APPLIED ISSUES

Fish community changes after minimum flow increase: testing quantitative predictions in the Rhône River at Pierre-Bénite, France

NICOLAS LAMOUROUX,* JEAN-MICHEL OLIVIER,† HERVÉ CAPRA,* MARC ZYLBERBLAT,‡ ANDRE CHANDESRIS* AND PASCAL ROGER*

*CEMAGREF, Biologie des Ecosystèmes Aquatiques, Lyon, France
†UMR CNRS 5023 Ecologie des Hydrosystèmes Fluviaux, Université Lyon 1, Villeurbanne, France
‡Compagnie Nationale du Rhône, Lyon, France

SUMMARY

1. Many aspects of the flow regime influence the structure of stream communities, among which the minimum discharge left in rivers has received particular attention. However, instream habitat models predicting the ecological impacts of discharge management often lack biological validation and spatial generality, particularly for large rivers with many fish species.

2. The minimum flow at Pierre-Bénite, a reach of the Rhône river bypassed by artificial channels, was increased from 10 to 100 m$^3$ s$^{-1}$ in August 2000 (natural mean discharge 1030 m$^3$ s$^{-1}$), resulting in a fivefold increase in average velocity at minimum flow. Fish were electrofished in several habitat units on 12 surveys between 1995 and 2004.

3. Principal components analysis revealed a significant change in the relative abundance of fish species. The relative abundance of species preferring fast-flowing and/or deep microhabitats increased from two- to fourfold after minimum flow increase. A change in community structure confirmed independent quantitative predictions of an instream habitat model. This change was significantly linked to minimum flow increase, but not to any other environmental variables describing high flows or temperature at key periods of fish life cycle. The rapidity of the fish response compared with the lifespan of individual species can be explained by a differential response of specific size classes.

4. The fish community at Pierre-Bénite is in a transitional stage and only continued monitoring will indicate if the observed shift in community structure is perennial. We expect that our case study will be compared with other predictive tests of the impacts of flow restoration in large rivers, in the Rhône catchment and elsewhere.

Keywords: dams, flow regime, habitat restoration, instream habitat model, large rivers

Introduction

Many aspects of the flow regime such as minimum flow, rate of flow change, flood frequencies and timing influence the structure of freshwater communities (Poff et al., 1997; Richter et al., 2003; Propst & Gido, 2004). Consequently, efforts to restore flow conditions to benefit river ecosystem health are increasing worldwide (e.g. database of The Nature Conservancy, http://www.nature.org/initiatives). Flow restoration projects can be viewed as natural experiments that should be designed, monitored and adapted through time with a strong cooperation between scientists,
managers and water users (Poff et al., 2003). Cooperation among these actors is, however, complicated by the high uncertainty of ecological models that predict the impacts of restoration scenarios. In particular, quantitative predictions of the ecological impacts of changes in flow regime often lack biological validation and spatial generality.

Minimum flow in rivers is one aspect of the flow regime that has received particular attention in scientific studies and water regulations, because it has been reduced by water abstraction and water diversion in many rivers. Low flows can be considered as 'bottleneck' conditions that provide critical stresses or opportunities for a wide array of fish specific life stages (Poff et al., 1997; Lamouroux et al., 1999c). Instream habitat models became popular over the last three decades for quantifying the impacts of minimum flow changes on fish populations (Bovee, 1982; Gore & Nestler, 1988; Lamouroux et al., 1999c). These models combine biological models that describe the preferences of fish in terms of velocity, depth and particle size, and a hydraulic model that estimates how the physical habitat varies with discharge. Despite abundant use of these models worldwide, the extent to which fish communities actually respond to minimum flow restoration at a site is largely unpredictable. 'Before–after' tests of the impacts of minimum flow restoration have generally focused on target populations (often salmonids) and yielded contrasting results (e.g. Harris, Hubert & Wesc, 1991; Phillips, Ory & Talbot, 2000; Jowett & Biggs, 2004; Souchon & Capra, 2004). We are not aware of such 'before–after' tests for fish communities in large rivers. Fish communities in natural large rivers are generally viewed as more diverse and less constrained by abiotic factors than communities in small streams. However, flow regulation in large rivers strongly modifies the environmental conditions in these systems, with potential consequences on community structure (Galat & Zweimüller, 2001).

In this paper, we analyse the fish community variations at Pierre-Bénite, a reach of the Rhône river bypassed by artificial channels (average natural discharge 1030 m$^3$ s$^{-1}$), between 1995 and 2004. Minimum flow in the reach was increased from 10 to 100 m$^3$ s$^{-1}$ in 2000 as part of a national restoration programme concerning the Rhône river. This case study provides a preliminary analysis of the impacts of minimum flow change on fish in a large regulated river, where multiple species coexist. It is also a unique opportunity to test the predictability of the changes according to an instream habitat model that was calibrated before 2000 (Lamouroux et al., 1999c).

This model combined a hydraulic model of the reach and models of fish hydraulic preference developed elsewhere in the Rhône basin. The model, run 'blindly' at Pierre-Bénite before minimum flow change, predicted higher relative densities of fish species preferring fast and/or deep hydraulic conditions after minimum flow increase.

