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Influence of site characteristics on fish community patterns in French reservoirs

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Abstract – The objectives of this paper are to describe the fish assemblages in French reservoirs and to relate them to the sites' characteristics. The results of 43 fishing surveys were collected and completed with environmental descriptors. Fish assemblages differ between salmonids-dominated mountain sites and lowland ones. The latter show higher species diversity and a distinction between rheophilic- and limnophilic-type communities. This distinction can be explained by the reservoir age, location in the catchment and depth. The response of fish communities to these variables was investigated by canonical correspondence analysis. It shows that rheophilic species are typically abundant in upper basin, deep and recently created reservoirs. The fish community response to the aging process corresponds to an addition of lowland standing waters species and an extinction of the native riverine ones. The structuring role of the sites' depth, location and age is discussed, considering their relationship with the water body trophic status.

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Key words: ageing process; environmental variables; fish community; France; reservoir

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Due to its geological and climatic history, the French territory has few lakes. The construction of dams in the past decades considerably increased the potential fish yield from freshwater bodies. These environments now sustain recreational fisheries which locally represent an important source of revenue in rural regions. However, the management of these fisheries, based on stocking and species introductions, is seldom efficient (Argillier et al. 2002) due to insufficient knowledge of these systems functioning. Yet few studies have investigated the relationship between European reservoir fish communities and site characteristics. The purposes of the present paper are to investigate the patterns of fish communities in French reservoirs and to identify the parameters structuring them. This requires a wide-scale community-level approach in order to detect general trends that cannot be assessed either by case studies or by species focused works (Tonn & Magnuson 1983).

The site → reach → catchment hierarchy proposed for rivers (Imhof et al. 1996) helps define the different scales of interactions governing freshwater systems. The dependence of riverine fish assemblages upon the catchment, natural and human features is now established (Marsh-Matthews & Matthews 2000). Lake fish fauna follows similar patterns (Jackson & Harvey 1989). Fish habitat characteristics also depend, at the lake scale, on its morphometry (Hondzo & Stefan 1996), macrophyte cover (Eadie & Keast 1984) and internal biochemical processes (Matthews 1998). The presence of deep areas favors the development of a pelagic fish community (Stefan et al. 1995), whereas the lake shoreline features condition the type of habitat available for littoral species (Eadie & Keast 1984; Mandrak 1995). Despite their apparent similarities, reservoirs cannot be considered as natural lakes due to numerous functional differences. Wetzel (1990) provides a comparative overview of how these systems function. The specificity of reservoirs essentially originates in their location in the catchment area with low hydraulic residence time and high organic, particulate and nutrient input loads. Dam operation also generates irregularly pulsed level fluctuations and water movements. These conditions lead to severe pressure on the living communities.

Major efforts have to be made to collect important datasets so that general trends in fish associations can be detected and related to the water bodies descriptors. This type of work was therefore carried out in few areas of the world and most of the cited literature originates from northern America. However, Godinho et al. (1998) showed the preponderance of longitudinal variables (elevation and temperature) and their correlates (rainfall) in structuring fish communities from Portuguese reservoirs. Similar observations were made earlier on riverine systems (Huet 1949; Illies & Botosaneanu 1963). The River Continuum Concept (Vannote et al. 1980) provides an energy-based framework to the biota distribution. Typically, the fish species richness increases downstream the river course (Oberdorff et al. 1993), resulting in a combination of zonation and downstream addition of species (Rahel & Hubert 1991). These similarities suggest that the processes governing reservoir fish communities could be midway between those occurring in lakes, as a result of an isolation limiting immigration possibilities (Magnuson et al. 1998) and the riverine continuity.

Materials and methods

The dataset

The dataset pools the information collected over 30 years for the needs of case studies. The sources are fully listed in Pronier (2000). Most of the 43 study sites are located in south-eastern France (Fig. 1), where the landscape is favorable to hydroelectric power generation. The main characteristics of these artificial lakes are summarized in Table 1. They represent a variety of environmental conditions (Table 2).

Ichtyological data were collected during either impoundment draining for dam investigation or gillnetting surveys. These surveys were carried out using two different sampling schemes. The first one is mostly empirical, relying on the setting of horizontal gillnet series overnight with knot-to-knot mesh sizes ranging from 10 to 60 mm in geometrical progression. The sampling sites are chosen so that the whole water column may be prospected and to cover most of the habitats diversity. The second methodology uses vertical gillnet series in the deep areas, whereas the littoral zone is sampled with multimesh gillnets. The nets are then set for approximately 24 h. These two methods proved to be equally efficient in terms of accuracy on species diversity and show overall similar distributions on the relative abundance of species (Irz 1998). The efficiency of both gillnetting methods was successfully compared with a total census of the standing stock on the occasion of the total draining of La Raviège and Treignac reservoirs (unpublished data).

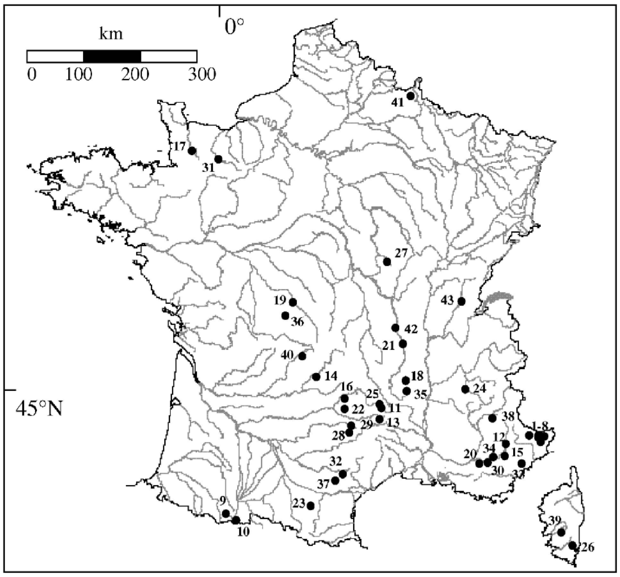

Fig. 1. Location of the 43 study sites on the French hydrographic network. The site numbers refer to Table 1.

From the overall 37 species present in the samples, only 22 were common enough to be kept for the analysis. The species that were omitted were either sparse (less than five occurrences) or not properly sampled by gillnetting. Some related species with similar habitat requirement were pooled into a single group (Table 3). The numerical relative abundance (RA) of each species was calculated as the ratio of the number of individuals per species versus the number of fish caught during the survey. These abundances were then encoded into three categories corresponding to the absence, low abundance, and high abundance of the species. The cut-off level between low and high abundances is the median relative abundance.

Environmental descriptors were chosen among the parameters available in the database. They were selected from the existing bibliography for their relevance in structuring fish communities.

