Fisheries Management and Ecology, 2004, **11**, 165–172

Contribution of native and non-native species to fish communities in French reservoirs

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Abstract Previous studies showed that only 20% of the variability in fish community structure in French reservoirs could be explained by site characteristics. In addition, no relationship was found between the relative abundance of species and stocking effort. Therefore, deliberate or uncontrolled introductions are likely to be the source of a great part of the observed communities. The objective of this study was to assess the importance of species introductions in French reservoirs. Fifty-one reservoirs were sampled to obtain species presence/absence data. Local native (LNaR) and non-native (LNNR) species richness were negatively correlated. LNaR was strongly correlated to the lake surface area, depth and catchment area, whereas LNNR was independent of environmental variables. Furthermore, LNaR was positively correlated to regional native richness. Conversely, local total richness was independent of regional total richness, but was related to the reservoirs' environmental characteristics. It was hypothesised that the native fish communities in French reservoirs are unsaturated and species introductions lead to saturated communities.

KEYWORDS: environmental factors, interspecific interactions, reservoir, species introduction, species richness.

Introduction

Introduction of fish species in France has a long history but records exist mostly for the last two centuries (Keith & Allardi 1997). The 23 introduced fish species currently present in the country's water bodies account for one-third of the total number of species. Therefore, they are likely to affect native fish communities.

Introduced piscivores have frequently reduced the populations of prey species, occasionally leading to their extinction (Townsend 1996; Chapleau, Findlay & Szenasy 1997), thereby reducing native richness (Whittier, Halliwell & Paulsen 1997; Findlay, Bert & Zheng 2000) and altering fish community structure (Godinho & Ferreira 1998). Furthermore, previously predator-less native fish communities could be more sensitive to predation pressure (Townsend & Crowl 1991).

Competitive interactions are subject to debate. Frequently, diet analyses show that native and introduced species feed on similar resources and in similar habitats, but the severity of feeding competition is difficult to prove unless prey resources are assessed. The problem becomes even more complex when considering that the interactions between two species are not restricted to feeding competition, but can depend on interactions with a third species (Bryan, Robinson & Sweetser 2002), and are influenced by habitat availability (Eklöv & Diehl 1994; Chick & McIvor 1997).

Ecologists have developed alternative methods and theories, frequently based on the niche theory (Hutchinson 1957), to assess directly interactions at the community level. Among those, the distinction between interactive and non-interactive communities (Cornell 1985; Cornell & Lawton 1992) is based on the hypothesis that local conditions result in a maximum carrying capacity. When species richness attains this capacity, interactive pressures are expected to condition subsequent community characteristics. Such communities are considered to be saturated. Conversely, species-poor communities, limited by regional biogeography, show limited niche overlapping and low interactions between species. Such situations provide greater chances for introduced species to develop and limits potential competitive risks with the original communities (Belkessam, Oberdorff & Hugueny 1997).

Local conditions strongly influence community characteristics (Eadie & Keast 1984; Hondzo & Stefan

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1996) by providing the framework in which the structuring processes take place. Therefore, reservoir fish community composition can be partially explained by their location in the catchment, climatic conditions and reservoir morphometry (Godinho, Ferreira & Portugal e Castro 1998; Irz, Laurent, Messad, Pronier & Argillier 2002). A hierarchical conceptual framework was proposed to integrate the various spatial and temporal scales involved in structuring lacustrine fish communities (Tonn 1990). Thus, local assemblages are regarded as a subsample of the global fish pool. Consequently, an understanding of the key processes responsible for the standing communities requires a multiscale approach as well as an assessment of the relative importance of biotic, abiotic and regional factors (Jackson, Peres-Neto & Olden 2001), to which human interventions must be added.

The objectives of this paper are to: (1) investigate the relationship between native and non-native richness at a local scale; (2) correlate local richness to environmental variables; and (3) analyse the relationship between local and regional richness to evaluate community saturation.

Materials and methods

The data set

The data used in this study originated from various sources. The aim of the collection was to gather, as exhaustively as possible, existing information on fish communities in French reservoirs. This was achieved on the basis of numerous, mostly unpublished, reports from research institutes, administrations and consultants. These studies were carried out for local purposes. They were not part of a national monitoring network and thus were not based on any standardised fish sampling strategy. As a result, data acquisition procedures showed strong heterogeneity. Most of the surveys were carried out with gill nets, either horizontal or vertical, but fish censuses were also carried out when reservoirs were being drained. To reduce the bias related to the differences in sampling methods, fish data were only used to derive the total number of species in the sample, expressed as the reservoir's total species diversity (LToR).