**Methods**

The Rhône river and the decennial restoration programme

The Rhône river is the largest river flowing through France (mean discharge >1700 m$^3$ s$^{-1}$ at the mouth). As other large rivers in Europe, it has had a long history of regulation and damming, especially during the 19th (embankment for navigation and flooding issues) and 20th (dams built for hydropower and other water needs) centuries (Bravard, 1987; Schiemer & Spindler, 1989; Fruget, 1992). Sixteen reaches of the French part of the river, each of length between 2 and 30 km, are bypassed by artificial channels. Minimum flows in these bypassed reaches range between 1/300 and 1/5 of the natural mean flow. When the maximum discharge processed by the power plants is exceeded in the artificial channels, bypassed reaches evacuate high flows and undergo major changes in hydraulic conditions. Most bypassed reaches have retained a longitudinal morphology close to natural conditions with sequences of pools, runs and riffles. Fish communities are also more similar to pre-impoundment than communities of artificial channels and reservoirs (Persat, 1988). However, species adapted to the fast-flowing and deep conditions of large flowing rivers (e.g. grayling, barbel, dace or the non-native nase) have suffered from the reduction in discharge (Persat, 1988; Lamouroux et al., 1999c), as in other large regulated systems in Europe and elsewhere (Galat & Zweimüller, 2001; Aarts, Van den Brink & Nienhuis, 2004).

Following a number of local and national initiatives, a decennial restoration programme of the Rhône river was implemented by the French government in 1998 with the general objective of restoring the ecological attributes of a large running river. The programme involves the rehabilitation of migratory pathways and
connections with secondary channels (Amoros, 2001) as well as the increase of minimum flow rates in some bypassed reaches of the river. A close cooperation between scientists, managers and water users was organised as part of the decennial programme, making it possible to define a common strategy for a consistent monitoring and evaluation of the various restoration operations (André & Olivier, 2003).

The bypassed reach at Pierre-Bénite

The bypassed reach at Pierre-Bénite is located 6 km downstream of the city of Lyon (Fig. 1). The reach is 10 km long and includes several marked riffles. Natural annual mean and minimum discharge rates at Pierre-Bénite are 1030 and 300 m$^3$ s$^{-1}$, respectively. At natural mean discharge the reach is 160 m wide and 3.7 m deep. The Pierre-Bénite dam regulates flow at the upstream end of the bypassed reach. The last 4 km of the bypassed reach are under the hydraulic influence of another reservoir situated further downstream (Vaugris dam) and hence our study only deals with the upstream, free-flowing 6 km of the reach (Fig. 1). No important tributaries discharge into the bypassed reach. The shorelines are partly embanked and several dikes provide a diversity of habitat conditions for juvenile fish along the banks (Nicolas & Pont, 1997). Several parameters of water quality (oxygen, conductivity, pH, nitrites, nitrates, ammonium, phosphates, carbonates and sulphates) were measured up to five times a year during the study (Lamouroux et al., 2004). All measurements were rated as good according to national criteria and as they did not change during our study they are not considered here. Water temperature was recorded daily in the bypassed section (except before 27 April 1995 and between 22 February 1999 and 06 May 1999) and typically varies at Pierre-Bénite between 4 °C in winter and 25 °C in summer (Fig. 2).

Before 2000, the minimum flow at Pierre-Bénite was 20 m$^3$ s$^{-1}$ between April and August and 10 m$^3$ s$^{-1}$ during the other months. In August 2000, minimum flow was increased to 100 m$^3$ s$^{-1}$ and because of this change average water depth at minimum flow doubled (from 1.2 to 2.1 m) and average velocity increased fivefold (from 0.07 to 0.35 m s$^{-1}$). Daily discharge rates, recorded in the reach during the study, confirm this change and reflect the typical flow regime of the Rhône river below Lyon (Fig. 3). The bypassed reach discharges high flows both in spring (glacial influence from the Alpes) and autumn–winter (pluvial influence), and discharges the minimum flow between high flow events.

Fish sampling

Twelve fish surveys were made in the bypassed reach between 1995 and 2004 at or around minimum flow; six before and six after 2000. Eight of the surveys were...
made in autumn (October 1995, September 1996, September 1998, September 1999, October 2001, September 2002, September 2003 and October 2004), the others in spring or early summer (July 1995, March 1996, June 2002 and June 2004). During each field survey, fish were collected by electrofishing in 23–50 independent habitat units (total number = 401; mean surface area 36 m$^2$; standard deviation 51 m$^2$) using an open-sampling technique adapted to large rivers (Vadas & Orth, 1993; Lamouroux et al., 1999c; Thévenet & Statzner, 1999). On average, a fish survey at Pierre-Bénite involved 33 habitat units of 36 m$^2$, i.e. a sampled surface area approximately equal to 0.2% of the total surface area of the reach. Although the efficiency of open electrofishing techniques in large rivers is difficult to assess, Thévenet & Statzner (1999) demonstrated that electrofishing habitat units of 50 m$^2$ was comparably efficient across species at depths <1.5 m, independent of the habitat conditions. Habitat units were sampled by wading when possible or from a small boat (EFKO type FE48000, generator 300–400 V, engine 9.5 kW). Within each habitat unit, fish were identified to species and measured. Habitat units were randomly chosen in pools, runs, riffles, at the channel centre or its margins and distributed proportionally according to habitat availability. However, portions of the reach deeper than 2 m could not be sampled because of the limits of electrofishing in deep conditions. Hence, habitat units were not similar between field surveys but were always selected with the same stratified random strategy. On average across surveys, habitat units were comparably distributed in pools, runs or riffles before and after minimum flow increase (3%, 74% and 23%, respect-
ively, before and 0%, 71% and 29%, respectively, after 2000). Similarly, units were comparably distributed at the channel margins or at the centre (58% and 42%, respectively, before and 53% and 47%, respectively, after 2000). The surface area of each habitat unit was measured (or visually estimated when measurement was difficult) and depended on the inherent variability of areas sampled without enclosures (e.g. at the centre channel, the area sampled partly depended on the flow velocity). Habitat unit depth was estimated as the average of three to 10 point measurements.