Table 1. Main characteristics of the studied reservoirs. Each reservoir is coded with three letters corresponding to its name and a number corresponding to a French administrative department.

Map number	Code	Name	River basin	Area (ha)	Altitude (m)	Mean depth (m)
1	BAS06	Basto	Coastal south	24	2341	5.9
2	CAR06	Carbon	Coastal south	6	2179	5
3	FOU06	Fourcat	Coastal south	4.5	2165	2.6
4	LLS06	Lac long sup.	Coastal south	12	2111	6.5
5	LMO06	La Muta	Coastal south	8	2274	5
6	NOI06	Noir	Coastal south	11	2278	4.7
7	TRE06	Trécolpas	Coastal south	1.4	2150	2.5
8	VER06	Vert	Coastal south	15	2221	7.1
9	CDL65	Cap de long	Garonne	118	2161	45
10	ESC65	Escoubous	Garonne	2	2235	3.5
11	ARM48	Mas d'Arman	Loire	12	1000	4.5
12	CAS04[a]	Castillon	Rhône	450	880	33.1
13	CHA19	Chastang	Dordogne	538	262	34.7
14	CHA48	Charpal	Garonne	180	1320	4.5
15	CHO04	Chaudanne	Rhône	70	790	22.8
16	COU12	Couesque	Garonne	260	290	21.6
17	DAT14	Dathée	Coastal north	44	160	2.5
18	DEV07	Devesset	Rhône	50	1074	4.74
19	EGU36	Eguzon	Loire	270	202	16
20	ESP04	Esparron	Rhône	330	360	24.24
21	GRA42[a]	Grangent	Loire	365	420	15.7
22	MAU12	Maury	Garonne	160	588	20.6
23	MON11	Montbel	Garonne	585	400	18
24	MON38	Monteynard	Rhône	657	490	41.87
25	NAU48	Naussac	Loire	1050	1000	18
26	OSP2A	L'Ospédale	Coastal south	42	949	6.8
27	PAN58	Pannecière	Seine	520	324	15.86
28	PAR12	Pareloup	Garonne	1260	805	12.5
29	PDS12	Pont de Salars	Garonne	190	720	10.8
30	QUI04[a]	Quinson	Rhône	191	404	20
31	RAB61	Rabodanges	Coastal north	97	125	4.64
32	RAV34	La Raviège	Garonne	439	662	10.2
33	SCA83	Saint-Cassien	Coastal south	374	147	16
34	SCR04[a]	Sainte-Croix	Rhône	2182	477	50
35	SMA07	Saint-Martial	Rhône	13	830	5
36	SPA87	Saint-Pardoux	Loire	330	360	7
37	SPE81[a]	Saint-Peyres	Garonne	211	670	16.43
38	SPO05	Serre-Ponçon	Rhône	3200	780	37.5
39	TOL2A	Tolla	Coastal south	115	560	30
40	TRE19	Treignac	Dordogne	101	513	7.4
41	VFO08	Vielles Forges	Meuse	136	320	3.3
42	VIL42	Villerest	Loire	800	316	22
43	VOU39[a]	Vouglans	Rhône	1600	429	37.8

[a] Sampled twice.

Table 2. Summary of the environmental characteristics of the studied reservoirs.

Parameter	Mean	SD	Range
Altitude above sea level (m)	947	753	125–2341
Distance to source (km)	36	47	0–177
Catchment area (km^2)	784	1435	1–6520
Lake area (ha)	396	632	1–3200
SLDF[a]	3.20	1.87	1.04–8.50
Perimeter (km)	22	23	0.1–107.0
Water level range (m)	12	15	0–60
Mean depth (m)	16	13	3–50
Reservoir age (years)	35	31	4–71

[a] Calculated as: $/\sqrt{4\pi\times\text{surface}}$.

Only long-term stable parameters were taken into account in order to provide a secondary source of data when the database was incomplete. This includes large-scale as well as local parameters (Table 2). The large-scale parameters, related to the position of the reservoirs in the watershed, were measured from 1/50 000th to 1/1 000 000th digitized topographical maps using Autocad® software. The lakes' area and perimeter were measured on 1/25 000th maps. These two parameters allowed to calculate the shoreline development factor (SLDF) characterizing the reservoir shape and ranging from 1 (round lake) to over 10 when the perimeter is very long when

Table 3. Species occurrence, frequency, average numerical relative abundance (RA) and average RA excluding the absence cases.

Common name	Group code	Species	Frequency (%)	Average RA (%)	Average RA when present (%)
Barbel	BAR	*Barbus barbus*	18	1.0	5.3
Black bullhead[a]	BBH	*Ictalurus melas*	13	1.4	11.1
Bleak	BLK	*Alburnus alburnus*	36	2.9	8.0
Bream	BRE	*Abramis brama* *Blicca bjoerkna*	44	5.3	12.1
Brown trout	BWT	*Salmo trutta fario* *S. trutta lacustris*	64	14.7	23.0
Common carp[a]	CAR	*Cyprinus carpio*	49	0.8	1.6
Chub	CHU	*Leuciscus cephalus*	54	2.8	5.3
Dace	DAC	*L. leuciscus* *L. leuciscus burdigalensis*	18	0.3	1.5
French nase	FNS	*Chondrostoma toxostoma*	13	0.8	6.4
Gudgeon	GUD	*Gobio gobio*	33	1.6	4.8
Perch	PER	*Perca fluviatilis*	72	13.3	18.1
Pike	PIK	*Esox lucius*	54	0.4	0.7
Pikeperch[a]	PKP	*Stizostedion lucioperca*	33	1.3	3.9
Pumkinseed[a]	PUM	*Lepomis gibbosus*	18	0.2	1.2
Rainbow trout[a]	RBT	*Oncorhynchus mykiss*	46	10.4	22.5
Roach	ROA	*Rutilus rutilus*	72	34.0	47.3
Rudd	RUD	*Scardinius erythrophthalmus*	36	3.0	8.5
Ruffe	RUF	*Gymnocephalus cernua*	21	0.6	3.0
Tench	TEN	*Tinca tinca*	62	1.6	2.6

[a] Introduced species.

the area is considered. The reservoir mean depth and the water level range, considered as the difference between the highest and lowest exploitation levels, were obtained from the dam operators.

Data processing

The relationship between fish diversity (i.e. the number of species present in each site) and several parameters was firstly studied by bivariate linear regression.

Further analyses, apart from the design of a longitudinal gradient index, were only carried out on the 33 reservoirs below 1500 m in altitude because all the fish populations in mountain lakes result from species introductions. Multivariate analysis was carried out using ADE-4 software (Thioulouse et al. 1997).

The faunal and environmental matrices were then analyzed separately. A correspondence analysis (CA) was processed on the species abundance indexes in order to identify the structure of the assemblages. The significance of between-species associations were then tested using Spearman correlation.