The reservoirs' catchment area, maximum depth, surface area and altitude were either extracted from the reports or taken from 1:25 000 to 1:100 000 topographical maps. The scope of the study was limited to sites located below 1100 m altitude as this appeared to be a reasonable threshold, excluding the rather distinct mountain reservoirs located on streams that did not originally host any fish populations prior to introductions. Such sites display little variability in species richness because they are limited to salmonids (Irz *et al.* 2002). Sufficient information was available for 51 reservoirs. The distribution of these sites in France is uneven (Fig. 1) and reflects both the actual distribution of reservoirs, which are mostly located in mountainous or hilly regions, and the degree of local interest for reservoir fisheries.

The classification of species as native, translocated or alien was based on historical records and riverine fish sampling (Keith 1998; Keith & Allardi 2001). This classification is given for each of the 10 hydrographic regions (Fig. 1). Species are considered as native if present in a catchment 5000 years BP, translocated when they were native in another French catchment, and alien when they were introduced from abroad. Tench, *Tinca tinca* (L.), was considered native in Côte d'Azur, as in the other mainland Mediterranean regions, despite the lack of precise information on the status of this species in Keith (1998) and Keith & Allardi (2001).

The reservoirs' (local) total species richness (LToR) could therefore be split into native (LNaR), translocated (LTrR) and alien (LAlR) richness. Local non-native richness (LNNR) is LTrR + LAlR. Regional total richness (RToR) was considered as the total species pool in each hydrographic region, regional

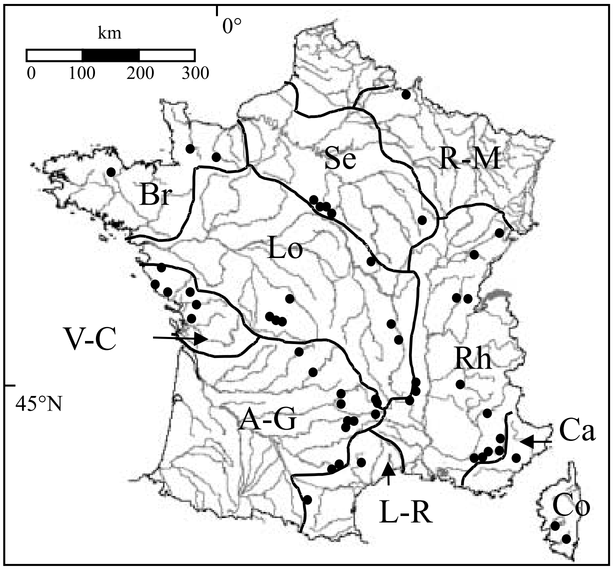

Figure 1. Map of France showing hydrographic regions (bordered by thick lines) according to Keith (1998) and location of the study reservoirs (solid circles). R-M: Rhine-Meuse; Se: Seine; Br: Bretagne; Lo: Loire; V-C: Vendée-Charente; A-G: Adour-Garonne, Rh: Rhône; L-R: Languedoc-Roussillon, Ca: Côte d'Azur, Co: Corse.

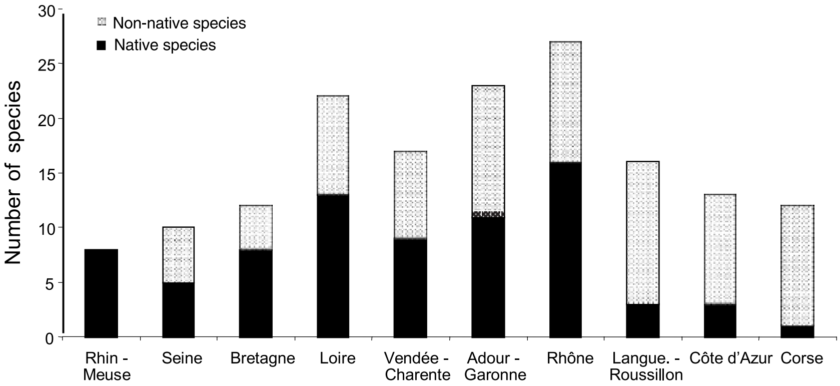

Figure 2. Number of native and non-native species recorded in the study reservoirs among hydrographic regions.

native richness (RNaR) being the total native pool in the region.