Describing community changes

Community changes were assessed using species richness and fish density (number of individuals per square metre) and the relative abundance of species (as percentage) calculated for each field survey (habitat units pooled). We tested if the means of these variables differed before and after the minimum flow change using t-tests. Principal components analysis (PCA) of species relative abundances was used to describe variations in community structure across surveys. In PCA, relative abundances were \( \ln(1 + x) \) transformed to downweight the influence of a few dominant species. We also tested if scores on the PCA axes differed before and after the minimum flow change using t-tests.

To test for the potential influence of rare but locally abundant species on our results, we repeated the PCA using the relative occurrence of species (percentage of habitat units where the species occurred) in surveys instead of the relative abundance. Finally, to test for the influence of the habitat types sampled on our results, we repeated the PCA on relative abundance using separately data sampled at the channel margins and data sampled at the channel centre.

Life stages of each species can be differently affected by environmental changes. For example, hydraulic changes modify simultaneously habitat conditions for adults, availability of nutrients, near bed spawning conditions and survival of fry. In addition, community responses to environmental changes are expected to occur over periods of several years, at least longer than the lifespan of species (around 5–6 years for fish of the Rhône river; >15 years for, e.g. nase). Therefore, we expect community changes during the study to be dynamic and size-dependent. We analysed the variations of the relative abundance of specific size classes to provide a better understanding of community dynamics. For this purpose, we defined two size classes for each of the 10 most abundant species of the study reach in order to separate individuals of the year and older fish. Size class limits were defined for each species and each survey using size histograms (limits ranged between 5 and 10 cm). For consistency, only autumn surveys were used for this analysis, as most young of the year are easier to catch and identify in autumn, i.e. at least 3 months after the main spawning period of most species (March to June; Cattaneò et al., 2001).

Linking community structure with annual environmental variables

Besides changes in minimum flow, annual variations in community structure across surveys can be due to a number of environmental characteristics (Grossman, Dowd & Crawford, 1990; Poff et al., 1997). In particular, the frequency of high flows and temperature patterns during key periods for fish population dynamics can explain annual community variations. This is particularly true in the context of the bypassed reaches of the Rhône river, where high flows (that contrast in magnitude with the minimum flow) and temperature are quite variable among years. Similarly, discharge and temperature conditions preceding field surveys may influence fish distributions during the survey and thus capture efficiency. For example, high flows preceding the survey may force fish to find refuges along the banks where they are more easily caught by electrofishing. Because of the paucity of surveys available we limited the description of the annual environment to seven variables describing low flows during the year and high flows and temperature during the reproduction period, the growth period and the 15 days preceding the surveys (see Table 2 for variable definitions). We tested the correlations between annual community patterns (survey species richness, survey fish density and coordinates on the PCA axes) and these seven annual environmental variables using autumn surveys (for consistency).

Testing predictions of fish community changes

A statistical instream habitat model was applied to several bypassed reaches of the Rhône river and its
main tributaries before the increase of minimum flow at Pierre-Bénite (Lamouroux et al., 1999b,c). The model was based on microhabitat preferences of the 14 more common species of the Rhône river. These microhabitat preferences were derived from electrofishing data (habitat unit samples) collected using the same methods as here but in other reaches of the basin (in two large tributaries of the Rhône, the Ain and the Ardèche, and in the bypassed reach of the Rhône at Montélimar, 150 km downstream from Pierre-Bénite). The model differed from conventional instream habitat model (e.g. Phabsim; Bovee, 1982) by the nature of its hydraulic component (based on statistical approaches and using simple input data) and its biological component (fish preference models were multivariate).