The environmental descriptors were submitted to a standardized principal components analysis (PCA) to study the correlation between these variables. This analysis of the environmental matrix allows selection of the variables providing the best description of the reservoirs for further analysis. Careful selection avoids most of the redundancy between the selected descriptors. A second PCA was then processed on the most correlated and redundant variables. The decomposition of the site scores on the first two components of the PCA enabled clustering of the sites and thus to summarize these parameters into a single ordinal variable.

The relationship between the selected environmental descriptors and the fish communities was investigated by means of canonical correspondence analysis (CCA) (Ter Braak 1986). CCA is an ordination method that selects a series of linear combinations of environmental variables called canonical axes, which are uncorrelated. This method was designed to relate the dispersion of the species to the environmental descriptors. Therefore, it meets the needs of community ecologists and was successfully used in aquatic research (Dolman 1990; Godinho et al. 2000). It is a nonsymmetric approach that provides an assessment of the faunal inertia that is explained by environmental variables. The main result of the CCA is an ordination diagram displaying the pattern of community variation (reservoirs and species) along the environmental variables (Ter Braak 1987).

The method possesses specific properties to deal with the nonlinear relationship between the taxa abundance and environmental gradients

(Ter Braak 1986). It also performs well in the case of a large set of response variables (Prodon & Lebreton 1994), even when strongly correlated (Ter Braak 1987). The limited number of data available led us to retain only four explanatory descriptors chosen in the light of the initial PCA. This choice avoids the awkward interpretation of the results when numerous descriptors are correlated and ensures a tight restriction of the species scores by the explanatory variables.

The stability and significance of CCA results was assessed by a Monte Carlo test. This test is nonparametric and is based on random permutations of the lines of the observed faunal matrix. A value of the part of faunal inertia due to the environment is calculated for each combination and allows the validation of the observed explained value with simulated values (Efron 1982).

Results

Species occurrence

The species most frequently observed in the fish assemblages are, in decreasing order of occurrence, perch, roach, brown trout, tench, pike and chub (Table 3). The dominant species in these assemblages are roach and perch, which indicates their aptness for reservoir environments. Some of the more widespread species, such as carp and pike, always remain at a low relative abundance.

Species diversity

Species diversity was plotted against each environmental variable which were previously log-transformed. The correlation was significant for the catchment area, reservoir area, distance to the source and mean depth (Fig. 2). The best descriptors to predict the number of species in a reservoir are the reservoir area ($R^2 = 0.67$) and its watershed area ($R^2 = 0.54$). No continuous relationship was found between fish diversity and altitude, though the average diversity significantly differ ($P < 0.001$) between lowland (below 1500 m; mean = 9.1 species) and mountain sites (mean = 1.8 species), which confirms that fish assemblages follow different patterns below and over the 1500 m elevation threshold.

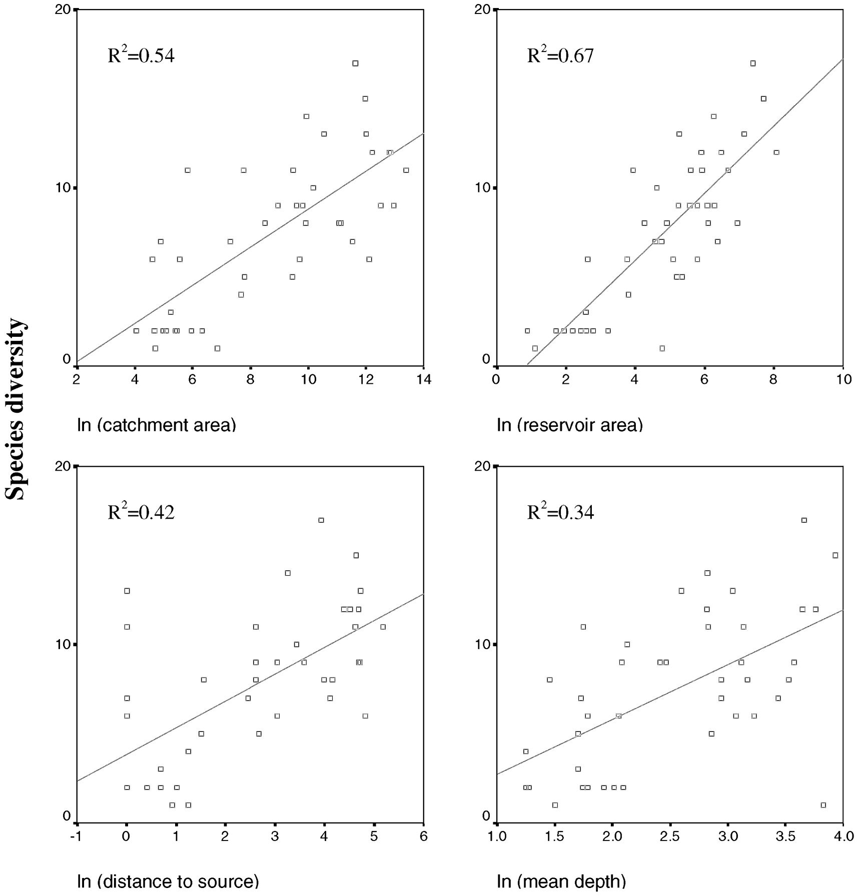

Fig. 2. Regression scatterplots of species diversity vs. the statistically significant variables.

Fish assemblages below 1500 m

The CA first axis clearly discriminates two types of fish communities (Fig. 3). The first one is composed of gudgeon, barbel, brown trout, French nase, chub and rainbow trout. These species are rheophilic and could originate from the riverine assemblages before the construction of the dams. The second group stretched along the second axis can be extended to the 13 other species, among which roach, perch, rudd and pike, i.e. limnophilic species are the most frequent. The opposition between tench, carp and pikeperch on one side, bream and bleak on the other side is difficult to interpret at this stage.

The between-species correlations confirm these results (Table 4). It shows the strong correlation among the first group of species, whereas the second group displays fewer significant correlations. The corresponding species represent an opposition to the first group but cannot be interpreted as a real assemblage due to their low co-occurrence rate.

Environmental descriptors of lowland sites

The PCA carried out on the environmental parameters provides an overview of their organization (Fig. 4). The correlation matrix is given in Table 5. Depth, water level range, perimeter and reservoir area, all site-scale characteristics, appear correlated. These parameters represent the size of the lake. The catchment area and the distance to the source are positively correlated, and opposed to the altitude. This opposition summarizes the location of the sites in the catchment. SLDF is simultaneously correlated to site-scale descriptors and to the location in the catchment. Mountain water bodies are close to the river source and typically round-shaped (low SLDF), with a small catchment area. These parameters increase for downstream sites. Reservoir age is independent from all the other parameters.

