

# Spatio-temporal patterns of fish assemblages in a large regulated alluvial river. *Freshwater Biology* (2009), 54, 1544-1559

RENAUD RIFFLART \*†, GEORGES CARREL\*, YANN LE COARER\* AND BENEDICTE NGUYEN THE FONTEZ †

\* Cemagref, UR HYAX, 13182 Aix-en-Provence, France.

† Université de Provence, UMR IMEP 6116, 13331 Marseille, France.

Correspondence: Renaud Riffart, Cemagref, UR HYAX, 3275 Route de Cézanne, CS 40061, 13182 Aix-en-Provence cedex 5, France.

E-mail: [renaud.riffart@cemagref.fr](mailto:renaud.riffart@cemagref.fr)

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**Précisions** : Dans la version publiée de l'article, trois espèces avaient été nommées sous leur ancienne dénomination scientifique : le chevaine (*Leuciscus cephalus* devenu *Telestes cephalus*), le toxostome (*Chondrostoma toxostoma* devenu *Parachondrostoma toxostoma*) et le blageon (*Leuciscus souffia* devenu *Telestes souffia*).

## SUMMARY

1. The River Durance, the last alpine tributary of the River Rhône, is a large, braided alluvial hydrosystem. Following large-scale regulation, flow downstream of the Serre-Ponçon dam has been maintained at 1/40th of previous annual mean discharge. To assess the effects of historical disturbances, fish assemblages and habitat use were analysed during five summers in a representative reach of the middle Durance.
2. Habitat availability and use were assessed with a multi-scale approach including the variables water depth, current velocity, roughness height of substratum, amount of woody debris and lateral/longitudinal location. Eighteen fish species were sampled by electrofishing in 289 habitat sample units.
3. Partial Least Square (PLS) regression showed that taxa were mainly distributed according to relationships between their total length and water depth/velocity variables. Fish assemblage composition was also related to roughness height as well as distance from the bank or to the nearest large woody debris. However, PLS regression revealed no significant differences in habitat selection between two periods of varying hydromorphological stability.
4. Fish distribution patterns and density were related to proximity to the bank and cover, indicating that local scale variables need to be considered in conservation and restoration programmes.

## INTRODUCTION

Natural disturbances such as floods or droughts are integral components of most freshwater ecosystems, and consequently organisms have evolved traits that enable them to survive, exploit and even depend on many kinds of disturbances (Townsend & Hildrew, 1994; Bunn & Arthington, 2002; Lytle & Poff, 2004). For example, fish can move to refuge areas during spates, avoid hostile conditions by spawning after floods and protect their eggs by excavating deep nests in gravel bottoms (Lytle & Poff, 2004). However, anthropogenic activities such as the regulation of rivers for hydropower often result in loss or modification of freshwater habitats (e.g. Nilsson *et al.*, 2005), by changing river connectivity (Aarts, Van Den Brink & Nienhuis, 2004; Hirzinger *et al.*, 2004), altering exchange processes (Brunke & Gonser, 1997) and fragmenting populations (Corbacho & Sanchez, 2001). Although fishes are primarily affected by alterations in hydromorphology (Ormerod, 2003), separating the effects of flow regulation from other anthropogenic impacts on the floodplain, such as extraction of gravel, water abstraction and pollution, has proven to be difficult.

The riverscape is a complex and heterogeneous system including lateral floodplain water bodies connected to the main channel. This lateral connectivity is frequently used by riverine fishes as seasonal habitat and plays a functional role as spawning or nursery grounds. Habitat disturbances affect fish life-histories, survival, reproductive success and ultimately population growth rate (Copp, 1989; Molls, 1999; Borchertding *et al.*, 2002; Dunham & Rieman, 1999). Although these impacts are well known, fish community responses are not well understood (Nilsson *et al.*, 2005). Disturbed wetlands have less species diversity (Chipps, Perry & Perry, 1994), and invasion of exotic and fugitive species is facilitated by habitat alterations (Meffe, 1984; Moyle & Light, 1996). Understanding the links between fish fitness and flow regimes

or other habitat variables is important for an effective watercourse management (Lytle & Poff, 2004).

In classical fish habitat studies, current velocity, water depth and substratum type are often used to explain spatial patterns and to calibrate predictive models (Gorman & Karr, 1978; Bovee, 1982). However, recent studies have shown that these variables alone are not adequate to understand and predict fish responses (Brosse & Lek, 2000; Mugodo *et al.*, 2006). For instance, in complex hydrosystems, like large gravel bed alluvial rivers associated to plurispecific fish communities (Souchon *et al.*, 2002), other habitat features are needed to predict fish assemblages (Powers *et al.*, 2003). Refuge availability and proximity to the riparian zone are two variables that have been shown to be strong predictors of fish assemblages (Copp & Jurajda, 1999; Schiemer, Keckeis & Flore, 2001). Both of these variables are proxies for the availability of refuges (Growth, Pollard & Gehrke, 1998) as well as shading zones, organic matter and favoured feeding areas (Gozlan *et al.*, 1999; Hirzinger *et al.*, 2004). Species richness (Powers *et al.*, 2003) and densities (Shields, Knight & Cooper, 1994) are also strongly correlated with channel width.

Although earlier studies often considered the importance of local scale variables as drivers of stream diversity, recent studies have shown the importance of catchment level variables (Ward & Stanford, 1989; Townsend *et al.*, 2003). Moreover, as mechanisms may operate on scales other than those at which patterns are observed they may be best understood by the assessment of relationships within smaller scale units, within large scale units (Levin, 1992; Moir, 2008). Consequently, relating processes identified at a local scale to large scale phenomena is a major challenge of both fundamental and applied ecology. For this reason, we describe habitat at local and mesohabitat scales. We study the importance of the classical

variables, water depth, current velocity and roughness height, as well as proximity to the bank, presence of large woody debris and channel width, as predictors of fish assemblages. Furthermore, using two distinct hydromorphological periods separated by almost 10 years we test the hypothesis that relationships between fish assemblages and spatial habitat are consistent among years. The study was carried out in a highly regulated river which has experienced stable low flow conditions and a significant decrease in minor floods since the construction of the Serre-Ponçon dam in late 1950's; dam construction resulted in flows of 1/40<sup>th</sup> of pre-regulated annual mean discharges. Finally, although much is known of the effects of flow regulation on salmonids (Murchie et al., 2008), our study focused on rheophilic cyprinids.

## **METHODS**

### ***Study area***

The catchment of the Durance River (14 322 km<sup>2</sup>), the last left-bank tributary of the Rhône River, starting at about 2400 m a.s.l. at the Franco-Italian border, merges with Rhône River some 320 km downstream. Having a Mediterranean climate, the Durance catchment receives less annual precipitation than other alpine tributaries of the Rhône (annual mean rainfall 720-900 mm in the Durance catchment; data from Météo-France, 1961-1990, AURELHY model). The upper Durance has a nival flow regime, not much influenced by glacial inputs, but the influence of Mediterranean climate increases with decreasing altitude (Pardé, 1925).

The study site is a reach of about one kilometre long, located near Manosque (Alpes-de-Haute-Provence, Latitude: 43° 50' 26" N, Longitude: 05° 51' 06" E) (Fig. 1). The study focused on the residual channel of the initial braided alluvial river pattern (Warner, 2000). Before flow regulation, annual discharge averaged 140 m<sup>3</sup>.s<sup>-1</sup>, and the natural minimum flow

was *c.* 24 m<sup>3</sup>.s<sup>-1</sup>. After flow regulation, discharge has markedly decreased (to *c.* 3.5 m<sup>3</sup>.s<sup>-1</sup>), with interspersed winter or spring flood events from intermediate sub-catchments (Fig. 2). Low discharge has resulted in a single channel, with few connections to residual side channels and backwaters, an increased remoteness of favourable structures for fish, such as shade and cover, and a reduction in river bank heterogeneity. The physical habitat is essentially built around gravel point, mid-channel, diamond and diagonal bars (Kellerhals & Church, 1989). These features explain the main physical characteristics of the regulated middle Durance River (Table 1).