As the scale at which the status of species is given is the hydrographic region in which the lake is located, some of the species that are considered as native could have been introduced into the lake from another catchment of the same region.

Analytical procedure

Spearman correlation was used to study the bivariate relationship between LNaR, LTrR, LA1R and LNNR. As LNNR is the sum of LTrR and LAlR, these variables could not be considered independent and the correlation coefficients were not derived. Between-regions comparison of the environmental variables was processed by one-way ANOVA. The relationship between richness and environmental variables was investigated by bivariate Spearman correlation due to clear non-normal distributions of the environmental variables.

Plotting local vs. regional richness is the classical method for testing community saturation (Cornell 1985). The relationship was assessed using linear, power and quadratic regression between the mean value of local richness of each region and the regional richness. Pooling local richness into a single mean value of a region is recommended instead of using individual values of local richness for each sampling station to avoid pseudo-replication (Srivastava 1999).

All the statistical analyses were performed with SPSS software (SPSS Inc. 1999).

Results

Regional distribution of fish species

The total number of species recorded in the 51 reservoirs was 34, but varied from eight in Rhine-Meuse to 27 in Rhône (Fig. 2). These differences can be related to both the number of reservoirs in each region and to the regional species pool. Ten of these species were present only in a single region (Table 1).

Apart from Rhine-Meuse, represented by a single reservoir in the data, native and non-native species were found in all the regions. However, the balance between native and non-native was also dependent upon regions. Languedoc-Roussillon, Côte d'Azur and Corse, all small coastal Mediterranean catchments, limited in native richness, showed high proportions of introduced species (Fig. 2). Conversely, the proportion of introduced species was around 40% in the Seine, Loire, Adour-Garonne and Rhône, all large regions. The number of introduced species was similar between reservoirs of species-rich and species-poor regions.

Relationship between native and non-native richness

At the regional scale, the relationship between RNaR and RNNR was not significant ($r^2 = 0.012$, $P = 0.77$) while the correlation between RNaR and RToR was strong (RToR = 18.5 + 1.06 RNaR, $r^2 = 0.80$, $P < 0.001$).

At the local scale, the only significant correlation was a negative one between LNaR and LNNR (Table 2). However, LTrR ($P = 0.12$) and LAlR ($P = 0.21$) were also negatively related to LNaR, whereas LTrR and LAlR were positively correlated ($P = 0.09$), showing that some reservoirs were more subjected than others to introductions from either origin (close or alien) and/or allow these species persistence. The negative correlation between LNNR and LNaR suggests that such lakes, hosting numerous non-native species, tend to be poor in native species.

Table 1. List of the species recorded in the study reservoirs. The status is given per hydrographic region. Regional richness were taken from Keith & Allardi (2001) for Corse, and from Keith (1998) for all other regions

	Rhine-Meuse	Seine	Bretagne	Loire	Vendée-Charente	Adour-Garonne	Rhône	Languedoc-Roussillon	Côte d'Azur	Corse
Number of reservoirs	1	5	3	7	6	10	14	2	1	2
Regional native richness	37	31	26	31	25	27	38	24	16	4
Regional total richness	51	53	39	58	40	53	58	48	40	19
Leucaspius delineatus					NN		NN			
Alburnus alburnus			N	N	N	N	N	N	N	
Barbus barbus						N	N			
Micropterus salmoides		NN		NN	NN			NN	NN	
Leuciscus soufia							N			
Blicca bjoerkna	N		N	N	N	N	N	NN	NN	
Abramis brama	N	N	N	N	N	N	N	NN	N	
Esox lucius	N	N	N	N	N	NN	N	NN	NN	NN
Carassius auratus										NN
Carassius carassius				NN	NN	NN	NN	NN		NN
Cyprinus carpio		NN	NN	NN	NN	NN	NN	NN	NN	NN
Leuciscus cephalus				N		N	N	N		
Coregonus sp.							N			
Salvelinus namaycush							NN			
Gambusia affinis holbrooki						NN				
Rutilus rutilus	N	N	N	N	N	NN	N	NN	NN	NN
Gobio gobio			N	N	N	N	N			NN
Gymnocephalus cernuus	N		NN	NN	NN	NN	NN			NN
Chondrostoma nasus							NN			
Misgurnus fossilis						NN	N			
Lota lota				N						
Salvelinus alpinus							NN			
Ictalurus melas		NN		NN	NN	NN	NN			
Perca fluviatilis	N	N	N	N	N	NN	N	NN	NN	NN
Lepomis gibbosus		NN		NN	NN	NN	NN	NN	NN	
Scardinius erythrophthalmus	N			N	N	N	N	NN	NN	NN
Sander lucioperca		NN	NN	NN	NN	NN	NN	NN	NN	NN
Silurus glanis				NN				NN		
Oncorhynchus mykiss			NN	NN		NN	NN	NN	NN	
Tinca tinca	N	N	N	N	N	N	N	N	N	NN
Chondrostoma toxostoma							N			
Salmo trutta				N		N	N			N
Phoxinus phoxinus						N				
Leuciscus leuciscus				N		N				

N, native; NN, non-native; blank, not recorded.

