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The effects of limnological features on fish assemblages of 14 Spanish reservoirs

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Abstract – The relationship of water quality and fish assemblages has been poorly documented in European reservoirs, despite being important for water management and ecological monitoring. We sampled the fish assemblages of 14 Spanish reservoirs by boat electrofishing in the littoral and multi-mesh gillnets in the limnetic zone. Simultaneously, we assembled eight physical descriptors and we measured 20 water quality features of the reservoirs. Multivariate analysis (ordination methods and generalised additive models) showed that altitude and trophic state (indicated by chlorophyll or nutrient concentrations) independently explained most of the variation of fish assemblages in these reservoirs. The most eutrophic reservoirs were dominated by common carp (*Cyprinus carpio*) whereas oligotrophic reservoirs presented other fish species intolerant to pollution rather native (such as brown trout, *Salmo trutta*). The absolute and relative abundance of common carp was strongly related to the trophic state of the reservoir and 40% of its variation was explained by total phosphorous concentration. Despite clear changes in species composition, there was no significant effect of water quality on overall fish richness or Shannon's diversity, suggesting that for such low richness assemblages species composition is a better indicator of cultural eutrophication of reservoirs than fish diversity.

Key words: fish community; water quality; trophic state; Iberian Peninsula; reservoir

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

Introduction

Reservoirs are of high ecological, economic and recreational importance. The assessment of water quality in reservoirs is essential because they are often one of the main sources of water for human consumption and irrigation. The implementation of the EU Water Framework Directive (Directive 2000/60/EC of the European Parliament and of the Council) urges to understand the response of ecological communities to degradation of water quality. The knowledge of fish ecology in European reservoirs is quite limited, particularly compared to that of natural lakes, and mostly comes from Eastern Europe (Kubečka 1993; Kubečka et al. 1998; Seda et al. 2000). Despite their apparent similarities, reservoirs present numerous functional differences with natural lakes that hinder their comparison (Wetzel 1990). Reservoirs have larger inputs of nutrients and particulate matter and stronger water-level fluctuation than natural lakes that lead to eutrophication and stress on their ecological communities.

Although several large natural lakes in Europe are well monitored and studied (Paxton et al. 1999; Gassner et al. 2003; Perga & Gerdeaux 2003), there are few studies directly relating water quality and fish assemblages in reservoirs (Godinho et al. 1998; Irz et al. 2002b). Moreover, although indices of biotic integrity are well developed in streams (Hughes & Oberdorff 1999; Oberdorff et al. 2002) and have been adapted to some U.S. reservoirs (Hickman & McDonough 1996; McDounough & Hickman 1999), the few studies available in lakes show that many of the traditional fish metrics do not respond well to known

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anthropogenic perturbation and will need considerable modification and validation (Schulz et al. 1999; Wanzenböck et al. 2002; Gassner et al. 2003). Therefore, studies directly relating fish assemblages and water quality in European reservoirs are urgently needed, particularly in countries such as France (Irz et al. 2002a) or the Iberian Peninsula, where there are numerous reservoirs but few natural lakes (except in high mountains above 1500 m of altitude).

More than 1200 large reservoirs are in use in Spain, mostly built in the second half of the 20th century and controlling about 40% of the total freshwater flow (Riera et al. 1992; Granado-Lorencio 1992). About 70% of Spanish reservoirs were eutrophic or hypereutrophic by 1992 (Alvarez Cobelas et al. 1992). The general limnology of many reservoirs is well known, including several comprehensive regional studies (Margalef et al. 1976; Riera et al. 1992), but they have generally not included the fish community, owing to methodological and financial constraints. Conversely, although there are several studies of reservoir fish, mostly on aspects of growth, reproduction or diet of fish in a single reservoir, very few relate them to water quality data (Granado-Lorencio et al. 1985; Sancho Royo & Granados Lorencio 1988). The response of fish assemblages to variation in water quality in Spanish reservoirs is thus largely unknown. The objective of our paper is to analyse the response of the fish populations at the community level to the variation in limnological features in a diverse set of contrasting reservoirs in northeastern Spain.

Methods

We studied the limnology and the fish assemblage of 14 reservoirs in Catalonia (Table 1), including some of the largest in Catalonia (Riba-roja, Sant Antoni, Susqueda, Escales, La Baells) and also some small reservoirs (Santa Fe, Riudecanyes, Foix) from small, coastal watersheds (Fig. 1). The main physical and limnological features of the reservoirs are summarised in Table 1. For each reservoir, we assembled the following general features: altitude, water capacity, age (construction year), watershed surface, reservoir surface, water storage at the sampling period, mean water storage the year before sampling and residence time of water.