Design of a longitudinal gradient index

Considering the strong correlations cited previously and the need to limit the number of explanatory variables for the CCA, a single longitudinal gradient index was searched for by means of PCA. The input parameters, altitude, distance to the river source, and catchment area, describe the location of the reservoirs on the hydrographic network.

The distribution of the 43 sites on the first two dimensions of the PCA enables the construction

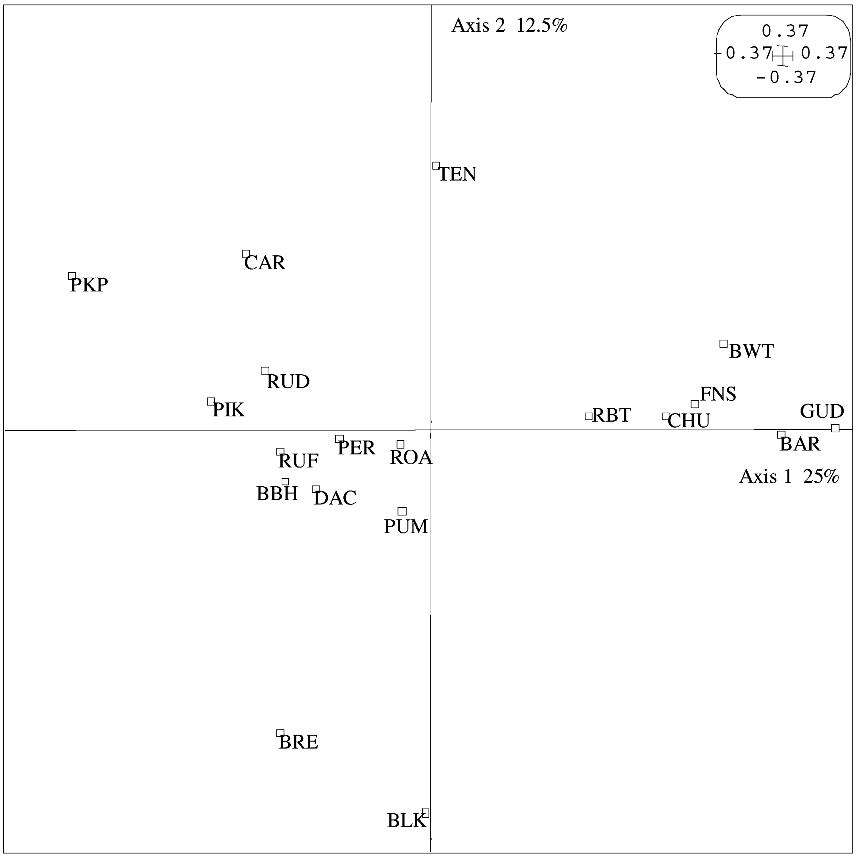

Fig. 3. Position of the fish taxa on the first two axis of the CA carried out on lowland sites ($N = 33$). The labels refer to Table 3.

of a longitudinal gradient index. This synthetic ordinal variable comprises five gradient classes, each corresponding to a group of reservoirs on the PCA diagram (Fig. 5). The fifth category contains all the mountain reservoirs.

The distribution of the environmental descriptors along the longitudinal gradient index is displayed in Fig. 6. These boxplots reveal the meaning of this index about altitude, distance to source and catchment area that were used to construct it. It also shows the homogeneous features of high-altitude reservoirs, apart from their age. It also appears that the index is correlated to SLDF, perimeter, and reservoir area. The longitudinal distribution of the sites also corresponds to strong morphological trends that oppose large, complex-shaped lowland reservoirs to small, round-shaped mountain ones. When class 5 sites are not considered, water level range ($P = 0.22$) and reservoir age ($P = 0.18$) are independent from the index, whereas it remains negatively correlated to the mean depth ($P < 0.001$).

The occurrence rate of the fish species can be plotted against the gradient index (Fig. 7). This gradient provides a good explanation for the distribution of some species. Bleak and bream occur mainly in lowland sites (1–3). On the other hand, rainbow trout and brown trout are present more in the mountain sites (class 5). Some species like barbel, gudgeon, tench and French nase are obviously restricted to intermediate conditions. Roach and perch, the most widespread species in the reservoirs, are present in almost all the sites with the exception of mountain water bodies.

Table 4. Spearman correlation between the species relative abundances in lowland sites.

	BAR	BBH	BLK	BRE	BWT	CAR	CHU	DAC	FNS	GUD	PER	PIK	PKP	PUM	RBT	ROA	RUD	RUF
BBH	−0.12	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
BLK	0.23	0.06	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
BRE	0.06	0.37*	0.52**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
BWT	0.38*	−0.18	0.09	−0.10	–	–	–	–	–	–	–	–	–	–	–	–	–	–
CAR	0.05	0.05	0.00	0.22	−0.06	–	–	–	–	–	–	–	–	–	–	–	–	–
CHU	0.55**	−0.12	0.16	−0.06	0.56**	−0.21	–	–	–	–	–	–	–	–	–	–	–	–
DAC	−0.13	0.16	0.22	0.31*	−0.08	0.01	0.03	–	–	–	–	–	–	–	–	–	–	–
FNS	0.78**	−0.02	0.08	0.07	0.29	−0.09	0.44**	0.02	–	–	–	–	–	–	–	–	–	–
GUD	0.40**	−0.09	0.14	−0.14	0.51**	−0.32*	0.27	−0.26	0.36*	–	–	–	–	–	–	–	–	–
PER	−0.31*	−0.02	0.02	0.08	−0.36*	−0.19	−0.14	0.01	−0.24	−0.32*	–	–	–	–	–	–	–	–
PIK	−0.09	0.03	0.12	0.19	−0.41**	0.28	−0.26	0.22	−0.13	−0.31*	0.29	–	–	–	–	–	–	–
PKP	−0.28	0.07	0.14	0.13	−0.32*	0.41**	−0.34*	0.29	−0.43**	−0.44**	0.08	0.22	–	–	–	–	–	–
PUM	0.02	0.14	0.22	0.37*	0.03	0.04	0.03	0.28	0.16	−0.06	0.15	0.01	−0.01	–	–	–	–	–
RBT	0.27	0.00	−0.05	0.06	0.29	0.04	0.12	−0.06	0.51**	0.29	−0.14	−0.15	−0.37*	0.32*	–	–	–	–
ROA	−0.06	0.12	0.11	0.10	−0.20	0.09	−0.24	0.26	−0.04	−0.08	−0.30*	0.17	0.13	−0.10	−0.08	–	–	–
RUD	−0.04	0.37*	0.07	0.28	−0.24	0.17	−0.11	−0.14	−0.08	−0.12	0.27	0.21	0.17	0.14	−0.06	−0.46**	–	–
RUF	−0.25	0.14	0.16	0.34*	−0.30*	0.22	−0.27	0.13	−0.13	−0.06	0.29	0.19	0.24	−0.01	−0.18	0.14	−0.03	–
TEN	0.06	−0.05	−0.16	−0.16	0.23	0.36*	0.05	0.02	0.13	0.01	−0.35*	0.02	0.14	0.03	−0.01	−0.05	0.07	0.03

*Correlation is significant at the 0.05 level.
**Correlation is significant at the 0.01 level.

