspond to stoneloach density expressed as the residuals of the GLM model with negative binomial distributed errors including all the variables in the final model out of the variables of interest. For these variables linear regression line is provided. (c) Relationship of mesohabitat variables and density of stoneloach. For variables retained in the final model residuals correspond to stoneloach abundance expressed as the residuals of the GLM model with normal distributed errors including all the variables in the final model out of the variables of interest. For these variables linear regression line is provided.

subsequently, simple variables could provide explicit schemes that may be useful to target further research, and to implement management options. However other variables such as food availability (not considered in this study) would probably account for part of the observed variations. Stream width was positively related to the probability of presence of stoneloach at the stream system scale, whereas it was negatively related with stoneloach density at the stream site scale. This pattern means that the probability of presence of the stoneloach is higher at sites with a large

*Table 2*. Environmental factors testing stoneloach density. Backwards model, with errors distributed as a negative binomial distribution and log link. The model explained 41% of the original deviance

| Effect | Estimate ± standard error | Chi-Square | df | $p$ |
|---|---|---|---|---|
| Intercept | 6.9420 ± 0.2488 | | | |
| Slope | −0.0321 ± 0.0078 | 9.00 | 1 | 0.0032 |
| Width | −0.0339 ± 0.0077 | 13.50 | 1 | 0.0002 |
| Temperature | | 0.17 | 1 | 0.6824 |
| Oxygen | | 1.38 | 1 | 0.2457 |
| Depth | | 0.80 | 1 | 0.3778 |
| Velocity | | 0.01 | 1 | 0.9135 |

Only variables with $p < 0.05$ are interpreted as statistically significant. For variables not included in the model no parameter estimate is presented and the Chi-square and $p$ values correspond to the values when added to the final model.

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

| Effect | Estimate ± standard error | $F$ | df | $p$ |
|---|---|---|---|---|
| Intercept | 8980.22 ± 697.08 | | | |
| Mud | −142.21 ± 37.69 | 14.23 | 1.21 | 0.0010 |
| Sand | | 0.18 | 1.20 | 0.6821 |
| Gravel | | 0.09 | 1.20 | 0.7765 |
| Stones | | 0.07 | 1.20 | 0.7932 |
| Pebbles | | 0.00 | 1.20 | 0.9847 |
| Cobbles | | 1.25 | 1.20 | 0.2801 |
| Boulders | | 2.10 | 1.20 | 0.1630 |
| Paving stones | | 1.33 | 1.20 | 0.2664 |
| Depth | | 0.75 | 1.20 | 0.4002 |
| Velocity | | 0.01 | 1.20 | 0.9122 |

The final model explained 40% of the original deviance. Estimates are provided for variables in the final model and correspond to the slopes obtained from the GLM model with normal errors and identity link. For variables not included in the model the significance when incorporated to the final model is given.

channel, but that populations are larger when they occur at sites with lower channel width. Previous studies suggested that stoneloach prefer small streams with heterogeneous substrates, although they are common in wide rivers (see Keith & Allardi, 2001). Specifically, Mastrorillo et al. (1996) highlighted that adult stoneloach require high proportions of shelter habitats providing protections against sunlight, because individuals chiefly have a nocturnal activity (Welton et al., 1983). Moreover, the presence of shelters provide refuges from predatory fishes (MacKenzie & Greenberg, 1998), e.g., Chub (*Leuciscus cephalus*, which can prey upon juvenile stoneloaches in large rivers (Watkins et al., 1997).

Slope was negatively correlated to both the probability of presence of stoneloach at the stream system scale, and to stoneloach density at the local scale. Slope has a key influence on the erosive force acting on substrate and bed scour in a given area (Cobb & Flannagan, 1990, Cobb et al., 1992), and, subsequently, on stream animals. The stoneloach is an unskilled swimmer (Balon, 1975). It is probably not able to maintain position under greater erosive forces (Roussel & Bardonnet, 1997), and/or may not find refuge habitats in areas with steeper slopes (Welton et al., 1983). Steeper slopes are rather characteristic of mountainous areas and could thus partially explain the negative correlation between stoneloach occurrence and elevation, and the absence of stoneloach at sites located above 1000 m a.s.l. Conversely, weaker slopes corresponded to the piedmont zone in our study area, which, according to Reyjol et al. (2003), favour higher fish densities in the Garonne stream system through a higher habitat heterogeneity. Moreover, stoneloach occurrence was more probable both at short distances from the source and at low elevations, i.e., in those streams having their source in piedmont zones, which fits with the above mentioned assumptions.

Among the 48 sites selected for population density analyses, oxygen ranged from 7 to 14 mg $l^{-1}$, and average temperature in summer ranged from 12.5 to 22 °C. Within theses ranges, oxygen and temperature were not key factors explaining variations in local fish density, certainly because the optimal temperature for the stoneloach is about 19 °C (Elliot et al, 1996), and all study streams were well oxygenated. Although water velocity may influence habitat use by stoneloach (Zweimüller, 1995), we found no particular effect of current velocity on stoneloach density at a site. Prenda et al. (1997) found stoneloach in pools, whereas Jones (1975) observed them in riffles; our study thus suggested the use of both habitats by the species in the Garonne stream system. Stoneloach generally inhabit depositional habitats (Prenda et al., 1997; MacKenzie & Greenberg, 1998), but our results suggested that individuals avoided clogged bottom (mud, silt). Such information supports the field observations that stoneloach usually take refuge under stones.

Because of its small body size and its benthic behaviour, the stoneloach 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. Spatial variations in stoneloach density were influenced by the location of populations within the stream system, with a marked preference for small rivers located at rather low elevations. Such ecosystems are characteristic of the piedmont zone of the Garonne river basin, which corresponds to the grayling zone (*Thymallus thymallus*) and the common barbel zone (*Barbus barbus*) according to Huet's well-known zonation (1949). The species may occur in a large range of sites within a large stream system, but the density of populations seemed to be governed by the suitability of physical habitat and hydraulic conditions. Scales below mesohabitat (i.e. microhabitat) were not considered in this study. However, our results showed the dependence of stoneloach on substrate composition. Given the small size of individuals, it is possible that they show some variability at microhabitat scales, but further investigations would be needed to verify this assumption.

By focusing on integrative variables at both spatial scales (e.g., elevation, slope), we emphasized the influence of river typology on a species' distribution. Such schemes are likely to provide insights to both managers and ecologists, because (i) the underlying local conditions which are associated to global river typologies are well known (see e.g., the River Continuum Concept by Vannote et al.(1980)), (ii) they may suggest subtle relationships that deserve more detailed study in subsequent research (e.g. population dynamics vs. temporal habitat dynamics), and/or (iii) 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 & Spindler,1989; Poulet, 2000). Most biomonitoring techniques for aquatic biota use extensive numbers of sites-specific data to allow predictions of the distribution of species to be expected in a given area, using a limited set of environmental characteristics (see e.g. review in Wright et al., 2000).

Substrate-based models (local scale) were usually successful in predicting the distribution of individuals at the 1–10 m in scale (Roussel et al., 1999; Hastie et al., 2000). However, large-scale (macrohabitat) descriptions based on few pertinent variables remain important to provide context (Strayer & 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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