Spring floods and temperature are main drivers of the fish assemblage of a Mediterranean regulated river (Durance River, France)

Les crues et la température printanières sont des déterminants majeurs de l'assemblage piscicole d'une rivière méditerranéenne régulée (Durance, France)

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RÉSUMÉ

La Durance, située dans le sud-est de la France, est une rivière dont le débit est fortement régulé, notamment pour la production d'électricité et l'irrigation. Néanmoins, la rivière conserve un caractère impétueux et une dynamique fluviale significative lorsque les crues ne peuvent plus être contenues par les barrages. Le peuplement piscicole de la Durance fait l'objet d'échantillonnages annuels depuis le début des années 1990. Dans cette communication, nous analysons les réponses du peuplement piscicole face aux variations interannuelles et saisonnières de l'hydrologie et du régime thermique sur 6 stations de moyenne et basse Durance suivies entre 1995 et 2011. Malgré la forte régulation du débit, le peuplement a répondu essentiellement à des événements hydrologiques non écrêtés par les ouvrages, en particulier à l'intensité des crues printanières. La température modulait la structure du peuplement en favorisant certaines espèces aux dépends d'autres moins thermophiles. La compréhension des effets des régimes hydrologiques et thermiques sur le peuplement piscicole de plusieurs sites et à long-terme est une clef de la gestion durable de la ressource en eau, notamment pour l'adaptation de débits environnementaux.

ABSTRACT

The Durance, located in the southeast of France, is a highly regulated river, mainly for hydropower production and irrigation purposes. Nevertheless, the river still has an impetuous character and a significant fluvial dynamics when floods exceed dams' capacity. The fish assemblage of the Durance River is monitored annually since the early 1990s'. In this paper, we analyse the response of the fish assemblage to inter-annual changes in the seasonal hydrology and temperature on 6 sites from the middle and lower Durance monitored between 1995 and 2011. Despite the high degree of flow regulation, fish assemblage variability was mainly linked to natural flow events resulting in dam spill-over, and in particular the magnitude of spring floods. Temperature influenced fish assemblage structure by promoting certain species at the expense of other less thermophilic ones. Understanding the effects of flow and thermal regimes on the fish assemblage at different sites and over the long term is a key step to go toward sustainable management of water resources, especially for the adaptation of environmental flows.

KEYWORDS

Crues, débits environnementaux, poissons, rivière alluviale, température
Floods, environmental flows, fish, alluvial river, temperature

1 INTRODUCTION

Damming and flow regulation are amongst the most severe human impacts on freshwater ecosystems at a global scale. However, attempts to mitigate their negative impacts are growing worldwide, and the restoration of altered flow regimes has now become a key challenge for the coming decades. Scientists took head on this major issue, and developed the 'environmental flows science' which aims at providing the theoretical and operational foundations to restore altered flow regimes. However, unravelling the relationships between changes in flow characteristics and subsequent biological responses put up as a prerequisite to propose new flow management rules.

Mediterranean rivers are characterized by their high summer temperature, their extremely variable flow regime, and most often high anthropogenic pressures. In South-Eastern France, the Durance River is extensively used for hydropower production and irrigation, which severely alter flow and temperature regimes. The regulation consists in a series of dams and by-passed sections, with most of the water flowing into canals parallel to the main by-passed channel. However, because peak floods regularly exceed upstream dam's capacity and spill into the by-passed (i.e. minimum-flow) sections, the 'regulated' flow regime can be extremely variable. Despite the heavy and ubiquitous footprint of hydropower all along the river course, the Durance still is a highly dynamic, alluvial river during high flow events.

Because of its high patrimonial and ecological values, the fish assemblage of the Durance River deserves significant conservation efforts. The changes in flow management rules implemented since 2007 in the medium reach of the river were a first step toward the restoration of the flow regime. Here, we aimed at identifying the major environmental driving forces of the fish assemblage structure. We analysed the long-term (1995-2011) spatial-temporal patterns of the fish assemblage at 6 sites located along a *ca.* 100 km reach of the Durance River. We investigated how year-to-year flow and temperature characteristics per biological seasons could explain annual changes in the fish assemblage structure.

2 MATERIAL ET METHODS

The sites were located at two hydroelectric schemes (i.e. Ste-Tulle and Mallemort), and were chosen so as to be representative of the geomorphological and mesohabitat characteristics of the river. The flow regime at the 6 sites could differ depending both on the minimum flow released by the upstream dam and the discharge of tributaries. Fish were sampled annually in late spring or summer by electrofishing, in 7-28 (mean = 18.1, sd. = 4.9) independent habitat units of several square meters per site. Fish monitoring started at a different year depending on the site (1995, 1997, 2003, or 2005), but all time series at least included 7 consecutive years and ended in 2011, resulting in n = 62 [site*year] combinations. The 11 most abundant species (% > 0.5) were considered in analyses. Individuals were separated in two ontogenetic stages, i.e. 0+ and >0+ fish. Daily flow and temperature time series for each of the 6 sites were described using variables reflecting median, high, and low conditions, overall variability, and magnitude and duration of particular events. Variables were computed for two 'biological periods', i.e. winter (November-February) and reproduction (March-June).

Species' densities per ontogenetic stage, flow and temperature variables were separately analysed using between- and within-sites Principal Component Analysis (PCAs). The relationships between annual fish and flow/temperature data were explored by correlation analysis (Pearson's *r*) using the within-sites PCAs axes as synthetic variables. General linear models (GLM) were used to test for the robustness of fish-flow relationships across sites.