Ordination of fish communities restricted by environmental descriptors

Only four variables were kept for the CCA. The longitudinal gradient index is the single large-scale input parameter, whereas mean depth, water level range and reservoir age characterize the water body itself. These descriptors were chosen to remove most of the redundancy in the data as well as to limit the number of explanatory variables.

A Monte Carlo test ($P < 0.001$, 1000 permutations) proves the significance of the analysis. It reveals that the four descriptors explain 20% of the variability within the fish assemblages (Table 6). The abundance of four species is well explained by the descriptors. Among these, barbel, French nase, and pikeperch are segregated along the first axis of the CCA biplot (Fig. 8). This axis accounts for 47% of the explained variability and can be interpreted by reservoir depth. The

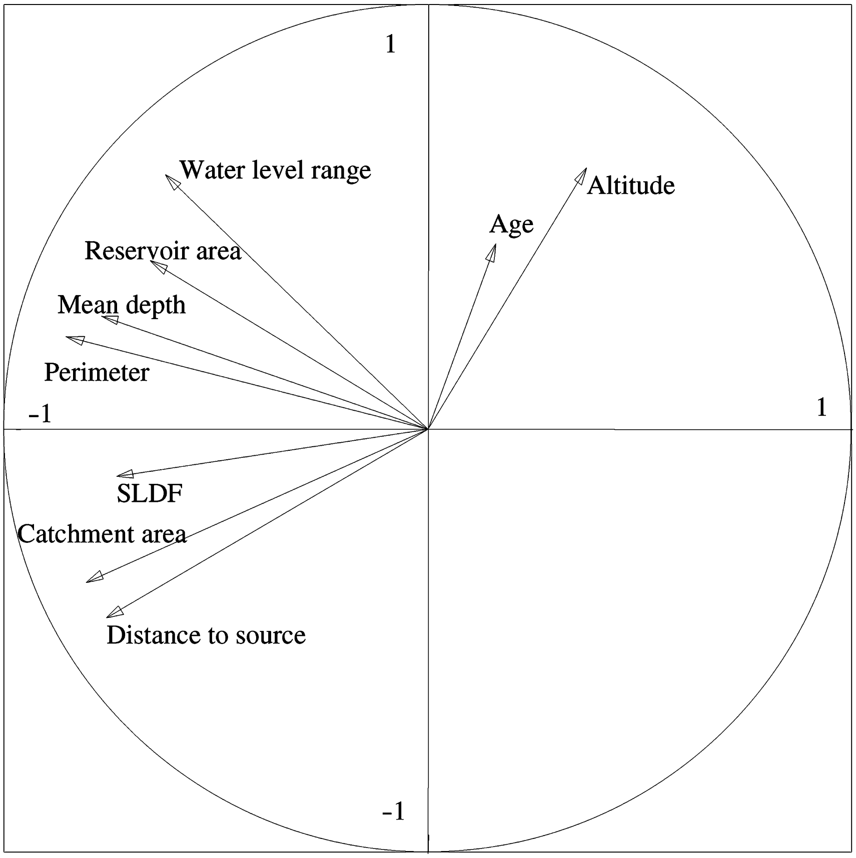

Fig. 4. Correlation circle of the PCA carried out on the environmental descriptors of 33 lowland sites.

abundance of French nase and barbel is positively correlated with this variable, whereas pikeperch populations are more abundant in shallow reservoirs. Depth is therefore the main parameter structuring the fish communities in the studied reservoirs. Along the second axis, which represents 26% of the explained variability, the longitudinal gradient is opposed to the age of the reservoir. These variables were not correlated during the previous analysis. These independent descriptors have an opposite effect on the fish assemblages. Bleak is more abundant in old and/or lowland reservoirs, whereas rainbow trout develops in young and/or elevated ones. The age since first filling also has an effect on pikeperch which is most abundant in old water bodies. The group of rheophilic species observed in correspondence analysis (RBT, FNS, BAR, BWT, and

Table 5. Correlation matrix resulting from the PCA carried out on the environmental descriptors of 33 lowland sites.

	Distance to source	Altitude	Catchment area	Reservoir area	SLDF	Water level range	Mean depth	Reservoir age	Perimeter
Distance to source	1.00								
Altitude	−0.43*	1.00							
Catchment area	0.85**	−0.30	1.00						
Reservoir area	0.30	0.03	0.38*	1.00					
SLDF	0.49**	−0.40*	0.56**	0.16	1.00				
Water level range	0.17	−0.02	0.25	0.43*	0.42*	1.00			
Mean depth	0.55**	−0.16	0.47**	0.64**	0.30	0.65**	1.00		
Reservoir age	−0.17	0.15	−0.26	−0.20	0.10	0.19	−0.14	1.00	
Perimeter	0.41*	−0.18	0.56**	0.65**	0.80**	0.57**	0.50**	−0.05	1.00

*Correlation is significant at the 0.05 level.
**Correlation is significant at the 0.01 level.

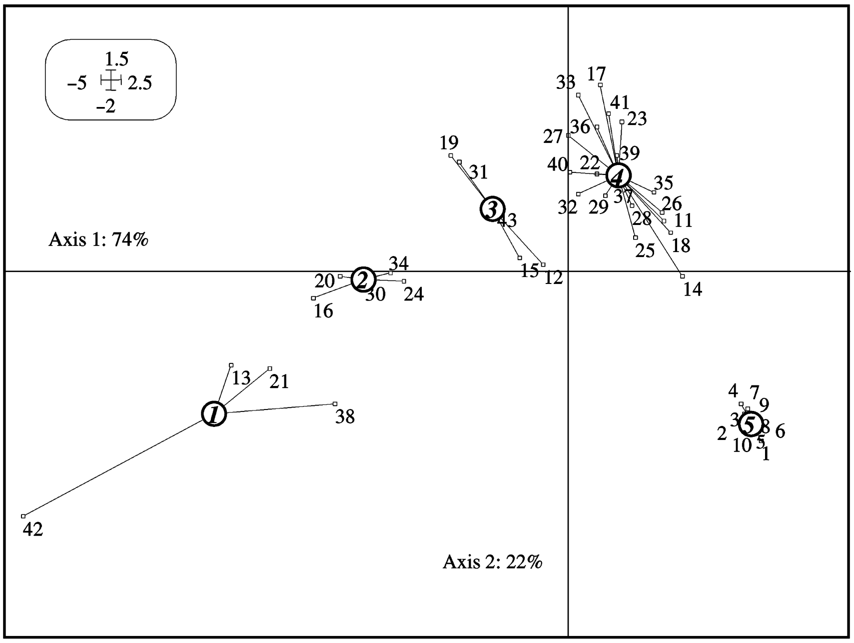

Fig. 5. Reservoirs scatterplot resulting from the PCA on the sites altitude, catchment area and distance to the source. The number inside each circle represents the inertia center of a class of gradient. The site numbers refer to Table 1.