### ***Fish assemblage***

Fish were sampled from 289 independent homogeneous sample units by diurnal electrofishing (EFKO F.E.G. 8000, 400–600 V, 6–10 A) using an open-sampling technique (Lamouroux *et al.*, 1999b; Thevenet & Statzner, 1999; Lamouroux *et al.*, 2006). As larger individuals have a better escape response, an adapted long anode of four metres was used to prospect deep areas and reduce fish escape. Surfaces varied between 4.5 and 110 m<sup>2</sup> (95% of units). Lamouroux *et al.* (1999a) showed that the area of sample units had a negligible impact on preference models.

All individuals were identified to species (except for young stages of the two species of the genus *Chondrostoma* which were grouped), and total length (TL ± 1 mm) measured. For analysis, each species was divided into size or taxa classes as: taxon 1 (0 < TL ≤ 30 mm), taxon 2 (30 < TL ≤ 60 mm), taxon 3 (60 < TL ≤ 90 mm), taxon 4 (90 < TL ≤ 120 mm), taxon 5 (120 < TL ≤ 150 mm), taxon 6 (150 < TL ≤ 300 mm), taxon 7 (300 < TL ≤ 450 mm) and taxon 8 (TL > 450). Rarest species were excluded from statistical analysis.

Annual sampling campaigns were carried out from July until September during five years, grouped in two periods (1995-1996-1997 and 2004-2005). Sampling was done when physical constraints linked to regulated low flow and water temperature were the highest and when all fish size classes, in particular the young-of-the-year, could be obtained (Gozlan *et al.*, 1999). The first period was characterised by flood events between each annual campaign, whilst the second period was characterised by a long and stable hydrological period due to the absence of high flow events (Fig. 2).

### ***Habitat characteristics***

A specific digital elevation model (DEM) was developed and used to describe hydraulic variability in the study reach (e.g. quantification of the proportions of velocity–depth classes). For a given flow and for any area of the aquatic space, it was possible to quantify the hydraulic diversity by calculating the percentages of volumes or horizontal surfaces in a depth–average velocity cross-classification. This representation in the velocity–depth plane is known as a hydraulic signature (Le Coarer, 2005; Le Coarer, 2007).

Geo-referencing of vertical measurements of depths and corresponding average velocities was done with a TCRA 1102 (© LEICA). Density of verticals increased according to the local heterogeneity of geomorphic units. Current velocities were measured using an electromagnetic current metre (FLO-MATE, portable model 2000). Discharge was gauged during each sampling period. Each year, the complete topography, depth and velocity measurements, gave a precise cartography of the study reach.

A more exhaustive habitat description was done for each of the individual sampling sub-units for fish. Within each sub-unit, a minimum of nine verticals of water depth and current

velocity were spatialised to build a triangular irregular network (TIN) of hydraulic description. Using the Hydrosignature concept, we defined nine depth-velocity crossed classes (i.e. hydraulic classes, Table 2). The lower velocity class limit ( $5 \text{ cm.s}^{-1}$ ) separates lentic zones and the upper value ( $30 \text{ cm.s}^{-1}$ ) corresponds to the observed critical velocity for suspended load transport. Values for depth were chosen according to Aadland's (1993) classification of stream habitat types.

Substratum type was characterized by measuring roughness height ( $k$ ), defined as the difference between the highest point on a particle and the minimal height of contact points of adjacent particles (Gordon, McMahon & Finlayson, 1992). A minimum of 10 values were measured in each sample unit and divided into five classes (Table 3). Large woody debris (LWD) was recorded as percent cover according to three classes ( $W1 < 10 \%$ ,  $10 \leq W2 < 50 \%$ ,  $W3 \geq 50 \%$ ). This form of assessment is well adapted to large systems presenting low density and discrete distributions of LWD (Maridet & Souchon, 1995; Thevenet, Citterio & Piegay, 1998). Segments were created from shorelines and cover percentages incremented into a GIS. The shortest distances were then measured from the centroid of each sample unit to each modality of cover ( $d_{W1}$ ,  $d_{W2}$  and  $d_{W3}$ ) and to the bank ( $d_{Bank}$ ). Channel width was also recorded ( $Width$ ) (Table 3). The last two variables were chosen according to the asymmetry of transversal fish distribution in a channel and the importance of instream ecotones (Bretschko & Waidbacher, 2001).

For the global approach, 10 types of visually distinguishable and biologically meaningful mesohabitats were identified (Table 4), and associated surfaces were evaluated each sampling year. Mesohabitat classes were defined according to the criteria proposed by Borsanyi (2004) and Malavoi & Souchon (2002).

## *Analysis*

### *Importance of habitat*

Partial Least Square regression (PLS) was used to quantify the influence of habitat variables on the spatial patterns of fish assemblages. As regression coefficients are not independent among fish taxa, they were ranked and analysis done on the first three variable ranks. Distances were square-root transformed and fish densities (abundance.m<sup>-2</sup>) were log (x+1)-transformed to account heteroscedasticity and deviations from normality. As values of coefficients associated to distances were inversely related to proximity to these structures, the signs of the coefficients were reversed and referred to as: *Bank*, *Wood1*, *Wood2* and *Wood3*. Bootstrapping was used to assess the distribution of the rank variables denoting the relative importance of each descriptive variable, according to Austin & Tu (2004) and adapted for study needs.

In order to transpose information collected at the sample unit scale to the reach scale, we used 10 000 simulations of the simulated surface areas of each mesohabitat, with a Dirichlet variable (Lange, 2002). Using parameters observed at the reach scale, we generated a bootstrapped data set in order to represent habitat diversity observed at the studied reach. Coefficients ranks were computed for the 10 000 resampled data sets using *pls* package for R (Kooistra *et al.*, 2001). Interpretation of the results focused on the first three variable ranks (rank one being the number of times the descriptive variable had the most influence on fish presence).

### *Importance of temporal stability*

Temporal stability of spatial relationships between the two sampling periods was tested using PLS. First, the same data processing as in previous analysis (bootstrapping including PLS regression) was carried out but restricted to 100 PLS regressions. The resulting two rank matrices were simplified: only taxa from the eight dominant species (blageon – *Leuciscus souffia*, stream bleak – *Alburnoides bipunctatus*, chub – *Leuciscus cephalus*, stone loach - *Barbatula barbatula*, barbel – *Barbus barbus*, minnow – *Phoxinus phoxinus*, sofie – *Chondrostoma toxostoma* and gudgeon – *Gobio gobio*) and habitat variables: (i) *Wood3* (proximity to the most complex LWD), (ii) *Bank* (proximity to the bank), (iii) *k1*, *kt* (*k2*, *k3* and *k4* grouped) and *k5* and (iv) *DIV1*, *DIV2*, *DIV3*, *D2V1*, *D2V2*, *D2V3* with depth limits ( $D1 \leq 30$  cm,  $D2 > 30$  cm) and velocity limits ( $V1 \leq 5$  cm.s<sup>-1</sup>,  $5$  cm.s<sup>-1</sup> <  $V2 \leq 30$  cm.s<sup>-1</sup> and  $V3 > 30$  cm.s<sup>-1</sup>) were used.

Simulated rank distribution of each variable for each taxon was compared using a *t*-test. The resulting p-values matrix was considered as an observed situation between the two data sets. New data sets were generated using the assumption that spatial relationships were similar among years. For this, and as bootstrapped Student *t*-statistic asymptotic properties were not known (Mason & Shao, 2001), permutation tests were performed (Manly, 1997). All sample units were combined and permutations were carried out in order to rebuild 1000 replicates of both data sets including data from all years. For each permutation, the same data processing was undertaken and the resulting distribution of statistics from these 1000 *t*-tests was considered as a theoretical situation (i.e. if there were no fish species preferences). The relative positions of the p-values associated to the observed situation within the distribution of the 1000 p-values obtained for the theoretical situation informed us about the probability of the observed situation under null hypothesis of stability of relationships among years.