3 RESULTS AND DISCUSSION

Spatial and temporal patterns were very similar for the two ontogenetic stages (thereafter only results for >0+ fish are presented). The assemblage structure displayed a clear longitudinal spatial pattern (between-sites inertia = 24.4%, P<0.001). The blageon (*Leuciscus souffia*) was typical of sites from the Ste-Tulle scheme located in the middle Durance. Sites of Bonpas and Cheval-Blanc in the lower Durance had high densities of minnow (*Phoxinus phoxinus*) compared to other species, possibly reflecting the effects of water releases from the Mallemort dam. The site of Cadenet had the highest overall mean densities.

Most of the variability (75.6%) in assemblage structure was due to year-to-year changes in fish densities. The first within-sites PCA axis (PC1) clearly discriminated years with low densities (e.g. 2008, 2009, 2010, 2011) from years with high densities (e.g. 2005, 2006, 2007) for all species. The second axis (PC2) separated species such as the barbel (*Barbus barbus*), the stream bleak (*Alburnoides bipunctatus*), the chub (*Squalius cephalus*) and the gudgeon (*Gobio gobio*), from the minnow and the two species of loach (*Barbatula barbatula* and *Cobitis bilineata*). The correlation

analysis (Table 1) revealed strong associations between the annual fish assemblage structure and annual flow/temperature characteristics.

PCA axis	PC1	PC2	PC1H	PC2H	PC1T	PC2T
PC1	1					
PC2	-0.024	1				
PC1H	**0.671**	-0.189	1			
PC2H	0.029	-0.1	-0.059	1		
PC1T	**-0.577**	**0.315**	**-0.852**	-0.143	1	
PC2T	0.162	0.001	0.229	-0.203	-0.048	1

Table 1 : Pearson's correlation matrix between within-sites PCA axes (Principal Components PC1 and PC2) for fish, flow (H), and temperature (T). In red are the significant ($p < 0.05$, not corrected) coefficients.

The overall density of the fish assemblage significantly decreased with the peak flood during the reproduction period (PC1 *vs* PC1H, r = 0.671). Directly looking at the relationship between the total fish density and the daily maximum flow (Fig. 1,left) confirmed a strong effect of the peak flow, which is similar across all sites (GLM, n = 62, $r^2 = 0.513$: $p_{Ln\_QMax}<0.001$, $p_{Site} = 0.002$, $p_{Site*Ln\_QMax} = 0.997$). High overall fish densities were also associated with warmer reproduction periods (PC1 *vs* PC1T, r = -0.577), but temperature was no more significant when the effect of peak flow was considered. However, warmer temperature during reproduction modulated the assemblage structure (PC2 *vs* PC1T, r = 0.315) and favored species such as the minnow and both stone and transalpine loaches, at the expense of barbel, stream bleak, gudgeon, and chub, similarly across sites (GLM, n = 55, $r^2 = 0.344$: $p_{DCX30\_TREP}=0.003$, $p_{Site} = 0.010$, $p_{Site*DCX30\_TREP}= 0.964$; Fig. 1, right).

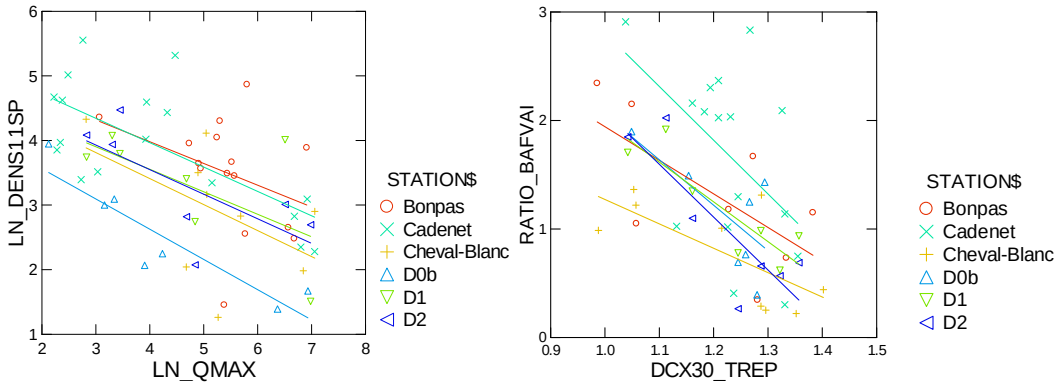

Figure 1: Relationships between overall fish density (LN_DENS11SP) and peak daily flow (LN_QMAX) during the reproduction period (left), and between the ratio of densities of (barbel+chub+stream bleak+gudgeon) / (stone and transalpine loaches+minnow; RATIO_BAFVAI) and the temperature continuously exceeded for 30 days (DCX30_TREP) during this same period.

Our results suggest that the natural flow variability, by means of spring floods, is a major determinant of the fish assemblage structure in the Durance River despite the severe flow regulation. Effects of floods were similar across all 6 sites over a 100 km long reach, even though the regulated flow regime and anthropogenic pressures could differ among sites. Spring floods could lower global fish abundances (for both 0+ and >0+ fish) presumably by inducing mortality in early-life stages, and/or by providing non-optimal habitat conditions for larger fish. Results also stressed the difficulty of disentangling the respective effects of flow and temperature, since both factors are highly correlated (Olden and Naiman 2010). At the Ste-Tulle hydroelectric scheme, positive effects of floods were demonstrated on the functioning of the whole aquatic ecosystem, including other taxonomic groups, and largely covered expected effects of the recent change in flow management rules (increase of the minimum flow and seasonal modulation; Gouraud et al. 2014). Given the large interannual variability of biological assemblages, a long-term biological monitoring should be set up to further highlight the effects of changes in flow management rules.

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