We studied water quality in a sampling point always located at the principal axis of the reservoir and *ca.* 100 m from the dam from 29 January to 16 May 2003 (one day per reservoir). In every sampling point we made a physical profile from the surface to the bottom with a multi-probe and we collected integrated water samples (0–8 m) for phytoplankton pigment analysis, using a plankton tube sampler. In the field, we measured temperature, conductivity, pH, redox potential, oxygen saturation and concentration, light energy in the photosynthetic radiation spectrum (400–700 nm, Li-Cor LI-193 SA) and nephelometric turbidity (Turo Technology Pty Ltd., Water Quality Analyser T-611, Sandy Bay, Tas., Australia) at 0 m of depth and we took a water sample for chemical analysis. We also measured Secchi disc depth.

At the laboratory, the surface water sample was analysed for suspended solids, nutrient concentrations and chlorophyll *a* contents. Suspended solids were measured by filtration (Whatman GF/F glass microfibre filter of 47 mm, Brentford, UK) and drying at 60 °C during 24 h. Nutrient concentrations (total particulate nitrogen and phosphorous, soluble reactive phosphorous, nitrate, nitrite, ammonium, chloride, sulphate and silicate) were measured by conventional spectrophotometric or chromatographic techniques. Alkalinity was measured following the Gran method (with an automatic Metrohm titration apparatus). The

Table 1. Physical and limnological features of the reservoirs studied. The water conductivity, alkalinity, total P and integrated chlorophyll refer to that of the study period. See Fig. 1 for location of the reservoir.

Reservoir name	Reservoir code	Altitude (m)	Age (years)	Basin surface (km^2)	Reservoir surface (ha)	Capacity (hm^3)	Conductivity (μS/cm)	Alkalinity (meq/l)	Total *P* (μM)	Integrated chlorophyll 0–8 m (μg/m^2)
Baells	BAE	630	28	532	367	115.4	517	3.25	1.12	7.29
Boadella	BOA	159	36	182	364	62.0	312	2.79	0.48	24.22
Camarasa	CAM	336	84	2850	624	113.0	246	1.80	1.72	12.39
Escales	ESC	821	49	152	400	154.0	213	1.77	0.41	4.09
Flix	FLI	41	56	82246	320	11.0	687	3.26	1.51	2.99
Foix	FOI	101	76	290	71	3.7	1270	4.63	10.70	443.34
Riba-roja	RIB	70	35	79177	2152	210.0	684	3.26	1.64	11.57
Riudecanyes	RIU	118	86	31	30	5.3	476	2.72	0.77	19.81
Sant Antoni	SAN	501	88	2070	927	205.0	222	1.71	1.51	6.22
Sant Ponç	SPO	530	47	318	139	24.4	431	3.00	0.34	15.17
Santa Fe	SFE	1080	71	5	6	1.0	38	0.39	0.89	110.21
Sau	SAU	425	41	1564	570	168.5	592	3.02	3.51	82.93
Susqueda	SUS	351	36	1850	466	233.0	491	2.60	2.33	21.76
Terradets	TER	372	69	2620	330	23.0	236	1.79	1.46	9.14