All analysis were conducted using R software version 2.2.1 © 2005 (R\_Development\_Core\_Team, 2005).

## RESULTS

### *Fish assemblages*

The studied reach of the middle Durance was characterised by 18 fish species from six families and was mainly dominated by rheophilous cyprinids (Table 5). Six species made up 85% of captures: five cyprinids (blageon, stream bleak, chub, barbel, minnow) and one balitorid, the stone loach. Four intermediate species counted for about 14% of captures: three cyprinids (nase - *Chondrostoma nasus*, sofie, gudgeon) and one cobitid, the spined loach (*Cobitis bilineata*). Eight rare species represented 1.3% of the total number of captures: three cyprinids (bleak – *Alburnus alburnus*, roach – *Rutilus rutilus* and tench – *Tinca tinca*), two percids (perch – *Perca fluviatilis* and Rhône streber – *Zingel asper*), one centrarchid (pumpkinseed – *Lepomis gibbosus*) and two salmonids (brown trout – *Salmo trutta* and rainbow trout – *Oncorhynchus mykiss*). Two species deserve particular attention: the Rhône streber, a threatened endemic species of the Rhône catchment, and the introduced spined loach. Thirty-one individuals of Rhône streber were recorded in 20 sample units during the five sampling campaigns. This species is considered as critically endangered in the International Union for Conservation of Nature and Natural Resources (IUCN) Red list of threatened species (Crivelli, 2006). The spined loach was also caught in the studied reach; first observed in the Durance River in 1996 after successive high floods, and captures increased from 14 specimens in the first period to 176 specimens in the second period.

Most individuals of the fish assemblage consisted of young-of-the-year and small species (*c.* 75 percent were < 90 mm). Only 0.65% of total fish catch were longer than 300 mm. For large cyprinids, adults > 300 mm accounted 0.8%, 2% and 6.5% of chub, barbel and nase, respectively.

### *Habitat characteristics*

Instream flow varied from 3.5 to 7 m<sup>3</sup>.s<sup>-1</sup>, and width of active channel varied from 7 to 202 m (mean 33 m) during the study period (Table 1). Cross-section flow velocities (mean 0.44 m.s<sup>-1</sup>, range 0.05 - 1.85 m.s<sup>-1</sup>) and water depth (mean 0.36 m, range 0.04 - 1.11 m) showed a predominance of shallow and lentic habitats. Deep areas > 60 cm covered 13.5% of the reach compared to 26.2% for shallow areas (*d* < 15 cm, Table 2). The proportion of large and shallow riffles increased. A first topographical survey of 3 300 m resulted in the presence of 10 riffles of 25 m or more with a depth < 15 cm (Dumont et al., 1993).

During regulated flow conditions the alluvial forest is almost always far from the channel and reached only during floods. Inputs of large woody debris from riparian forest to the channel were highly reduced. The scarcity of immersed LWD was indirectly shown by the average minimal distance between sample units and woody debris (*d*\_W3: 64 m, *d*\_W2: 81 m, *d*\_W1: 84 m, Table 3), i.e. twice the width of the active channel.

The first 16 principal components of the PLS regression were kept in order to explain at least 25 % of the spatial patterns individual taxa. Including more components did not improve model fit. The first three ranks obtained from the coefficients of the PLS regression (Appendix 1) revealed strong relationships between fish length and hydraulic classes. A well

defined pattern for the largest species (chub, barbel and nase) was exhibited. Some hydraulic classes were strongly avoided, such as d1v1 by large taxa, d1v4 by minnow and d4v1 by bleak (Aal 2 & 3), blageon (Lso 4 & 5), chub (Lce 2 to 6), nase (Cna 4 & 5) and all taxa of spined loach.

Habitat characteristics were important predictors of fish assemblage composition. Presence or proximity of LWD had a significant effect on the largest specimens of sofie, gudgeon, perch, chub, blageon, nase and barbel, and also on all size classes of stream bleak. LWD was also the most important variable for nase (Cna 6), gudgeon (Ggo 4 & 5) and perch (Pfl 6). By contrast, other taxa, bleak (Aal 3 & 4), young sofie (Cto 3) and barbel (Bbs 3) and Rhône streber (Zas 2) were negatively correlated with LWD. A positive effect of bank proximity was also observed for almost all species, particularly for the youngest fishes, in relation to low depths close to the bank. Bank proximity was also important for some large taxa such as chub, barbel and perch. Conversely, bank proximity was not important for spined loach, and Rhône streber was negatively correlated with this variable. Regarding channel width, most of the species occupied the narrow sections of the river, except Rhône streber (taxa 3, 4 & 5) which showed a preference for large channels and an avoidance of bank proximity. All sizes of species caught in lentic sub-units (chub, spined loach, perch) but also some rheophilous taxa (bleak, gudgeon, blageon) were associated to the lowest roughness height values (k1). The largest rheophilic species (nase, sofie, barbel, blageon) were associated to the highest k values (k5) recorded in narrow and curved sections of the channel with the highest hydraulic classes. In some areas, rheophilic species were associated to heavy blocks used for bank stabilisation.

Our results show the importance of habitat for the endangered Rhône streber and two loaches (stone and spined loach). Small individuals (< 60 mm) were mainly associated with d2v3

while the larger individuals ( $> 60$  mm) were only associated with d2v4 (d2v3 were partly avoided). Rhône streber inhabited mid-channels in wide sections. Roughness height followed a gradient in intermediate k classes according to the fish size (k4 was avoided by taxa 3 and 4). The stone loach was mainly found in fast-flowing shallow zones (overall  $< 0.05$  m) and appeared to be directly influenced by proximity to the bank or to the largest woody debris. By contrast, the spined loach was only observed in null velocity areas; according to rank values, this species was associated to the presence of very fine (k1) substratum.

### *Temporal variability*

Hydromorphological changes in the river bed and instream LWD after high-level floods showed the most marked changes between the two time periods (Fig. 2). Although % bank line with LWD did not differ among years (range 2.6% in 1996 to 7% in 1995), distance to the nearest and highest complex LWD (d\_W3) did differ between the two periods (Period 1:  $99 \pm 21$  m, Period 2:  $35 \pm 5$  m, Mann-Whitney test,  $P < 0.001$ ) (Table 6). Distances to the bank did not differ (Period 1:  $4.9 \pm 0.8$  m, Period 2:  $6.1 \pm 0.8$  m,  $P = 0.078$ ), whereas roughness height classes differed significantly for k1 and k5. Silted areas increased in 2005 and roughness height increased in the last two years (Table 3).

As the river channel was not restructured between 2004 and 2005, the sampled surface associated to k1 in 2005 (10.8 %) was about twice that of other years (mean 5.3%). Furthermore, in the second period, a reach section was running along rocks protecting a motorway, increasing "artificially" high roughness height values (sampled surface associated to k5 was about 2.5% in 2004-2005, whereas it was less than 0.6% for the other three years).

In spite of changes in habitat characteristics, no major differences in fish-habitat relationships were noted between the study periods (Table 6). The importance of bank characteristics was the same between periods except for stream bleak (Abi 4). Only one strong ecological change concerned proximity to the nearest large woody debris (blageon, Lso 5) and roughness height (stream bleak, Abi 2 for k1). Similarly, few differences were noted for hydraulic classes between periods (Table 2). The most important changes were noted in D2V1 class for chub (Lce 2 & 6) and in D2V3 for barbel (Bbs 6). Observed differences in hydrosignatures were mainly related to deep classes ( $d > 60$  cm). A deepening of the channel against the artificial bank reinforcement consecutive to its lateral migration explained the highest proportion of deep classes during the second period.