The statistical habitat model predicted two types of attributes of fish communities from hydraulic conditions in reaches at minimum flow. First, relative density indices (RI values) for the 14 species were averages of the ln(1 + density) of species across all habitat units sampled in the reach (all surveys pooled, density being the number of individuals in 0.1 m³), rescaled to sum to one across the 14 species considered here. As the relative proportions introduced above, RI values reflected the expected weight of the different species in the community. However, because based on local ln(densities) their definition was more complex. Ln(densities) are particularly interesting to use because their variations are less sensitive to random error in estimates of fish abundance or habitat unit volume (see permutation tests in Lamouroux et al., 1999a). Second, two community indices (CSI1 and CSI2) were defined as linear combinations of RI values and summarised the predictions of relative densities at the community level. Specifically, predicted CSI1 and CSI2 were defined from a PCA on predicted RI values in the Rhône catchment (i.e. for different reaches pooled). CSI1 was strongly linked to the longitudinal morphology of reaches; predicted to be high when the RI values of riffle-dwelling species were predicted to be high. CSI2 reflected the expected effect of minimum discharge rate; predicted to be high when the RI values of ‘midstream’ species preferring fast-flowing and deep microhabitats were predicted to be high.

Lamouroux et al. (1999c) showed that the observed values of CSI1 and CSI2 of reaches (derived from electrofishing data) were precisely predicted from hydraulics at minimum flow in 12 different reaches of the Rhône river and its tributaries (including our study reach at Pierre-Bénite before minimum flow increase). Observed RI values were not well predicted across sites because of zoogeographic differences between the Upper Rhône (upstream from the city of Lyon) and the Lower Rhône river. However, observed differences in RI values between close sites (i.e. pairs of close reaches with different hydraulic conditions) were well predicted by the model. This validation showed the potential of a regional instream habitat model for predicting fish community variations across sites related to hydraulics. Based on these results, Lamouroux et al. (1999b) simulated how minimum flow changes at a site should modify RI and CSI values. The minimum flow increase at Pierre-Bénite is the first occasion for testing these predictions. The habitat model predicted an increase ofCSI2 at Pierre-Bénite after minimum flow change, with higher RI values for species preferring both fast-flowing and/or deep habitat (barbel, bleak, nase, dace and spirlin; see Table 1 for scientific names). CSI2 at Pierre-Bénite after minimum flow increase should have the highest value of all bypassed reaches of the Rhône. By contrast, CSI1 values (and thus RI values of riffle-dwelling species) were not expected to change because they are essentially linked to the longitudinal morphology of reaches (proportions of pools versus riffles). Riffle-dwelling species should have contrasting responses to the increase in minimum flow, depending on their preferences for water depth.

To test the predictions of Lamouroux et al. (1999b,c), observed changes in RI values at Pierre-Bénite due to minimum flow increase (differences between before and after flow restoration) were compared with those predicted from hydraulics at minimum flow (i.e. from the statistical instream habitat model). Additionally, we tested if the observed CSI2 value at Pierre-Bénite after minimum flow increase reached the highest value of all bypassed reaches of the Rhône river and if the observed CSI1 value did not change, as predicted by the habitat model.

**Results**

A strong annual variability in discharge patterns among years was noted during the study. For example, 1999 and 2001 were ‘wet’ years with short periods at the minimum flow, whereas the duration of
minimum flow was high in ‘dry’ years, 1996 and 2003 (Fig. 3). Two floods of return period >10 years occurred in March 2001 and November 2002, with a maximum daily discharge >3400 m$^3$ s$^{-1}$ in the bypassed reach. Temperature patterns were also variable among years (Fig. 2), e.g. the summer 2003 was particularly warm. However, water temperature did not show any increasing trend during the study period despite a context of global warming in the region (Daufresne et al., 2003).

### Describing community changes

A total of 9771 fish belonging to 32 species were sampled during the study period. Neither survey species richness ($P = 0.92$) nor density ($P = 0.16$) differed before and after minimum flow increase (t-tests). Survey richness varied between 16 (June 2002) and 26 species (September 1998), indicating that all species were not sampled during each survey. Survey fish density varied between 0.16 (June 2002) and 1.61 individuals m$^{-2}$ (September 2002).

The relative abundances of species reflect a predominance of a limited number of species both before and after minimum flow increase (Table 1). Chub and roach were the most abundant species during both periods and 10 species represented 93% of the fish captured (chub, roach, bleak, stone loach, gudgeon, barbel, pumpkinseed, white bream, nase and spirlin). However, the relative abundance of six of the 12 most abundant species changed significantly after minimum flow increase (Table 1). Bleak, nase, spirlin,