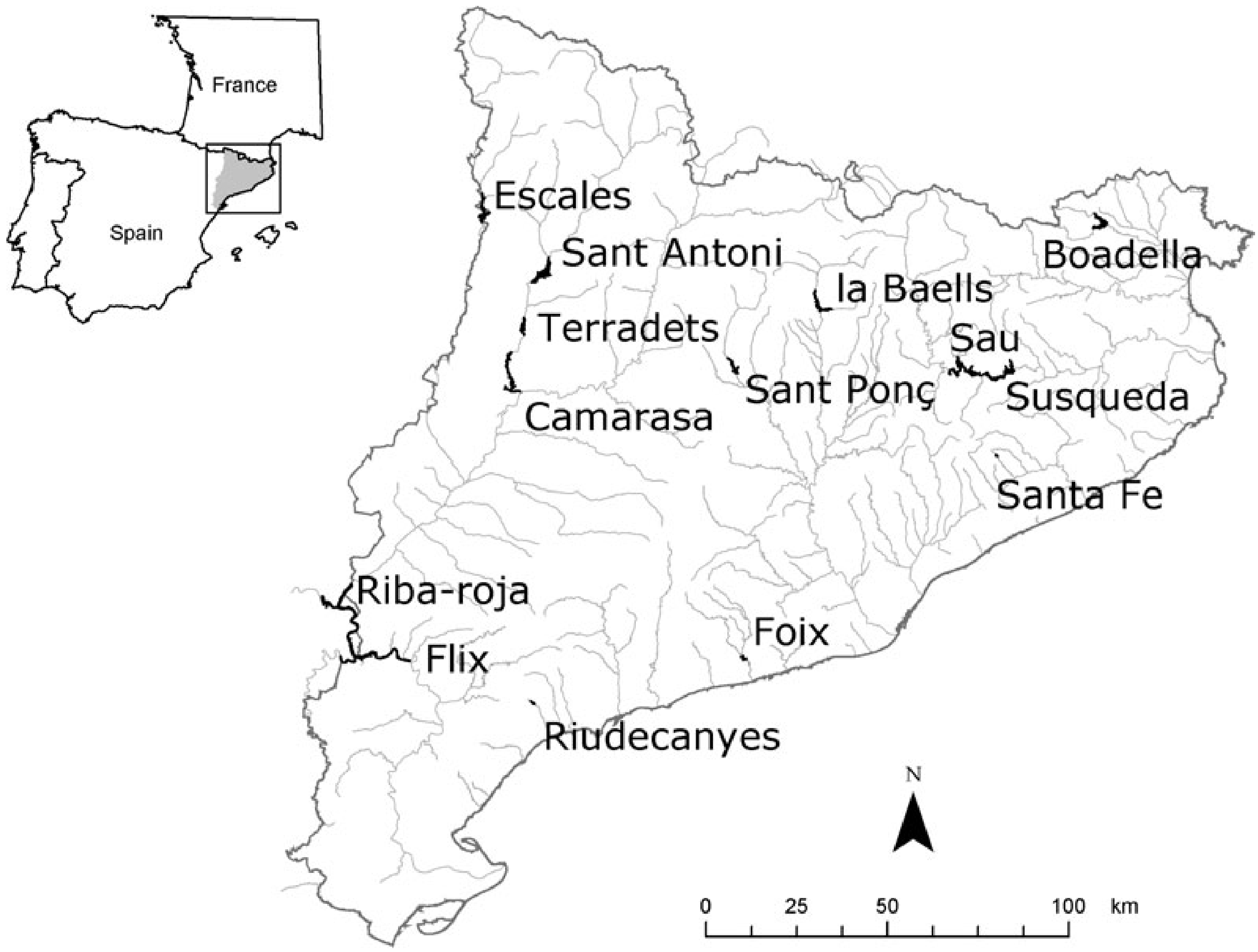

Fig. 1. Location of the 14 reservoirs studied in the Catalan river network.

chlorophyll *a* contents, collected on Whatman GF/F glass microfibre filters, was analysed by using the trichromatic method (Jeffrey & Humphrey 1975).

Fish were sampled from the 14 reservoirs from 19 February to 6 May 2003 by daylight boat electrofishing in the littoral and multi-mesh gillnets in the limnetic zone. The electrofishing boat was equipped with a 5.0-GPP Smith-Root Inc. (Vancouver, WA, USA) engine (providing up to 1000 V and 16 A) and two to nine transects of about 500–1000 m of distance were done in each reservoir depending on its size. Catch per unit effort (CPUE) of electrofishing transects was computed as the number of fish caught per electrofishing time (provided by the engine in seconds) divided by 100. For each electrofishing transect the percentage of vegetation cover and percentage of refuge were also estimated.

Multi-mesh gillnets were 50 × 1.5 m in size with 10 panels of 5 m length with meshes ranging from 31 to 260 mm (stretched mesh). Meshes were interspersed within the net (to avoid confusion of the mesh size with environmental gradients) and followed a geometric progression (to optimise efficiency). Depending on the reservoir surface, four to seven multi-mesh gillnets were set in each reservoir overnight at 10 m of depth in the water column or at the bottom. CPUE of gillnets was computed as the number of fish caught per net. A total of 3618 fishes from 19 different species (Table 2) were captured, measured (total length to the nearest millimetre) and (most of them) released.