## **DISCUSSION**

River topography and quantitative hydraulic characterisation of habitat (Le Coarer & Dumont, 1995; Le Coarer, 2005; Le Coarer, 2007) were used to define the hydraulic heterogeneity of each sub-unit. Traditionally, water depth and current velocity are considered as independent parameters, although they are intimately associated, for example, in characterisation of physical flow (Stewardson & McMahon, 2002), ecological mesohabitat evaluation (Orth, 1995) and fish habitat use (Mosley, 1983; Aadland, 1993). Bivariate classes (depth/velocity) and use of fish size classes highlighted taxa distributions according to the size, physiological adaptation and ecological affinity to hydraulic conditions. Taxa followed well-defined gradual distribution in hydraulic classes.

Our results show the importance of habitat characteristics for fish assemblages, but also that depths used by taxa, especially large individuals, were probably a "compulsory" adjustment to

physical conditions rather than a real preference in the Durance (Boyer, 2004). Only 13.5% of the study reaches consisted of deep mesohabitat ( $d > 60$  cm), which is known to be important in the life history of large rheophilous species (Baras & Cherry, 1990; Lucas & Batley, 1996; Huber & Kirchhofer, 1998; Allouche, Thevenet & Gaudin, 1999). Hence, the scarcity of deep mesohabitat is likely responsible for the low number of large individuals recorded in our study. Only 0.8% of chub, 2% of barbel and 6.5% of nase individuals captured were  $> 300$  mm. Although sampling effort may have underestimated the density of large individuals, our findings support previous studies on the regulated Durance (Bouchard, 1996; Dumont et al., 1993). The low number of large individuals could also be associated to fitness which may be negatively affected by physical constraints, such as low availability of LWD, decrease in mean current velocity, lack of deep areas and alteration of temperature patterns. All of these disturbances have been shown to affect the growth rate of salmonids (Swales, 1988; Fausch & Northcote, 1992) and chub (Bouchard et al., 1998) in the river Durance.

The finding that substratum roughness height value ( $k$ ) was a robust predictor of fish assemblages was expected as it indirectly estimates hydraulic shelter created by substratum elements. A previous study in a salmonid-rich part of the regulated Durance showed a significant positive relationship between mean size of brown trout and mean  $k$  value in sub-units (Carrel *et al.*, 1992). The importance of the  $k1$  class is related to fine sediments associated with low velocity; only *Cobitis bilineata* can be considered as having a real affinity to fine sediment substratum (Slavik *et al.*, 2000). Intermediate  $k$  classes had no clear influence on the spatial patterns of individual taxa, with the exception of Rhône streber. Our results corroborate Rhône streber habitat observations on the Beaume River, a tributary of the Ardèche River (Labonne, Allouche & Gaudin, 2003). The  $k5$  class appears naturally in the

deepest areas and in artificial rocks protecting the bank (second period). The large substrate elements are mainly used as cover for the largest specimens.

Woody debris was among the first three variables selected in our models, and its importance is clearly highlighted regarding the influence of LWD on rank values. This strong relationship is likely related to the overall low amount of LWD in the study reaches, but also its importance for instream hydrology and shelter. The largest woody debris (and associated distances: d\_W2 and d\_W3) had the most influence on fish assemblages. Thevenet, Citterio & Piegay (1998) showed that wood jams containing large wood had greater potential for aquatic communities. Likewise, Angradi *et al.* (2004) showed the importance of LWD for increasing habitat heterogeneity, by increasing the hydraulic roughness of the bed and creating specific habitats, for fish assemblages.

Species richness and spatial responses of taxa were relatively stable, despite large hydromorphological changes during flood events. The main differences between the study periods were associated with changes in morphological characteristics following natural high flood events and siltation during long periods of stable low flow. The significant changes in distances to the nearest LWD observed between the two periods could be linked to migration patterns of the channel, thereby underpinning the importance of contact with forested bank. Our results showed low LWD densities in the channel in addition to the highest densities unusually being found in the channel sections reaching overhanging residual alluvial forests. Differences observed for Wood3 were explained by greater distances to these LWD during the first period. For example, distances for blageon to the nearest largest LWD were clearly distinct between the first (mean 78.3 m) and second (14.5 m) periods. For bank variability, the differences observed for stream bleak were explained by the shorter distance to the bank

recorded the first year ( $1.8 \pm 1.1$  m in 1995) compared to the other years ( $6.1 \pm 0.9$  m). The only difference exhibited in roughness height was associated with stream bleak for k1 and was related to the increase in silted areas in 2005.

Spatio-temporal relationships for hydraulic classes showed the regulated Durance to be relatively stable during the study period. Significant differences concerned chub for class D2V1 and barbel for class D2V3. Chub preferred habitats with low water velocity, greater depth and wood shelter (Appendix 1). During the first study period, chubs were often sampled in sub-units close to or inside wood cover, i.e. woody debris functioned as a hydraulic refuge. The observed differences were therefore related more to the choice of hydraulic class limits than to a real change in velocity preference of the species. Barbel was associated with deep, fast-flowing habitats located along rip rap. Despite high levels of disturbance, both fish assemblages and spatio-temporal relationships of individual taxa to habitat characteristics appeared relatively stable.

Prior to large scale regulation of the middle Durance River the fish community was practically unknown, except for some rare historical data published in cartographical archives. Studies by Kreitman (1932) and Leger (1934) provide historical data on fish assemblages in the Rhône River and Upper Durance catchment, respectively. A comparison of current with past conditions showed fish assemblages in the main channel to be similar, with the exception of eel (*Anguilla anguilla*), which has totally disappeared from the middle Durance, and the recent arrival of *Cobitis bilineata*. Indeed, before the first capture of a cobitid in the Durance, *Cobitis taenia* was considered as the only spined loach present in France, mainly limited to the Seine and the Rhine catchments (Keith & Allardi, 2001). The diversity of hydrosystems inhabited by *C. bilineata* could explain its rapid and successful colonisation of the River

Durance (Kottelat & Freyhof, 2007). By contrast, the distribution of the endemic percid *Zingel asper* has dramatically decreased in the Rhône River catchment (Laroche & Durand, 2004). Therefore, a population of the endemic *Zingel asper* in the highly regulated middle Durance can be considered as a positive element for its conservation.

Many studies have demonstrated that an efficient restoration plan cannot rely solely on small-scale actions such as implantation of artificial instream structures or rehabilitation of the main channel (Pretty *et al.*, 2003). Potential recovery of fish assemblages in the Durance River is driven by the necessity of promoting the development of lateral and off-channel habitats within the river corridor. Sustainable management implies an efficient rehabilitation scheme including a regulated instream flow that should be more adapted to fish needs. Coupling information on mesohabitat and at reach scale was demonstrated to be the best way of assessing and predicting fish spatial assemblages (Parasiewicz & Walker, 2007). Although restoration would require improving natural hydro-geomorphological dynamics in order to increase habitat heterogeneity, with connections to remnant side channels or backwaters, it would be most effective when used together with other strategies such as water quality management. Consequently, explaining how these abiotic and biotic factors interact over a range of temporal and spatial scales should be a major goal of lotic fish ecologists (Schlosser, 1995).

In regulated rivers, many landscape attributes have been shown to have strong effects on processes determining fish population dynamics. The functional terrestrial-aquatic ecotone and its influence on temporal and spatial variation in resource or cover supply were shown to significantly affect the distribution fish species and assemblages. Large-scale spatial habitat relationships and their effects on resource use and fish movement are likely to be most

relevant for modelling. Presence of refuges from harsh environmental conditions and their influence on fish survival and emigration/immigration rates must be taken into account to increase fish populations.