Table 2. Spearman correlation coefficients between local species richness

	Native richness	Translocated richness	Alien richness
Native richness	1		
Translocated richness	−0.220	1	
Alien richness	−0.180	0.235	1
Non-native richness	−0.286*	nc	nc

nc, Not calculated. *$P < 0.05$.

Influence of environmental variables

The sites displayed a wide range of variation in environmental characteristics (Table 3). Comparison of the environmental variables showed that only altitude presents significant between-regions differences ($P < 0.001$). The reservoirs of Corse, Rhône, Loire and Adour-Garonne were higher in altitude than those of the Seine and coastal regions.

The relationship between these variables and reservoirs' species richness showed that catchment area, lake area and maximum depth were positively correlated to LToR and LNaR but not to the richness in

Table 3. Range of variation of environmental variables

	Altitude (m)	Catchment area (km^2)	Lake area (ha)	Maximum depth (m)
Minimum	13	1	4	2
Maximum	1074	6520	3200	135
Mean	392	82.5	358	37.6
SD	297	1490	587	33.7

Table 4. Spearman bivariate correlation coefficients between species richness and reservoir characteristics

	Altitude	Catchment area	Lake area	Maximum depth
Native richness	0.141	0.500***	0.433**	0.288*
Translocated richness	−0.018	0.170	0.214	0.247
Alien richness	−0.183	−0.279*	−0.184	−0.155
Non-native richness	−0.056	−0.09	0.038	0.005
Total richness	0.092	0.407**	0.435**	0.395**

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

introduced species (Table 4). The only exception was the negative correlation between LAlR and catchment area. Altitude was never a significant factor. Only native and total richness displayed environment-related patterns for the variables considered.

Saturating effect of species introductions?

The local-regional richness plot (Fig. 3) showed that LNaR was correlated to RNaR. The linear model fitted the data best ($n = 10$, $r^2 = 0.52$, $P = 0.012$) with no sign of reaching an asymptotic value, suggesting that native communities could be unsaturated. The slope was 0.195 and the intercept did not significantly differ from zero. Conversely, LToR appeared to be independent of RToR ($n = 10$, $r^2 = 0.081$, $P = 0.43$). Such an independence could result from a local saturation in species.

Discussion

Regional scale

Fish species introductions are widespread in French reservoirs and occur in all regions, which is consistent with previous results obtained on rivers (Keith & Allardi 1997). When such introductions are voluntary, they generally aim at enhancing recreational fisheries and are carried out without any prior analysis of their chances of success or of their potential impact on native communities (Argillier, Pronier & Changeux 2002). These observations prove that reservoirs generally provide a favourable environment for the establishment of non-native species.

The number of introduced species in a region is interesting on a regional scale, but it is difficult to interpret because it depends on both the frequency of introduction attempts and the success rate of these attempts. However, it appears quite constant among regions and independent of the regional native pool. This suggests that the invasibility of species-poor regions is not markedly greater than that of species-rich ones.

Local scale

At the local scale, the negative correlation between native and non-native richness suggests that the success of introductions could be superior in species-poor environments, which would be consistent with other results showing that species-poor communities were in some cases less resilient to invaders (Lodge 1993). Furthermore, management authorities may be

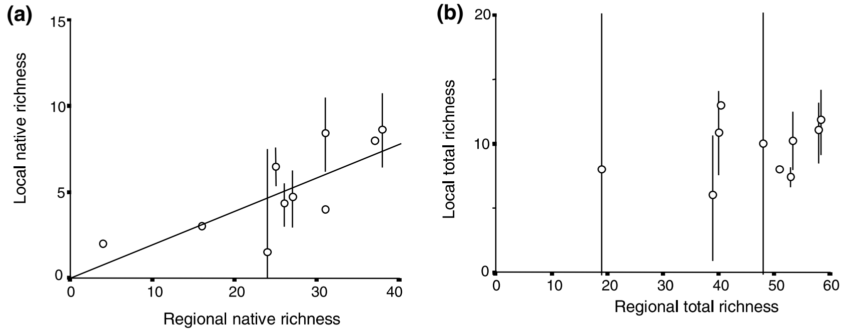

Figure 3. Relationship between regional and local species richness: (a) native richness; (b) total richness. Bars represent 95% confidence interval for the mean value.

more inclined to introduce species when recreational fisheries appear limited by local richness.