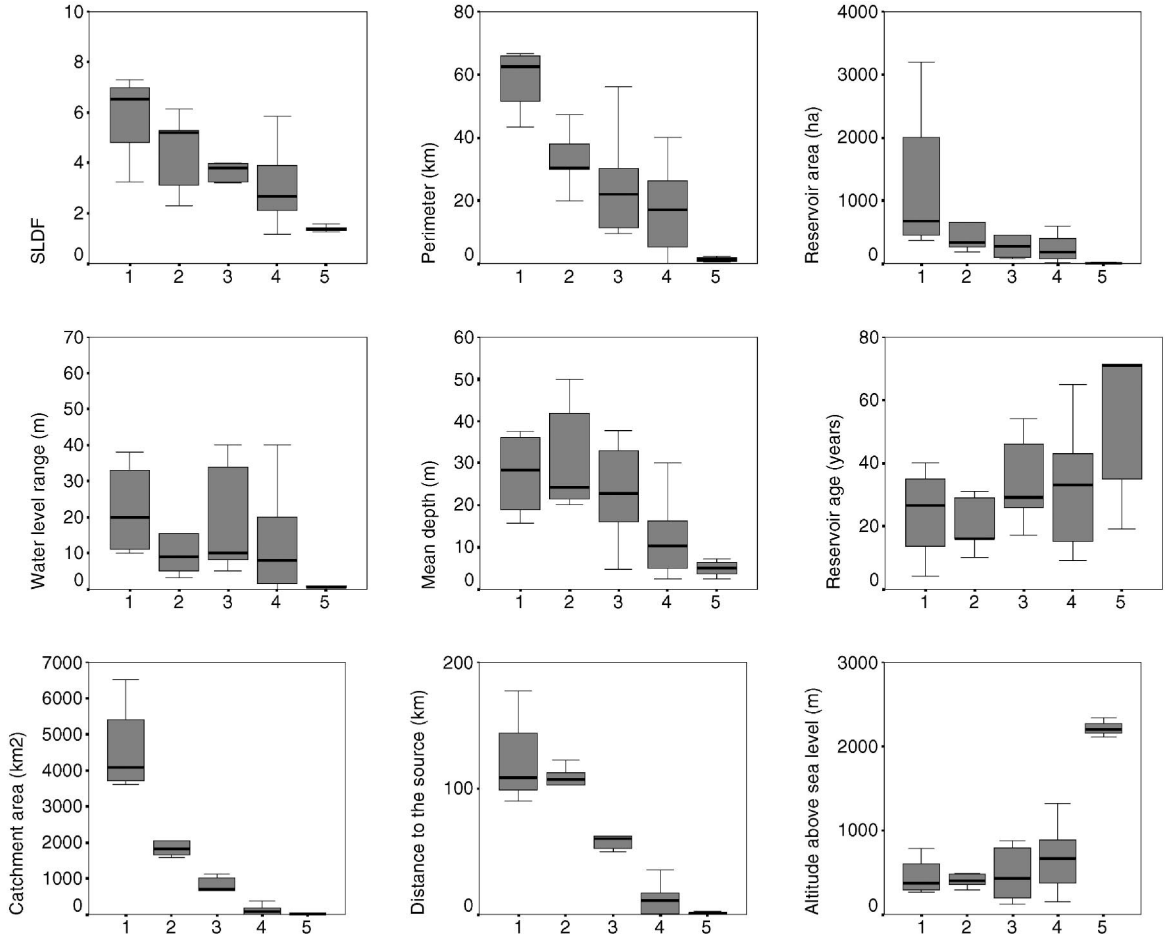

Fig. 6. Boxplot representation of the geographical and morphological signification of the longitudinal gradient index.