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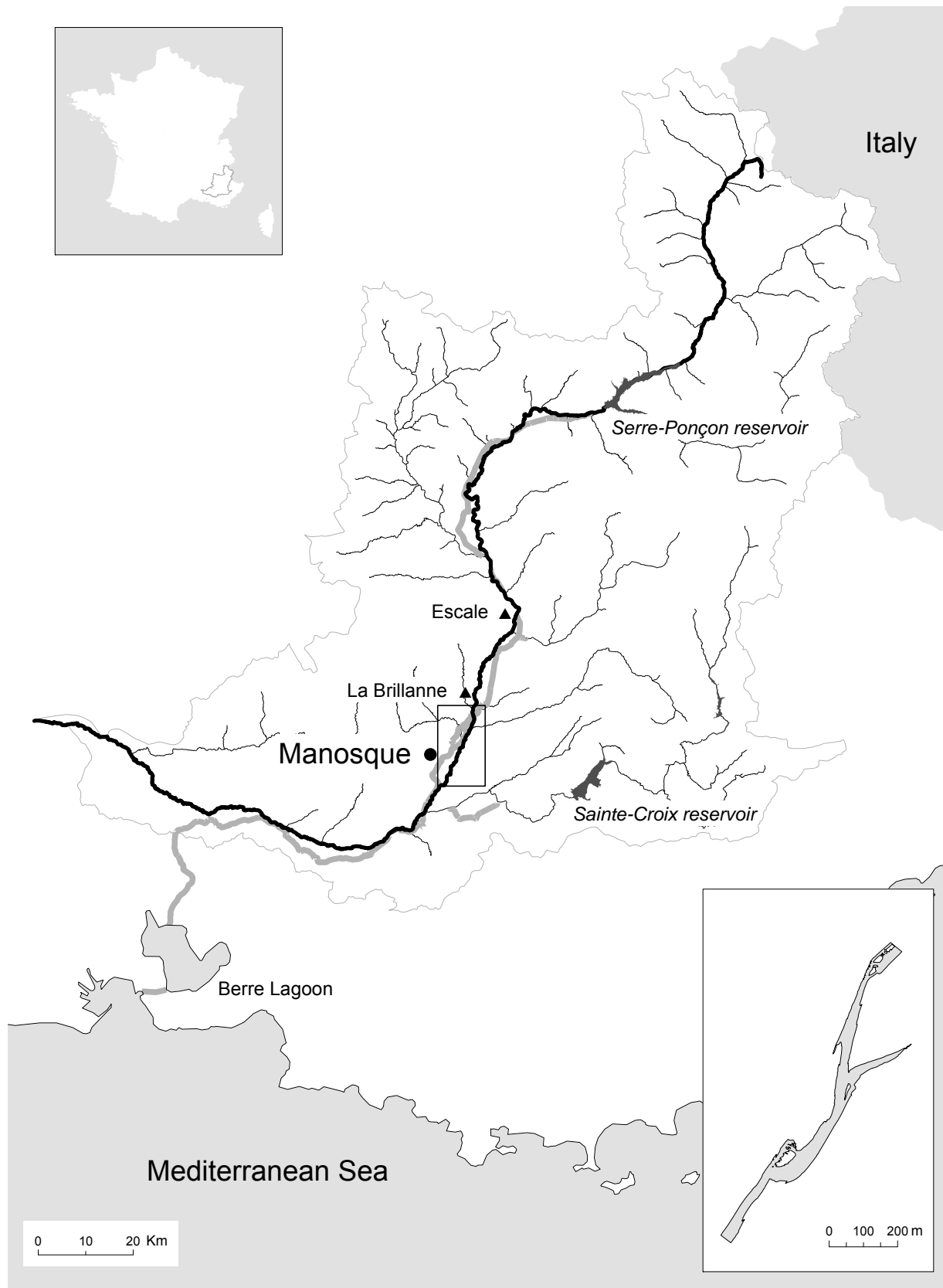


Figure 1: The Durance River basin, its main tributary network (Strahler order  $\geq 3$ ) and the study site located near Manosque (Alpes-de-Haute-Provence). A thick grey line outlines the canal supplying 14 hydropower stations from Serre-Ponçon dam to Berre Lagoon. For clarity, all hydropower stations are omitted from the map. Escale and La Brillanne are gauging stations (see Figure 2). The bottom-right insert shows the studied river reach during the two final years, 2004 and 2005. Document sources: U.R. Hydrobiologie - Cemagref Aix-en-Provence, ©IGN, BD CARTHAGE® RMC.

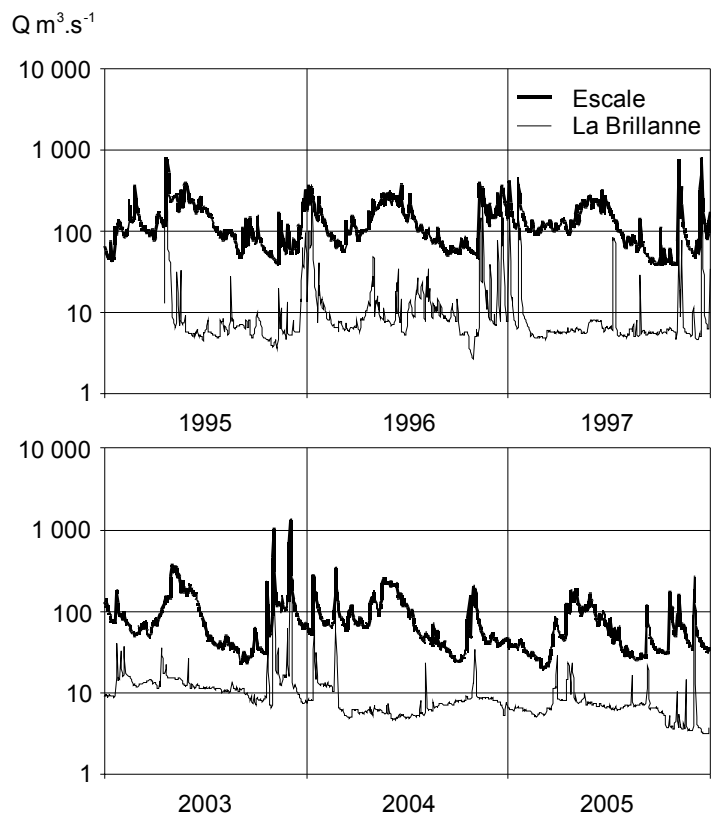


Figure 2 - Time-series of mean daily discharge of the Durance River at Escale and at La Brillanne for the two study periods: 1995-1997 and 2003-2006. At Escale (44°05'11"N, 6°00'45"E), natural discharge is reconstructed and close to the historical Durance stream flow. At La Brillanne (43°56'04"N, 5°53'37"E), current discharge corresponds to regulated instream flow and includes partial flows from tributaries located between the two gauging stations. Data from the French Hydrology Data Bank HYDRO of the Ministry for Ecology, Sustainable Development and Spatial Planning (<http://www.hydro.eaufrance.fr/>).

Table 1 – Main hydromorphological variables of the study site. Mean values were calculated with 1164 transects at 5 m intervals along the curvilinear axis of the channel. W: width of the channel, dm: mean depth of transect, dM: maximal depth of transect, V: mean velocity and Slope: surface water slope.