### Table 1

<table>
<thead>
<tr>
<th>Species code</th>
<th>Common name</th>
<th>Scientific name</th>
<th>Total abundance</th>
<th>% pre</th>
<th>% post</th>
</tr>
</thead>
<tbody>
<tr>
<td>CHE Chub</td>
<td>Leuciscus cephalus (L., 1758)</td>
<td>2337</td>
<td>24.4</td>
<td>18.9</td>
<td></td>
</tr>
<tr>
<td>GAR Roach</td>
<td>Rutilus rutilus (L., 1758)</td>
<td>1857</td>
<td>20.0</td>
<td>17.4</td>
<td></td>
</tr>
<tr>
<td>ABL Bleak</td>
<td>Alburnus alburnus (L., 1758)</td>
<td>1340</td>
<td>10.9</td>
<td>22.2*</td>
<td></td>
</tr>
<tr>
<td>LOF Stone loach</td>
<td>Barbatula barbatula (L., 1758)</td>
<td>901</td>
<td>13.5</td>
<td>2.7*</td>
<td></td>
</tr>
<tr>
<td>GOU Gudgeon</td>
<td>Gobio gobio (L., 1758)</td>
<td>854</td>
<td>8.0</td>
<td>7.7</td>
<td></td>
</tr>
<tr>
<td>BAF Barbel</td>
<td>Barbus barbus (L., 1758)</td>
<td>564</td>
<td>4.8</td>
<td>7.8</td>
<td></td>
</tr>
<tr>
<td>PES Pumpkinseed</td>
<td>Lepomis gibbosus (L., 1758)</td>
<td>493</td>
<td>8.4</td>
<td>2.8</td>
<td></td>
</tr>
<tr>
<td>BRB White bream</td>
<td>Blicca bjoerkna (L., 1758)</td>
<td>465</td>
<td>2.4</td>
<td>7.7*</td>
<td></td>
</tr>
<tr>
<td>HOT Nase</td>
<td>Chondrostoma nasus (L., 1758)</td>
<td>174</td>
<td>0.7</td>
<td>3.2*</td>
<td></td>
</tr>
<tr>
<td>SPI Spirlin</td>
<td>Alburnoideae bipunctatus (Bloch, 1782)</td>
<td>150</td>
<td>0.9</td>
<td>2.4*</td>
<td></td>
</tr>
<tr>
<td>CHA Sculpin</td>
<td>Cottus gobio (L., 1758)</td>
<td>97</td>
<td>1.4</td>
<td>0.7</td>
<td></td>
</tr>
<tr>
<td>PER Perch</td>
<td>Perca fluviatilis (L., 1758)</td>
<td>68</td>
<td>0.5</td>
<td>1.3*</td>
<td></td>
</tr>
<tr>
<td>ROT Rudd</td>
<td>Scardinius erythrophthalmus (L., 1758)</td>
<td>59</td>
<td>0.5</td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>PSR Topmouth gudgeon</td>
<td>Pseudorasbora parva (Temmick and Schlegel, 1842)</td>
<td>52</td>
<td>0.6</td>
<td>0.1</td>
<td></td>
</tr>
<tr>
<td>SIL Wels</td>
<td>Silurus glanis (L., 1758)</td>
<td>52</td>
<td>0.4</td>
<td>0.8</td>
<td></td>
</tr>
<tr>
<td>VAN Dace</td>
<td>Leuciscus leuciscus (L., 1758)</td>
<td>45</td>
<td>0.2</td>
<td>0.7</td>
<td></td>
</tr>
<tr>
<td>VAL Minnow</td>
<td>Phoxinus phoxinus (L., 1758)</td>
<td>43</td>
<td>0.0</td>
<td>0.0</td>
<td></td>
</tr>
<tr>
<td>TAN Tench</td>
<td>Tinca tinca (L., 1758)</td>
<td>40</td>
<td>0.4</td>
<td>0.4</td>
<td></td>
</tr>
<tr>
<td>BOU Bitterling</td>
<td>Rhodeus sericeus (Pallas, 1776)</td>
<td>39</td>
<td>0.4</td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>GRE Pope</td>
<td>Gymnocephalus cernuus (L., 1758)</td>
<td>39</td>
<td>0.4</td>
<td>0.4</td>
<td></td>
</tr>
<tr>
<td>ANG Eel</td>
<td>Anguilla anguilla (L., 1758)</td>
<td>25</td>
<td>0.3</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>EPI Threespine stickleback</td>
<td>Gasterosteus aculeatus (L., 1758)</td>
<td>22</td>
<td>0.2</td>
<td>0.3</td>
<td></td>
</tr>
<tr>
<td>PCH Catfish</td>
<td>Ictalurus melas (Rafinesque, 1820)</td>
<td>13</td>
<td>0.1</td>
<td>0.3</td>
<td></td>
</tr>
<tr>
<td>SAN Pike perch</td>
<td>Stizostedion lucioperca (L., 1758)</td>
<td>9</td>
<td>0.1</td>
<td>0.1</td>
<td></td>
</tr>
<tr>
<td>CAA Goldfish</td>
<td>Carassius auratus (L., 1758)</td>
<td>8</td>
<td>0.0</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>TAC Rainbow trout</td>
<td>Oncorhynchus mykiss (Walbaum, 1792)</td>
<td>8</td>
<td>0.1</td>
<td>0.0</td>
<td></td>
</tr>
<tr>
<td>BLE River benny</td>
<td>Salaria fluviatilis (Asso, 1801)</td>
<td>5</td>
<td>0.1</td>
<td>0.0</td>
<td></td>
</tr>
<tr>
<td>BRO Pike</td>
<td>Esox lucius (L., 1758)</td>
<td>4</td>
<td>0.0</td>
<td>0.1</td>
<td></td>
</tr>
<tr>
<td>CCO Common carp</td>
<td>Cyprinus carpio (L., 1758)</td>
<td>4</td>
<td>0.0</td>
<td>0.0</td>
<td></td>
</tr>
<tr>
<td>BRE Bream</td>
<td>Abramis brama (L., 1758)</td>
<td>2</td>
<td>0.0</td>
<td>0.0</td>
<td></td>
</tr>
<tr>
<td>TOX Soiffe</td>
<td>Chondrostoma toxostoma (Vallot, 1837)</td>
<td>1</td>
<td>0.0</td>
<td>0.0</td>
<td></td>
</tr>
<tr>
<td>TRF Brown trout</td>
<td>Salmo trutta (L., 1758)</td>
<td>1</td>
<td>0.0</td>
<td>0.0</td>
<td></td>
</tr>
</tbody>
</table>

*Significantly different from % pre (t-test, $P < 0.05$).
white bream and perch increased between two- and 4.3-fold, whilst stone loach decreased by a factor of five. Although not significant individually, the relative abundance of barbel and dace were greater, while sculpin, pumpkinseed and topmouth gudgeon were lower after minimum flow increase. However, the relative abundance of any species considered separately was highly variable among surveys (e.g. barbel, Fig. 4).