Data analysis

The two matrices (fish abundance and limnological variables) were mostly analysed with ordination techniques. Variables were analysed with both indirect (principal component analysis or detrended correspondence analysis) and direct (canonical correspondence analysis) gradient techniques. Indirect gradient analysis only uses the species × sample matrix in the ordination whereas in direct techniques the ordination results are constrained to optimise their linear relationship to the environmental variables (usually physicochemical). Indirect and direct gradient analyses

Table 2. Fish species collected in the reservoirs studied. Figures are abundances (CPUE) with multi-mesh gillnets. Native status refers to Catalonia. '+' = species recorded by electrofishing only; '–' = species not detected in the reservoir. See Table 1 for reservoir code.

Scientific name	Species code	Common name	Native	BOA	SAU	SFE	SUS	FOI	RIU	FLI	RIB	SAN	TER	BAE	SPO	CAM	ESC
Abramis bjoerkna	ABJ	White bream	No	–	–	–	–	–	–	–	–	0.050	–	–	–	–	–
Alburnus alburnus	AAL	Bleak	No	–	1.166	–	+	0.991	–	+	+	–	–	+	0.416	0.408	0.419
Anguilla anguilla	AAN	Eel	Yes	–	–	–	–	+	–	+	–	–	–	–	–	–	–
Barbus graellsii	BGR	Barbel	Yes	–	0.068	–	0.167	–	–	–	0.159	0.907	0.808	–	–	–	0.636
Barbus haasi	BHA	Barbel	Yes	–	–	–	–	–	–	–	–	–	–	–	–	–	0.771
Carassius auratus	CAU	Goldfish	No	–	–	+	–	+	–	–	–	–	–	–	–	–	–
Chondrostoma miegii	CMI	Nase	Yes	–	–	–	–	–	0.369	–	–	–	+	–	–	–	0.711
Cyprinus carpio	CCA	Common carp	No	+	0.517	+	0.302	0.871	0.413	+	0.100	0.469	+	+	0.060	0.151	0.060
Lepomis gibbosus	LGI	Pumpkinseed	No	+	–	–	+	–	–	–	+	–	–	–	+	–	–
Micropterus salmoides	MSA	Largemouth bass	No	+	–	–	+	–	+	+	+	+	–	+	+	+	–
Perca fluviatilis	PFL	European perch	No	0.050	–	–	–	–	–	–	–	–	–	–	–	–	–
Phoxinus phoxinus	PPH	Minnow	Yes	–	–	–	+	–	–	–	–	–	–	–	–	–	+
Rutilus rutilus	RRU	Roach	No	0.413	0.697	–	–	–	–	0.301	1.107	–	–	–	–	0.080	–
Salaria fluviatilis	SFL	Freshwater blenny	Yes	–	–	–	–	–	–	–	–	–	+	–	–	+	–
Salmo trutta	STR	Brown trout	Yes	–	–	0.075	+	–	–	–	–	+	+	–	+	–	0.191
Sander lucioperca	SLU	Zander	No	0.201	–	–	–	–	–	+	0.367	0.151	0.060	0.100	–	0.100	–
Scardinius erythrophthalmus	SER	Rudd	No	–	–	–	–	–	0.556	+	–	–	–	1.105	0.095	0.100	–
Silurus glanis	SGL	Wells	No		–	–	0.050	–	–	+	–	–	–	–	–	–	–
Squalius cephalus	SCE	Chub	Yes	+	–	0.395	–	–	–	–	–	–	–	–	–	–	–

are complementary because although direct gradient analyses provide an ordination using the two matrices in a single analysis, indirect techniques are often more robust (McCune 1997) and can show species gradients because of unmeasured environmental variables. Except for principal component analysis (performed with SPSS 12), the program CANOCO 4.5 (ter Braak & Šmilauer 2002) was used for all multivariate analyses, downweighting rare species and log-transforming species abundances and most environmental variables. Canonical correspondence analysis (CCA) was used as the direct technique because a detrended correspondence analysis (DCA) showed that the first axis had a gradient length larger than four standard deviation units, suggesting a long gradient and that a unimodal response model technique was preferable. The environmental variables in CCA were selected using the forward selection of CANOCO, which tests the significance of the variables with Monte Carlo permutation tests (499 permutations).

For the environmental variables highlighted in previous analyses, we also fitted generalised additive models (GAMs) (Lepš & Šmilauer 2003), as available in the CANOCO program, to fit the response of CPUE of fish species to the environmental variables. GAMs are an extension to generalised linear models that, unlike more conventional regression methods, do not require the assumption of a particular shape for the species distribution along the environmental gradient (Lepš & Šmilauer 2003; Yuan 2004). The model complexity of GAMs was selected by the stepwise selection procedure using the Akaike information criterion (AIC), as available in CANOCO 4.5. AIC considers not only models for goodness of fit but also parsimony, penalising very complex models. Species without an adequate candidate model (e.g., rare species for which there is no evidence of response to the gradient) are automatically deleted by this procedure.