	W (m)	dm (m)	dM (m)	V (m.s <sup>-1</sup> )	Slope (%)
Mean	32.8	0.32	0.59	0.42	0.39
Standard deviation	16.2	0.18	0.32	0.24	0.54
Minimum	7.4	0.04	0.06	0.05	0.01
Maximum	202.5	1.11	2.05	1.85	3.05

Table 2 – Variables and their codes obtained by depth (d) and current velocity (v) cross tabulation. The numerical value of each variable is the percentage area of the cross class in the total area considered. The sum of the 16 variables of the cross table equals 100%. Values are indicated for the whole five year period and for both distinct periods.

depth (cm)	Codes				Total ( 5 year period)				Velocity (cm.s <sup>-1</sup> )
	0 < v ≤ 5	5 < v ≤ 30	30 < v ≤ 60	v > 60	0 < v ≤ 5	5 < v ≤ 30	30 < v ≤ 60	v > 60	
d > 60	<b>d4V1</b>	<b>d4V2</b>	<b>d4V3</b>	<b>d4V4</b>	<b>2.3</b>	<b>4.5</b>	<b>4.6</b>	<b>2.1</b>	
30 < d ≤ 60	<b>d3V1</b>	<b>d3V2</b>	<b>d3V3</b>	<b>d3V4</b>	<b>2.3</b>	<b>9.4</b>	<b>10.9</b>	<b>11.5</b>	
15 < d ≤ 30	<b>d2V1</b>	<b>d2V2</b>	<b>d2V3</b>	<b>d2V4</b>	<b>2.0</b>	<b>7.7</b>	<b>11.0</b>	<b>5.4</b>	
0 < d ≤ 15	<b>d1V1</b>	<b>d1V2</b>	<b>d1V3</b>	<b>d1V4</b>	<b>8.6</b>	<b>12.9</b>	<b>4.3</b>	<b>0.4</b>	
<b>First period : 1995 to 1997</b>									
depth (cm)					<b>Second period : 2004 - 2005</b>				
d > 60	<b>0.1</b>	<b>3.1</b>	<b>5.8</b>	<b>0.9</b>	<b>4.7</b>	<b>6.0</b>	<b>3.3</b>	<b>3.4</b>	
30 < d ≤ 60	<b>1.6</b>	<b>11.9</b>	<b>10.8</b>	<b>10.6</b>	<b>3.1</b>	<b>6.8</b>	<b>11.1</b>	<b>12.4</b>	
15 < d ≤ 30	<b>1.8</b>	<b>9.3</b>	<b>11.8</b>	<b>5.5</b>	<b>2.3</b>	<b>6.0</b>	<b>10.2</b>	<b>5.2</b>	
0 < d ≤ 15	<b>9.2</b>	<b>13.7</b>	<b>3.4</b>	<b>0.4</b>	<b>7.9</b>	<b>12.0</b>	<b>5.3</b>	<b>0.4</b>	
Velocity (cm.s <sup>-1</sup> )									

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Table 3 – Habitat variables, their modalities and values for each year. Minimal distances were calculated from the sample unit centroid to the nearest three cover modalities and to the nearest bank. The width of the channel was measured at the level of the sample unit centroid and on a line perpendicular to the water current direction. The frequency distribution of roughness height values in a given sample unit gives the percentage of each size class (variable  $k_i$ ).

Variables and Codes		1995		1996		1997		2004		2005	
<i>Cover percentage and distance associated</i>		Mean ( $\pm$ sd)	[Min. - Max.]	Mean ( $\pm$ sd)	[Min. - Max.]	Mean ( $\pm$ sd)	[Min. - Max.]	Mean ( $\pm$ sd)	[Min. - Max.]	Mean ( $\pm$ sd)	[Min. - Max.]
< 10 %	<i>d_W1</i>	282 ( $\pm$ 282)	[5 - 861]	80 ( $\pm$ 96)	[0.3 - 348]	30 ( $\pm$ 22)	[0.8 - 80]	58 ( $\pm$ 62)	[0.6 - 285]	37 ( $\pm$ 42)	[0.1 - 199]
< 50 %	<i>d_W2</i>	52 ( $\pm$ 60)	[0.1 - 191]	191 ( $\pm$ 136)	[1.2 - 464]	52 ( $\pm$ 33)	[2.1 - 110]	48 ( $\pm$ 53)	[0.4 - 226]	53 ( $\pm$ 57)	[0.3 - 244]
> 50 %	<i>d_W3</i>	137 ( $\pm$ 183)	[0.1 - 574]	100 ( $\pm$ 90)	[0.1 - 329]	46 ( $\pm$ 37)	[0.2 - 113]	34 ( $\pm$ 34)	[0.01 - 154]	36 ( $\pm$ 33)	[0.2 - 155]
<i>Other variables</i>											
Distance to the bank (m)	<i>dBank</i>	4 ( $\pm$ 4)	[0.1 - 21]	5 ( $\pm$ 4)	[0.3 - 19]	6 ( $\pm$ 5)	[0.4 - 19]	6 ( $\pm$ 6)	[0.1 - 27]	6 ( $\pm$ 5)	[0.1 - 20]
Chenal width (m)	<i>Width</i>	20 ( $\pm$ 12)	[4 - 48]	18 ( $\pm$ 10)	[3 - 46]	27 ( $\pm$ 12)	[4 - 44]	25 ( $\pm$ 12)	[2 - 55]	25 ( $\pm$ 11)	[6 - 50]
<i>Substrate roughness height and frequencies (ki)</i>											
[ 0 - 0.0625 cm [	<i>k1</i>	3.9 ( $\pm$ 16.3)	[0 - 100]	8.4 ( $\pm$ 23.6)	[0 - 100]	8.7 ( $\pm$ 25.5)	[0 - 100]	6.1 ( $\pm$ 17.6)	[0 - 100]	22.7 ( $\pm$ 34)	[0 - 100]
[ 0.0625 - 1.6 cm [	<i>k2</i>	18.8 ( $\pm$ 22.7)	[0 - 93.3]	7.9 ( $\pm$ 12.1)	[0 - 44.4]	22.7 ( $\pm$ 20.1)	[0 - 76.9]	22.3 ( $\pm$ 21.6)	[0 - 78.6]	14.6 ( $\pm$ 17.2)	[0 - 64.7]
[ 1.6 - 6.4 cm [	<i>k3</i>	47.7 ( $\pm$ 20.3)	[0 - 92.3]	47.1 ( $\pm$ 19.7)	[0 - 86.6]	44.7 ( $\pm$ 23.2)	[0 - 80]	49.4 ( $\pm$ 24.3)	[0 - 100]	39.7 ( $\pm$ 26.7)	[0 - 90]
[ 6.4 - 25.6 cm [	<i>k4</i>	29.3 ( $\pm$ 24.5)	[0 - 76.9]	35.9 ( $\pm$ 22.9)	[0 - 86.6]	23.8 ( $\pm$ 19.7)	[0 - 70]	17.9 ( $\pm$ 18.2)	[0 - 75]	19.8 ( $\pm$ 23.2)	[0 - 80]
[ 25.6 - 204.8 cm [	<i>k5</i>	0.2 ( $\pm$ 1.6)	[0 - 10]	0.6 ( $\pm$ 2.2)	[0 - 12.5]	0 ( $\pm$ 0)	[0 - 0]	4.2 ( $\pm$ 14.4)	[0 - 78.9]	3.1 ( $\pm$ 12.8)	[0 - 90]

Table 4 - Definition and codes of the 10 mesohabitats according to the following physical variables: wave height of the water surface, surface water slope, current velocity and depth [adapted from Malavoi & Souchon (2002) and Borsany et al. (2004)].

Water surface	Slope	Velocity	Depth
Waves < 5cm	> 0.4%	> 30 cm.s <sup>-1</sup>	> 60 cm
		< 30 cm.s <sup>-1</sup>	< 60 cm
	< 0.4%	> 30 cm.s <sup>-1</sup>	> 60 cm
		< 30 cm.s <sup>-1</sup>	< 60 cm
Waves > 5cm	> 0.4%	> 30 cm.s <sup>-1</sup>	> 60 cm
		< 30 cm.s <sup>-1</sup>	< 60 cm
	< 0.4%	> 30 cm.s <sup>-1</sup>	> 60 cm
		< 30 cm.s <sup>-1</sup>	< 60 cm

Table 5 – List of the 18 species sampled in the middle Durance study site and their abbreviation (Abb.). For each species, total number of fish caught (N), relative abundance (%), number of sample units (Nsampl) and species occurrence (Occ.) in percentage, minimal (TLm) and maximal (TLM) total length in mm are indicated. The last column indicates the three groups of species according to their relative abundance. Group 1: main species, > 5%. Group 2: intermediate species, from 1 to 5%. Group 3: rare species, < 1%. Five species were excluded from data analysis: roach, tench, the two salmonids and pumpkinseed.