The first PC axis explained 36% of the variance in relative abundances and clearly discriminated surveys made pre- and postrestoration ($t$-test, $P < 0.001$; Fig. 5), thereby supporting the changes in species proportions described above. The 1999 survey appeared as an exception, with a position on the PCA close to postrestoration surveys. The second PC axis, explaining another 18% of the variance in relative abundances, did not discriminate pre- and postrestoration surveys ($t$-test, $P = 0.46$) but identified surveys with relatively higher proportions of stone loach and lower proportions of roach and pumpkinseed within both periods (e.g. October 1995, September 1999 and October 2001). Similarly, three additional PCAs made on species occurrence, or using habitat units sampled in one habitat type (channel margins or centre) discriminated surveys pre- and postrestoration on their first ($t$-tests, $P = 0.005$, $P = 0.005$, $P = 0.01$, respectively) but not on their second ($t$-tests, $P = 0.88$, $P = 0.13$, $P = 0.72$, respectively) axes.

Changes in relative abundance of the 10 predominant species at Pierre-Bénite were dynamic and size-dependent (Fig. 6). For species whose relative abundance increased after minimum flow change (i.e. bleak, nase, white bream, spirlin and barbel; Table 1), this increase was essentially because of the catch of numerous young of the year. Small fish of these species had a higher cumulated relative abundance in and after 1999. The cumulated relative abundance of large fish of these species tended to be higher after 2001, but this effect is less clear (Fig. 6a). By contrast, for the other species (chub, roach, stone loach, pumpkinseed and gudgeon), the cumulated relative abundance of large fish was lower in and after

### Table 2

<table>
<thead>
<tr>
<th>Environmental variable</th>
<th>Richness</th>
<th>Density</th>
<th>PCA-axis1</th>
<th>PCA-axis2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low flows*</td>
<td>0.07</td>
<td>0.26</td>
<td>0.93</td>
<td>0.16</td>
</tr>
<tr>
<td>High flows – reproduction†</td>
<td>-0.34</td>
<td>-0.44</td>
<td>-0.42</td>
<td>0.87</td>
</tr>
<tr>
<td>High flows – growth‡</td>
<td>-0.49</td>
<td>0.39</td>
<td>-0.14</td>
<td>0.12</td>
</tr>
<tr>
<td>High flows – survey§</td>
<td>0.19</td>
<td>0.02</td>
<td>-0.11</td>
<td>0.53</td>
</tr>
<tr>
<td>Temperature – reproduction*</td>
<td>0.27</td>
<td>0.49</td>
<td>0.01</td>
<td>-0.46</td>
</tr>
<tr>
<td>Temperature – growth**</td>
<td>0.49</td>
<td>-0.05</td>
<td>-0.23</td>
<td>-0.05</td>
</tr>
<tr>
<td>Temperature – survey††</td>
<td>-0.08</td>
<td>0.15</td>
<td>-0.28</td>
<td>-0.38</td>
</tr>
</tbody>
</table>

*Number of days with discharge <25 m$^3$ s$^{-1}$ from the reproduction period to the sampling period, i.e. between March and August.
†Number of days with discharge >500 m$^3$ s$^{-1}$ for the reproduction period, i.e. March to June.
‡Idem for the growth period, i.e. July and August.
§Idem for the 15 days preceding the survey.
*Average daily temperature for the reproduction period – $n = 6$ for this variable because of missing temperature values.
**Idem for the growth period.
††Idem for the 15 days preceding the survey. Limits of periods are from Cattaneò et al. (2001).
The cumulated relative abundance of small fish of these species was lower in 2003 and 2004 (Fig. 6b).

Linking community structure with annual environmental variables

Survey species richness and density in autumn were not significantly correlated with any of the annual environmental variables describing low or high flows or temperature conditions (Table 2). Scores of autumn surveys on the first PC axis were only significantly correlated with low flows ($R^2 = 0.86$, $P < 0.01$), consistent with the separation of pre- and postrestoration surveys on this axis (Fig. 5). Scores on the second PC axis were correlated with high flows during the reproduction period ($R^2 = 0.76$, $P < 0.01$), i.e. high flows during the reproduction period favoured stone loach compared with roach and pumpkinseed.