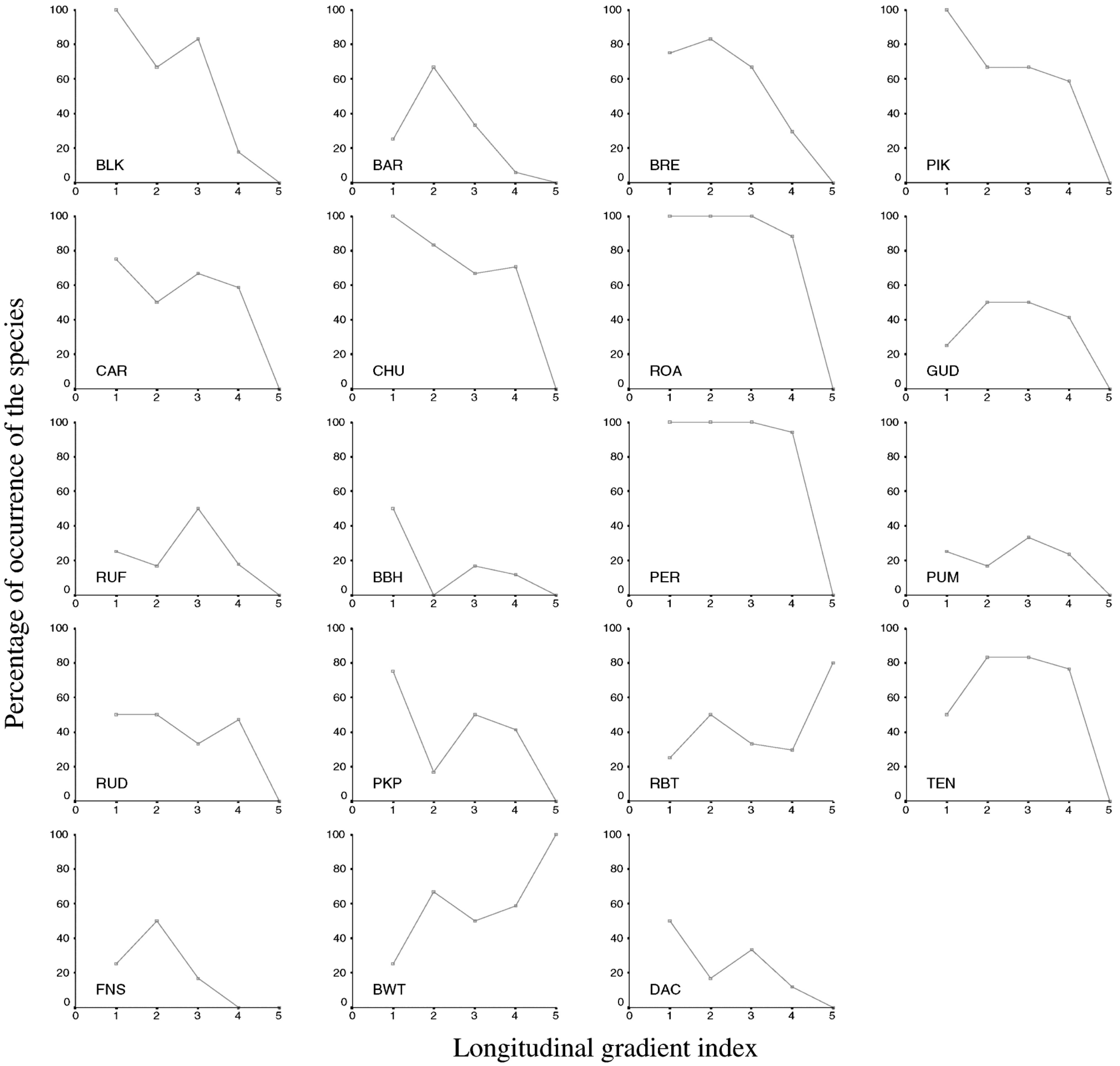

Fig. 7. Occurrence rate of the species along the longitudinal gradient.

GUD) appears characteristic of young reservoirs. The variation in abundance of perch is partly explained by the descriptors (27% of the variability explained). Its position on the biplot suggests that it is a species of intermediate longitudinal gradient and reservoir age. Water level range does not appear to be a good structuring variable for this dataset.

Discussion

The dataset processed in the present study reveals general patterns of the fish assemblages encountered in French reservoirs.

The observed taxa associations can be clustered into three types that are mountain sites, recently built lowland reservoirs, and older lowland reservoirs. The latter group is much more heterogeneous than the other two. The communities are influenced by local and regional parameters, and whereas reservoir morphology influences the abundance of particular species, large-scale descriptors tend to affect the assemblages.

The increase in species diversity with the reservoir size is coherent with the trends observed in Ontario lakes (Minns 1989) and northern Wisconsin lakes (Tonn & Magnuson 1982). This can be related to the relationship between the

Table 6. Projected inertia decomposition on a CCA subspace for the 19 species.

	Environmental subspace ($\times 10^{-3}$)	Orthogonal subspace ($\times 10^{-3}$)	Total inertia ($\times 10^{-3}$)	Explained inertia (%)
BAR	3.98	5.41	9.39	42.38
BBH	1.06	5.22	6.27	16.86
BLK	3.31	5.99	9.30	35.57
BRE	1.63	7.52	9.15	17.8
BWT	2.16	6.88	9.04	23.93
CAR	1.14	8.30	9.44	12.05
CHU	0.80	6.35	7.15	11.19
DAC	0.59	7.03	7.62	7.7
FNS	3.82	3.91	7.73	49.43
GUD	0.37	12.73	13.10	2.82
PER	1.41	3.89	5.30	26.67
PIK	1.83	7.31	9.14	20.04
PKP	4.00	7.43	11.44	35.01
PUM	0.21	7.72	7.92	2.59
RBT	2.11	4.29	6.40	32.9
ROA	0.30	4.91	5.21	5.72

water body surface area and the heterogeneity of its habitats (Eadie & Keast 1984; Benson & Magnuson 1992). The significance of the regressions between fish diversity and catchment area, distance to the source and reservoir depth should be interpreted with care, considering the numerous correlations linking these descriptors. However, the effect of the catchment size on the fish communities can be considered indirectly through the downstream increase in nutrients loads, dissolved minerals, and conductivity. The longitudinal gradient index designed on the basis of the site location descriptors could also be regarded as a temperature, a trophic or a quality gradient. This longitudinal-based structure confirms the results of Godinho et al. (1998) on Portuguese reservoirs, although the species and sites characteristics are to a large extent different.

High-altitude rivers typically sheltered no native fish populations prior to human introductions of salmonids in the Pyrénées (Delacoste et al. 1997). This can be generalized to most mountain areas in France, and fishery legislation in such sites prohibits practices tending to sustain other fish taxa. Therefore, fish communities in mountain reservoirs are more likely to reflect human actions than biotic responses to environmental conditions.

Depth is the main parameter structuring fish communities in reservoirs below 1500 m in altitude. This observation suggests a trophic interpretation

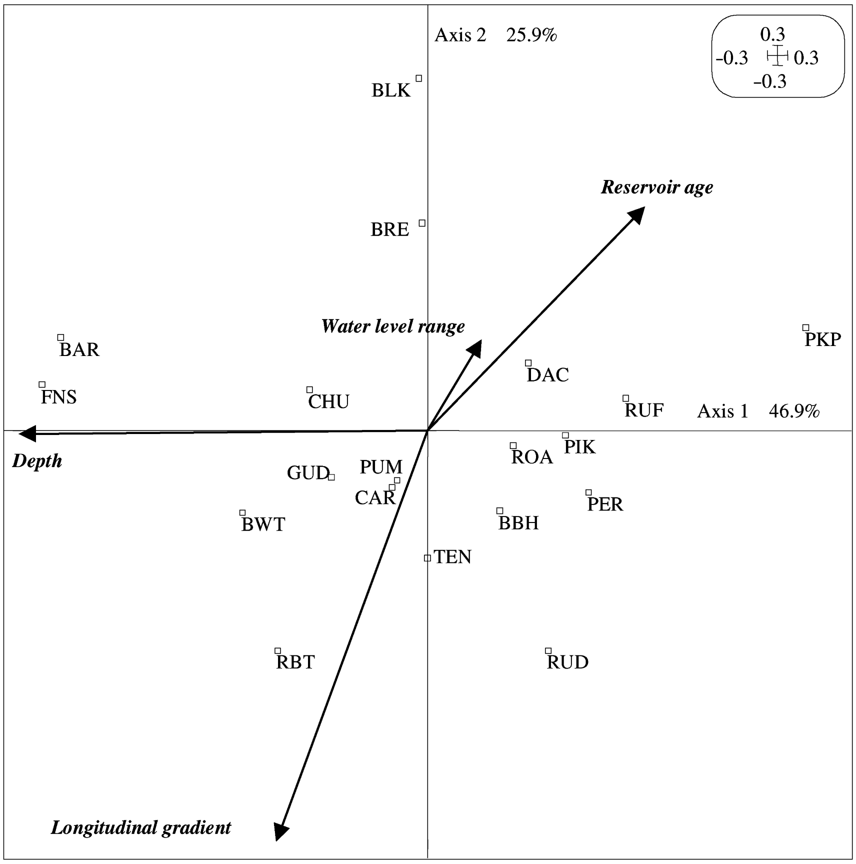

Fig. 8. CCA biplot superposing the environmental descriptors and the fish species. The scale box indicates the maximum value of the axis for the fish species. The maximum value of the axis is set to 1 for the descriptors.