		Abb.	N	%	Nsampl	Occ.	TLm	TLM	Group
<b>Cyprinidae</b>									
<i>Leuciscus souffia</i>	Blageon	Lso	2318	19.46	191	0.66	17	165	1
<i>Alburnoides bipunctatus</i>	Stream bleak	Abi	2045	17.17	191	0.66	11	132	1
<i>Leuciscus cephalus</i>	Chub	Lce	1730	14.52	165	0.57	17	558	1
<i>Barbus barbus</i>	Barbel	Bbs	1463	12.28	197	0.68	16	610	1
<i>Phoxinus phoxinus</i>	Minnnow	Pph	965	8.10	95	0.33	14	68	1
<i>Chondrostoma nasus</i>	Nase	Cna	520	4.36	92	0.32	28	525	2
<i>Chondrostoma toxostoma</i>	Sofie	Cto	480	4.03	89	0.31	20	237	2
<i>Gobio gobio</i>	Gudgeon	Ggo	449	3.77	104	0.36	15	130	2
<i>Alburnus alburnus</i>	Bleak	Aal	45	0.38	25	0.09	18	160	3
<i>Rutilus rutilus</i>	Roach	Rru	6	0.05	5	0.02	32	107	3
<i>Tinca tinca</i>	Tench	Tti	1	0.01	1	< 0.01	173	173	3
<b>Balitoridae</b>									
<i>Barbatula barbatula</i>	Stone loach	Bba	1599	13.42	160	0.55	22	85	1
<b>Cobitidae</b>									
<i>Cobitis bilineata</i>	Spined loach	Cbi	190	1.59	48	0.17	31	102	2
<b>Percidae</b>									
<i>Perca fluviatilis</i>	Perch	Pfl	51	0.43	19	0.07	66	190	3
<i>Zingel asper</i>	Rhône streber	Zas	31	0.26	20	0.07	40	155	3
<b>Centrarchidae</b>									
<i>Lepomis gibbosus</i>	Pumpkinseed	Lgi	5	0.04	4	0.01	85	97	3
<b>Salmonidae</b>									
<i>Salmo trutta</i>	Brown trout	Str	12	0.10	10	0.03	61	240	3
<i>Oncorhynchus mykiss</i>	Rainbow trout	Omy	3	0.03	2	0.01	290	350	3
<b>Total number of fish</b>			<b>11913</b>						

Table 6 – Analysis of temporal effects: p-values of t-test for comparison between two time periods (1995-1996-1997 and 2004-2005). Abbreviations were explained in Methods - Analysis - Importance of temporal stability. Total abundances were mentioned for each period and for each taxon. Critical values were adjusted with a Dunn Sidak procedure to account for multiple comparisons (Sokal & Rohf, 1995). The correction of the multiple comparisons will lead to conservative tests (Sokal & Rohf, 1995) therefore an upper alpha risk than the usual 0.05 could be assumed and we suggest 0.2. Significances were coded as standard proposed by (Leahey, 2005): \*p <= 0.2, \*\*p <= 0.1, \*\*\*p <= 0.05. Variables considered as having no relevant influence on fish presence according to results from previous analysis are shown as grey.

	Minnow		Stream bleak			Gudgeon			Blageon					Cho_2	Sofie		
	Pph_1	Pph_2	Abi_2	Abi_3	Abi_4	Ggo_2	Ggo_3	Ggo_4	Lso_1	Lso_2	Lso_3	Lso_4	Lso_5		Cto_4	Cto_5	Cto_6
Wood3			*		*		*										
Bank					*												
k1			**														
kt																	
k5																	
D1V1			*												*		
D1V2												*					
D1V3		*															
D2V1													*				
D2V2																	
D2V3																	
Period 1	171	506	185	766	85	70	121	45	90	459	324	123	26	141	11	15	21
Period 2	99	171	433	194	255	63	39	96	25	518	314	360	71	76	36	31	89

	Barbel					Chub						Stone loach	
	Bbs_2	Bbs_3	Bbs_4	Bbs_5	Bbs_6	Lce_1	Lce_2	Lce_3	Lce_4	Lce_5	Lce_6	Bba_2	Bba_3
Wood3			*										
Bank													
k1													
kt													
k5													
D1V1													
D1V2													
D1V3												*	
D2V1							**			*	**		
D2V2													
D2V3					**								
Period 1	158	106	95	44	201	188	230	172	118	68	65	776	129
Period 2	224	67	154	157	173	61	329	129	176	74	106	484	121

Appendix 1 – Number of times (expressed in percentages) each variable belongs to the first three ones explaining fish presence. Abbreviations were previously explained in part Methods. Information about sign of PLS coefficients was kept in order to inform about attractiveness or avoidance of relationships. For simplification and readability of the tables, percentages less than 5% have not been indicated. Values were formatted as following: *italic* (from 5 to 25), *italic bold* (from 25 to 50) and **bold** (over 50).