Testing predictions of fish community changes

Of the 14 species included in the habitat model of Lamouroux et al. (1999c), 13 were present at Pierre-Bénite, representing 91% of the fish captured during our study. For these 13 species the observed changes in RI values between the pre- and postrestoration periods were significantly related to those independently predicted from hydraulics by the habitat model ($R^2 = 0.42$, $P = 0.02$, slope not different from 1; Fig. 7). RI values for barbel (BAF), bleak (ABL), nase (HOT) and spirlin (SPI) increased as expected or more; RI values for gudgeon (GOU) decreased less.
than expected and RI values for pumpkinseed (PES) and stone loach (LOF) decreased more than expected after minimum flow change.

The two synthetic indices related to the proportion of riffle-dwelling (CSI1) and ‘midstream’ species (CSI2) changed as predicted by the habitat model at Pierre-Bénite after minimum flow increase (Fig. 8). CSI1 did not change after minimum flow increase and was low compared with many other reaches of the Rhône and its tributaries. By contrast, CSI2 increased and reached the highest value observed in bypassed reaches of the Rhône river.

Discussion

Our study provides the first analysis of a minimum flow increase below a dam in a large river with many species. Only 4 years after flow restoration at Pierre-Bénite (i.e. August 2000), several of our results indicate a significant, predicted change in fish community structure related to minimum flow enhancement. First, surveys made before and after minimum flow increase were clearly separated along the first axis of a PCA of specific relative abundances. The 1999 survey appeared as an exception in this analysis, with a community structure close to that observed after minimum flow change. However, 1999 was hydrologically an unusual year, with very few days at low flows (n = 38) compared with the previous years (n > 71). Second, a change in community structure across autumn surveys (PCA axis 1 scores; Fig. 5) was significantly related to the number of days at low flows in spring and summer, but not to any other annual environmental variable describing high flows and annual temperature at key periods of fish life cycle. Third, the observed change in community structure was observed for different treatments of
our data (analyses of the relative abundance of individual species, PCA of relative abundance and occurrences, separate analyses of data collected along the margins or at the channel centre). Finally, changes in specific density and community structure indices observed at Pierre-Bénite match those predicted from an independent habitat model and are consistent with the knowledge of species microhabitat preferences.

Most species whose relative abundance increased at Pierre-Bénite prefer deep and/or fast-flowing hydraulic conditions. For example, bleak is a pelagic species (Copp, 1992) preferring intermediate velocities (Lamouroux et al., 1999a; Bruslé & Quignard, 2001). Both nase, which migrated to France from central Europe via artificial channels at the end of the 19th century and barbel are rheophilic species typical of large, fast-flowing rivers (Nelva, 1988; Bruslé & Quignard, 2001). Spirulin, also a rheophilic species, prefers oxygenated habitats with intermediate depths (Lamouroux et al., 1999a; Bruslé & Quignard, 2001). Nase, barbel and spirilin are also lithophilic species that spawn on gravel or cobble in fast-flowing habitats. The increase of the relative abundance of white bream and perch were less expected because these species generally avoid fast-flowing habitats. Perch, however, is not abundant at Pierre-Bénite and white bream was often caught in macrophyte patches where it spawns and where velocity is locally reduced. Overall, the minimum flow increase at Pierre-Bénite favoured fluvial species that have been largely affected by the regulation of the large rivers in the Rhône (Persat, 1988; Lamouroux et al., 1999c) and elsewhere (Schiemer & Spindler, 1989). Among the species whose relative abundance decreased, we note both species avoiding fast flows (pumpkinseed and topmouth gudgeon) and small rheophilic species that avoid deep water (stone loach and sculpin) (Bruslé & Quignard, 2001).

Estimating fish abundances in large rivers is difficult, often resulting in high levels of uncertainty (Persat & Copp, 1990). A fish survey at Pierre-Bénite covered only 0.2% of the total surface area of the reach and as many stream fish are notoriously gregarious (Bruslé & Quignard, 2001) their capture in our habitat units is variable. In this context, our quantitative estimates of a particular species proportion should be considered as potentially biased. It is only the number of species affected by flow restoration, the consistency of observed changes for different treatments of the data and the predictability of these changes that enable us to conclude on a significant change in community structure. It is not surprising that fish community changes were essentially observed for community variables depending on the relative abundance of species (Daufresne et al., 2003), as these type of variables are better estimated by our sampling design than other fish community descriptors (richness and density). Estimates of survey richness and density were probably affected by the limits of fish sampling in large rivers. The difference of fish density estimated for example in June 2002 (0.16 individuals m⁻²) and 3 months after in September 2002 (1.61 individuals m⁻²) illustrates these difficulties. Moreover, survey species richness was always lower than the total species richness of the reach (32, all surveys pooled) and its variations were because of the uncertain capture of a number of rare species (e.g. trout, pike perch, bream and river blenny; see Table 1). A study of these community descriptors would require more intensive sampling effort in space and time (see also Lamouroux et al., 1999c) and our difficulty to interpret their temporal variation is an obvious limit of our study.