related to the food resource availability. Deep water bodies submitted to temperate climate are seasonally stratified. These conditions are more favorable to pelagic fishes which are able to feed in open waters than to the benthivorous species then limited to the shallow littoral areas. Several biological and chemical processes have been shown to depend on the depth of the water body that was therefore included in the expression of synthetic models to assess the trophic status or to predict fish yield (Ryder et al. 1973). This interpretation of the effect of depth on fish communities is common with natural lakes, but reservoir-specific features increase the depth effect. A deep reservoir means that the dammed river had a steep slope. These intermediate riverine systems were described by Verneaux (1981) as, from upstream to downstream, brown trout, grayling (*Thymallus thymallus* L.) and barbel zones. French nase and barbel appear to be the species performing best in deep reservoirs, accompanied to a lesser extent by chub, bleak, rainbow trout, bream, gudgeon and brown trout, whereas pikeperch, ruffe, pike and perch are most abundant in shallow reservoirs. Furthermore the strong correlation between the reservoirs mean depth and their water level range can be considered as a general characteristics of these systems. The level fluctuations, whose effects have so far been difficult to distinguish from the effects of depth, also limit the possibilities for stable and rich benthic invertebrate and macrophytic communities to colonize the substrate. Such artificial and unpredictable conditions represent severe pressure for various functions of the fish life cycle. Most of the recorded fish species feed, at least at one development stage, on benthic invertebrates (Billard 1997). Their low abundance represent a resource gap. The absence of aquatic vegetation also considerably reduces the survival of juveniles due to the lack of shelters from predators and prevents some species to reproduce in the absence of suitable spawning habitat. The last direct impact of level variations is the risk for the eggs of shallow spawners to become emerged during lowering periods.

The CCA shows that the water body depth is a better explanatory variable of the fish community than the water level range. Nevertheless, the effects of level variations should be further investigated to draw general conclusions. A more precise description of the variations, including daily and seasonal fluctuation regimes, would provide more pertinent results than the simple annual level range.

Man-made reservoirs can be regarded as particularly interesting environments due to their youth. Their rapid evolution, in comparison to natural hydrosystems, provides valuable information on the ecological successions following a major environmental disruption. Fish communities appear sensitive to reservoirs' aging process. The fish fauna of a newly built reservoir essentially originates from the dammed river. The dominant species at that stage are either rheophilic and limited to the mouth of the tributaries or come from the river pools. Few of them are generalist enough to remain competitive in a lacustrine environment. Pelagic habitats are to a large extent unexploited as these species find better living conditions in littoral shallow areas (Fernando & Holcik 1991). In most cases, the fish stock does not increase until species adapted to standing waters are introduced. Obviously, such management practices alter the natural evolution of biotic communities. Nevertheless, our observations show that the structuring role of site characteristics is not occulted by anthropogenic actions. Indeed, as shown by Argillier et al. (2002), stocking is rather inefficient in such environments. We hypothesize that species introductions do not challenge our approach, firstly because all the sites are similarly submitted to these practices, and secondly because the success of an introduced species depends on whether it meets favorable environmental conditions or not. Therefore, the abundance of the species can be regarded as a response to habitat characteristics despite stocking and introductions.

The brutal habitat disturbance due to the construction of the dam is followed by a rapid evolution in the created environment. Some authors consider three stages in this biogeochemical evolution. A short time after filling, a 'trophic upsurge' results from the nutrients' availability from inundated soils, then productivity decreases and then stabilizes at a level controlled by the external nutrients' loads from the inflow (Popp et al. 1996). In spite of the lack of water quality data, this model does not seem to fit our observations. French reservoirs appear sensitive to progressive eutrophication, the first algal blooms occurring a few decades after initial filling (unpublished data). Fish community response to these habitat alterations is quite similar to the pattern described by Kubecka (1993) with a shift from the original riverine community to cyprinids-dominated communities with important perch populations. Such a process certainly is accelerated by species introductions. The ultimate stage is characterized by the dominance of cyprinids, particularly bleak, and pikeperch that can be considered as the typical old reservoirs predator. These species are considered to be tolerant towards water quality and their adaptive ability allows their populations to develop in unstable environments. Communities therefore seem to reflect the eutrophication trend.

The opposite effect of reservoir age and longitudinal gradient index shows that the response of fish assemblages to the aging process is similar to a progressive slide towards downstream-type communities. This confirms the trophic interpretation of the observed taxa successions, considering a longitudinal productivity gradient as a general feature of riverine systems.

Conclusions

This work provides an original overview of the features of fish communities in French reservoirs and highlights the different types of factors structuring them. Though the investigations were limited to easily collectable descriptors of the studied reservoirs, the general patterns in the species associations can be interpreted functionally. In the absence of reference conditions due to their artificial origin, reservoir fisheries management does not include any conservation purposes. Species introductions are widespread and accelerate the successions while reservoirs age. Further research aiming at designing a model to predict the fish potential yield and species adaptability should require the collection of water quality data.

Resumen

1. El objetivo de este trabajo es describir los ensamblajes de peces de los embalses franceses y relacionarlos con las caracteristicas de las localidades. Los resultados de 43 muestreos fueron complementados con descriptores ambientales. Los ensamblajes de peces difirieron entre localidades de montaña dominadas por salmonidos y los de tierras bajas. Los embalses de montaña reflejan mas acciones humanas (repoblaciones e introducción de especies) que respuestas bioticas a las condiciones ambientales. Por debajo de los 1500 m de altitud, la diversidad de especies es mayor y se pueden distinguir comunidades reofilicas a limnofilicas. Esto puede estar relacionado con la edad, la profundidad y la localizacion geografica de la cuenca.

2. La respuesta de las comunidades a estas variables fue investigada a traves de Analisis de Correlacion Canónica. Los parámetros ambientales explicaron un 20% de la dispersión de las especies. Las comunidades estan influenciadas por parametros locales y regionales. Mientras que la morfologia del embalse determina la abundancia de algunas especies, descriptores a gran escala tienden a afectar a los ensamblajes. Las especies reofilicas son tipicamente abundantes en las cuencas superiores, profundas y en los embalses recientemente creados. La respuesta de la comunidad de peces a la edad de los embalses tiende a ser la adición de especies de aguas quietas y a la extinción de especie de río. Discutimos ademas el papel estructural de la profundidad de las localidades, la edad y la localizacion, considerando estas relaciones con el estado trófico y su significado en términos de habitat.

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