Coef (+)	<i>Phoxinus phoxinus</i>			<i>Alburnoides bipunctatus</i>				<i>Alburnus alburnus</i>				<i>Gobio gobio</i>					<i>Leuciscus souffia</i>						<i>Chondrostoma toxostoma</i>										
	RK_1 to 3	Pph_1	Pph_2	Pph_3	Abi_1	Abi_2	Abi_3	Abi_4	Aal_1	Aal_2	Aal_3	Aal_4	Ggo_1	Ggo_2	Ggo_3	Ggo_4	Ggo_5	Lso_1	Lso_2	Lso_3	Lso_4	Lso_5	Lso_6	Cho_1	Cho_2	Cto_3	Cto_4	Cto_5	Cto_6				
Wood1	14	11	14		11	10	23			15		11	6		8	6			24	5					20	5	21						
Wood2					<b>39</b>	<b>55</b>		11					7		<b>38</b>	<b>66</b>				9	19	<b>37</b>					16		8				
Wood3					11	<b>25</b>	21		12					7		16						13					16						
Bank	<b>28</b>	<b>62</b>	9		<b>74</b>	21	<b>35</b>	<b>31</b>	<b>37</b>	<b>29</b>		23	18	6		10	15	<b>27</b>	17			5	10	<b>41</b>	<b>30</b>	10	7						
Width	7															8																	
k1					6					<b>93</b>	14		10			<b>36</b>				10	<b>25</b>	23	<b>53</b>				5	9		8			
k2								11									18	12						16									
k3																	22																
k4			11						20																23								
k5																						23								23			
d1v1	23								<b>53</b>				<b>61</b>					<b>54</b>						10									
d1v2	23												<b>40</b>					22					<b>56</b>										
d1v3	<b>52</b>	<b>66</b>	<b>62</b>											<b>28</b>				<b>23</b>	<b>68</b>							<b>62</b>	9						
d1v4																												<b>48</b>					
d2v1	<b>60</b>	24	17		<b>46</b>	5		<b>44</b>					<b>30</b>	<b>68</b>		7	22	<b>65</b>	13							18	8						
d2v2	11	<b>45</b>											8	<b>56</b>	<b>55</b>	<b>26</b>			<b>48</b>	<b>97</b>	<b>74</b>	10			20	<b>45</b>	<b>85</b>	<b>79</b>	5				
d2v3					17	10			9				6						9	<b>26</b>				<b>62</b>		17							
d2v4						8	7	20																									
d3v1			21		11						<b>53</b>				6	<b>27</b>	23														<b>53</b>		
d3v2							16		7	<b>43</b>	10				<b>51</b>												8	<b>46</b>					
d3v3					<b>55</b>	<b>23</b>	<b>44</b>				7					7	10												12				
d3v4							20					13																		7			
d4v1							7							<b>61</b>	23	23		6				<b>47</b>											
d4v2	16	11	<b>68</b>		<b>33</b>	<b>58</b>		10	<b>54</b>			<b>65</b>					25				15				<b>74</b>	18	6						
d4v3											6																			5			
d4v4																														17			
Coef (-)	<i>Phoxinus phoxinus</i>			<i>Alburnoides bipunctatus</i>				<i>Alburnus alburnus</i>				<i>Gobio gobio</i>					<i>Leuciscus souffia</i>						<i>Chondrostoma toxostoma</i>										
RK_1 to 3	Pph_1	Pph_2	Pph_3	Abi_1	Abi_2	Abi_3	Abi_4	Aal_1	Aal_2	Aal_3	Aal_4	Ggo_1	Ggo_2	Ggo_3	Ggo_4	Ggo_5	Lso_1	Lso_2	Lso_3	Lso_4	Lso_5	Lso_6	Cho_1	Cho_2	Cto_3	Cto_4	Cto_5	Cto_6					
Wood1				6				11	9		<b>33</b>																						
Wood2						<b>78</b>			16	<b>75</b>	<b>78</b>	11		7						18													
Wood3			24		7				6	6		18													7		<b>76</b>						
Bank																																	
Width		9	18				<b>87</b>	<b>30</b>	8		<b>31</b>	9	12	20	<b>81</b>	20		6	12	<b>66</b>	21	12	19	<b>41</b>	17	<b>41</b>	<b>53</b>	<b>71</b>	<b>37</b>				
k1								25										<b>38</b>															
k2												7											21										
k3																																	
k4							8		<b>27</b>		14	6			18	10					10	16						<b>27</b>	9				
k5	9	18	13		10								7		6				18								18		6				
d1v1				6	<b>41</b>	10	<b>56</b>		7				12	<b>53</b>	<b>66</b>	16					<b>42</b>	<b>63</b>	<b>38</b>				11		<b>42</b>	<b>44</b>	<b>30</b>		
d1v2																													5				
d1v3												8												7									
d1v4	<b>29</b>	22	<b>38</b>		10									10				14	<b>26</b>							22							
d2v1										9												13			5						17		
d2v2								10																									
d2v3																																	
d2v4																																	
d3v1	9						23	6				<b>30</b>	7				10																
d3v2												7											14										
d3v3								6																									
d3v4																																	
d4v1				6					<b>39</b>	<b>30</b>									7	<b>48</b>	<b>70</b>										<b>61</b>		
d4v2																								5									
d4v3																																	
d4v4																																	<b>34</b>

Coef (+)	<i>Leuciscus cephalus</i>								<i>Barbus barbuis</i>								<i>Chondrostoma nasus</i>										
	Rk_1 to 3	Lce_1	Lce_2	Lce_3	Lce_4	Lce_5	Lce_6	Lce_7	Lce_8	Bbs_1	Bbs_2	Bbs_3	Bbs_4	Bbs_5	Bbs_6	Bbs_7	Bbs_8	Cho_1	Cho_2	Cna_3	Cna_4	Cna_5	Cna_6	Cna_7	Cna_8		
Wood1		7						5				6					6		20	22				5		6	
Wood2		9		11	57	41	30	12			10		8	47	31	29							47	10	11		
Wood3						8	31	6				36	9			20	40						13				
Bank		17	20	26	9	15	14	38	9		12	20		14	16	28	37	15		41	30				17		
Width																											
k1		43	57	45	23	56						7		45	39							14	40				
k2		13						13	53		50		7							16				7			
k3																										11	
k4								7									19			23							
k5																13	60						37	56	20		
d1v1		91									53									10							
d1v2											54	36								56							
d1v3		23	38									74									62						
d1v4													12				6				22						
d2v1		75	24			9		16	11		23	6		16	15						18				11		
d2v2				6	7							23	70	30							20	61	44	38	18		
d2v3											17	67	7							62		8					
d2v4													15	60													
d3v1			60	73	80	79	82	23	54						57	27									70	80	
d3v2													11	25											9		
d3v3								38							6							9		37			
d3v4								17	5					11	13	27	15							9	13		
d4v1									7																		
d4v2			6	7	9	5		9													74	65	16				
d4v3									5								12	10							37	43	
d4v4									43								71								87	85	
Coef (-)																											
Rk_1 to 3	Lce_1	Lce_2	Lce_3	Lce_4	Lce_5	Lce_6	Lce_7	Lce_8	Bbs_1	Bbs_2	Bbs_3	Bbs_4	Bbs_5	Bbs_6	Bbs_7	Bbs_8	Cho_1	Cho_2	Cna_3	Cna_4	Cna_5	Cna_6	Cna_7	Cna_8			
Wood1								9	13						10												
Wood2											56					24				9							
Wood3									7										7					6	10		
Bank																										8	
Width		11		7				30	7		18		31	21		44	7	37		41	17	51	17	14	14	13	8
k1		6								11								7									
k2														18	11											7	
k3																		5									
k4													7		8	11							8				
k5			10																		18						
d1v1				19	33	30	12	13			21	12	41	23	32	13					11	17	14	17	17		
d1v2								7					15											8			
d1v3										5						6	18			7							
d1v4		13	15								13										22						
d2v1				11	13		10					9				8		8					5		23	18	
d2v2							11																				
d2v3																									9	13	
d2v4																		16								5	
d3v1		20									8		7											15			
d3v2								5																	9	12	
d3v3								10			6														16	18	
d3v4																											
d4v1			64	77	80	66	67					10		35	23									73	80		
d4v2		10						22				6					18	14		5					6	9	
d4v3																											
d4v4																											

Coef (+)	Barbatuta barbatula			Cobitis bilineata			Perca fluviatilis				Zingel asper				
	Rk_1 to 3	Bba_1	Bba_2	Bba_3	Cbi_2	Cbi_3	Cbi_4	Pfl_3	Pfl_4	Pfl_5	Pfl_6	Zas_2	Zas_3	Zas_4	Zas_5
Wood1			7										15	23	24
Wood2					11	11			21	47	67				20
Wood3		6	14	17			7								
Bank		15	6						8	25	15		9		
Width								6					13	12	30
k1					17	91	69	97	63	55	48				
k2												12			
k3													56	44	
k4			6												45
k5											43				
d1v1		31			88							29			
d1v2		67	93	36	61										
d1v3		30	77	77		12				5					
d1v4		43	38	44											
d2v1		7			30	15				35	34				
d2v2				5											58
d2v3		28	6	7								72			
d2v4		11		14								14	80	70	
d3v1			6		35	68	75	83	84						
d3v2													25		
d3v3						5	16								19
d3v4														39	
d4v1								54		61	32				
d4v2															
d4v3															
d4v4															
Coef (-)	Barbatuta barbatula			Cobitis bilineata			Perca fluviatilis				Zingel asper				
Rk_1 to 3	Bba_1	Bba_2	Bba_3	Cbi_2	Cbi_3	Cbi_4	Pfl_3	Pfl_4	Pfl_5	Pfl_6	Zas_2	Zas_3	Zas_4	Zas_5	
Wood1		7													
Wood2		12		20								43			
Wood3										11		9			
Bank												31		6	31
Width		9								13		36			
k1															
k2			7	22				22		26	22				9
k3											7				
k4													42	36	
k5			5												
d1v1				12		7		7	7						
d1v2															16
d1v3												21			
d1v4													9	8	
d2v1						19		15	29			7			
d2v2		5								8					
d2v3													12	14	6
d2v4															
d3v1															
d3v2					11									8	16
d3v3													5	13	
d3v4															
d4v1			8	9	40	76	76		73						
d4v2		5										7			
d4v3															
d4v4			14												