Our study suggests a very rapid change in species relative abundance that was observed since 2001 and even during the ‘wet’ year 1999. The rapidity of the fish response was unexpected, because most fish species at Pierre-Bénite have life cycles of 5 years or more (Bruslé & Quignard, 2001). Furthermore, former observations of fish community response to environmental changes suggested responses over a longer period (e.g. Matthews, Schorr & Meador, 1996; Eklov et al., 1998; Pegg & McClelland, 2004). Our analysis of size class responses provides a rational explanation for this rapid change. Species whose relative abundance increased at Pierre-Bénite may have benefited from an immediate higher reproduction success, because it is essentially the relative proportion of small fish of these species that increased. The increase of relative abundance of large individuals of these species is less evident and was not immediate after minimum flow change. Minimum flow increase may have enhanced the usable area and the spawning conditions (generally fast-flows on coarse substrate) of species preferring deep and fast-flowing hydraulic habitats. By contrast, it is essentially the large individuals of species whose relative abundance decreased that are responsible for the rapidity of the

observed community change (Fig. 6). This suggests that adults of these species either had higher mortal-
ities after minimum flow change or escaped from the
reach to find more suitable hydraulic conditions (e.g. downstream of our study reach in Vaugris reservoir).
The modification of hydraulic conditions in dike fields
along the shoreline, following minimum flow
increase, may also have influenced the survival of
young of the year (Nicolas & Pont, 1997). Overall, the
different responses of specific size classes and the
high variability of community patterns observed
across surveys after minimum flow change reveal
that the fish community at Pierre-Bénite is in a
transitional phase. Continued monitoring of the fish
life stages will indicate if the changes observed at
Pierre-Bénite are perennial or not.

In addition to the (transitional) change in commu-
nity structure observed after minimum flow increase,
the annual variability of the environment may explain
a minor part of the variability in community structure
across surveys. In particular, we found a significant
correlation between the frequency of high flows
during the reproduction period and the second PC
axis of relative abundance. High flows (and maybe
their indirect action on substrate) favoured the repro-
duction of stone loach, a species spawning in clear
riffles (Bruslé & Quignard, 2001), despite the general
decrease of this species because of minimum flow
increase. A more intensive sampling design, including
regular sampling from March to September, would
probably allow a more precise interpretation of the
observed inter-annual variability.

The case-study of Pierre-Bénite supports the idea
that fish community responses to hydraulics are
partly predictable in large rivers. It expands the scope
of the few studies indicating an impact of minimum
flow increase on fish populations in smaller streams
(Phillips et al., 2000; Jowett & Biggs, 2004). Large
rivers are inhabited by species that are adapted to
depth, fast-flowing systems (Persat, 1988; Schiemer &
Spindler, 1989; Penczak & Kruk, 2000; Galat &
Zweimüller, 2001), i.e. the main channel of large
rivers cannot be viewed as ‘highways’ where fish only
transit (Junk, Bailey & Sparks, 1989). Moreover, the
results obtained at Pierre-Bénite match general expec-
tations derived from the application of instream
habitat models in different countries (Lamouroux &
Jowett, 2005). Indeed, habitat values derived from
instream habitat models are sensitive to two hydraulic
axes in many rivers: a geomorphological axis (corre-
spending to our index CSI1) where riffle-dwelling
species contrast with pool-dwelling ones, and a
discharge rate axis (corresponding to our CSI2) where
midstream species adapted to fast-flowing and deep
microhabitats contrast with others (Lamouroux &
Jowett, 2005). Correspondingly, rheophilic species had
contrasted response to minimum flow enhancement at
Pierre-Bénite. Rheophilic, midstream species prefer-
ring intermediate or high water depth were favoured
by the minimum flow increase at Pierre-Bénite
relative to other rheophilic, riffle-dwelling species
preferring shallow conditions (stone loach, sculpin).
Rheophilic species as a whole are often used in
biomonitoring for indicating the effects of physical
modifications of rivers (Oberdorff et al., 2002), or in
general definitions of habitat guilds (e.g. Aarts et al.,
2004). Our case study suggests the need to refine guild
definitions in such studies, by separating rheophilic
species sensitive to discharge management from
species sensitive to morphological changes of the
streambed (i.e. weir addition or removal, manage-
ment of the bed morphology). Pierre-Bénite is the first
of six reaches of the Rhône river where minimum flow
has been or should be increased. We expect this case
study to be a base for a quantitative comparison of
other experiences of flow restoration in large rivers, in
the Rhône catchment and elsewhere.

Acknowledgments

Financial support was provided by the Compagnie
Nationale du Rhône (CNR), the Agence de l’Eau
Rhône-Méditerranée-Corse, the Diren Rhône-Alpes,
and the Syndicat mixte du Rhône des îles et des lônes
(SMIRIL). Sylvie Valentin coordinated the fish surveys
before 1999. Georges Carrel, Richard Johnson, Michael
Ovidio, Yves Souchon and anonymous reviewers
provided helpful comments.

References

Aarts B.G.W., Van den Brink F.W.B. & Nienhuis P.H.
(2004) Habitat loss as the main cause of slow recovery
of fish faunas of regulated large rivers in Europe: The
transversal floodplain gradient. River Research and
Applications, 20, 3–23.
Amoros C. (2001) The concept of habitat diversity
between and within ecosystems applied to river side-


(Manuscript accepted 15 June 2006)

© 2006 The Authors, Journal compilation © 2006 Blackwell Publishing Ltd, Freshwater Biology, 51, 1730–1743