Environmental disruptions, such as dam construction, have also been proven to provide favourable conditions for the establishment of new species by modifying the competitive ability of native fauna (Moyle & Light 1996). The damming of the river also considerably alters the initial riverine habitat, thereby modifying the ecological niches available. The possibilities for the initial lotic fish species to occupy these niches are probably reduced because most of them may not be adapted to lentic conditions, which explains that in some cases in the years following the initial filling colonisation of a water body was restricted to its upper part and shallow areas (Fernando & Holcik 1991).

However, the success of introduced species also depends on their ability to cope with habitat conditions and environmental variability (Brown & Moyle 1997). The environmental variables considered in this study are not correlated to the number of introduced species, which shows that the reservoirs' physical features do not represent a major pressure on the number of non-native species, either translocated or alien. This does not mean that the fate of introduced species is independent of environmental conditions, but rather that whatever habitats are available, some of the introduced species find suitable conditions to settle. Native fishes exhibit patterns related to environmental variables. Catchment area can be considered as an indicator of the diversity of habitats upstream from the lake, whereas lake depth and surface area are related to the within-lake habitat diversity. Therefore, their positive correlation with native and total richness indicates the classical increase in richness with habitat diversity (Eadie & Keast 1984). It also suggests that migratory movements between the lake and the upstream hydrographic network have to be considered, which is confirmed by the presence in the data of numerous obligatory riverine species (according to Penczak & Kruk 2000).

The absence of an altitude effect is more puzzling because altitude is frequently recognised as a surrogate for the longitudinal succession of habitat conditions from upstream to downstream (Irz *et al.* 2002). It is possible that the range of variation in the sites' altitude (0–1074 m) was insufficient to make altitude an important explanatory variable to species richness.

Man-induced saturation?

The plots of local vs. regional richness (Fig. 3) suggest that native fish communities in reservoirs would be unsaturated (Cornell & Lawton 1992). In France, this had already been observed in small coastal streams (Belkessam *et al.* 1997; Oberdorff, Hugueny, Compin & Belkessam 1998) but not at a larger scale nor in lentic systems. In reservoirs, local native richness is limited because potential natural colonisation is restricted to a subsample of the upstream species pool that is sufficiently adapted to lentic environments. Therefore, native richness is likely to be below the levels leading to strong interaction between species, particularly when considering that the reservoir generally increases the diversity of habitats compared with the initial river.

Conversely, no linear relationship was found between local and regional total richness. This does not strictly prove that communities are saturated (Srivastava 1999). However, the strong relationships found between LToR and the environmental variables would be expected under a control of LToR by local conditions. Furthermore, the negative correlation between LNNR and LNaR, for which several interpretations were given above, could also reflect the impact of introductions on native communities and therefore a strong level of interspecific competition.

Comparing patterns of native and non-native richness suggests that introductions may be so frequent that they lead to increases in richness until communities become saturated, i.e. when no niche remains vacant.

Conclusion

In the absence of precise monitoring of lentic systems, including data on the extinction of native species at the local scale, the type of approach developed contributes to the understanding of the processes involved in structuring fish communities. In an applied perspective, it provides valuable information for the assessment of management practices because further introductions in already saturated communities could result in local extinction and thereby in a reduction in biodiversity.

Preliminary results from natural lakes (unpublished data) tend to confirm the hypothesis of man-induced saturation of fish communities. Further work will be carried out to check the trends observed in a broader framework for both natural and man-made lakes, with more attention to the underlying assumptions and analytical procedure.

Acknowledgments

We would like to thank the numerous persons and institutions who provided data for this study, Conseil

Supérieur de la Pêche, Ecole Nationale Supérieure d'Agronomie de Toulouse, Université Paul Sabatier Toulouse III, Institut National de la Recherche Agronomique, Université de Franche Comté and Electricité de France. We thank T. Oberdorff for his useful comments on the initial version of the manuscript.

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