The relationship between fish diversity (total species richness and Shannon's index of diversity for both limnetic and littoral samples) with annual mean total phosphorus (P) was also assessed through linear correlation.

Results

Indirect gradient analysis

Many of the variables were interdependent and the first two axes of the PCA (Fig. 2), respectively, explained 27.4% and 21.5 % of the total variation. The strongest correlations were between conductivity, alkalinity and oxygen and nutrient concentrations: SRP-nitrite, $r = 0.84$; SRP-total N, $r = 0.84$; SRP-conductivity, 0.79 and altitude-nitrite, $r = -0.73$. These variables were all positively correlated and opposed to altitude and Secchi disc depth and mean depth. The first PCA axis summarised these correlations displaying a trophic state gradient, in part related to altitude, from the most eutrophic, lowland reservoirs (Foix, Riudecanyes, Sau and Susqueda) to oligotrophic, higher altitude reservoirs (Escales, Sant Antoni). At one extreme of the gradient, only Foix reservoir is hypereutrophic, with severe problems of cultural eutrophication owing to human activity in the drainage basin (Marcé et al. 2000).

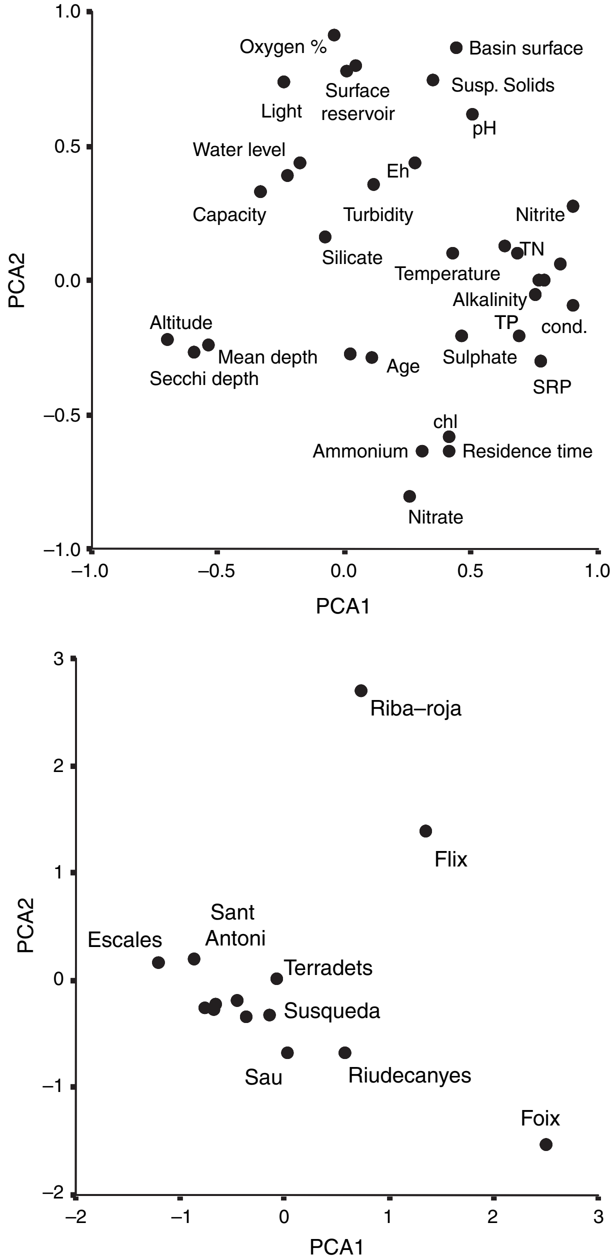

Fig. 2. Principal components analysis of limnological variables for the reservoirs studied. Top, factor loadings of the variables; bottom, reservoirs scores for the first two principal components.

The second PCA axis distinguishes the two last reservoirs from the Ebro river (Riba-roja and Flix) from the rest of reservoirs (Fig. 2). These two reservoirs, in addition to a large basin surface, display different limnological features (higher values of percentage of oxygen, light penetration, suspended sediments, turbidity, pH and lower chlorophyll concentration and residence time) because of the high water flow (Ebro is the Iberian river with most water flow), which implies high turbidity and suspended sediments but low phytoplankton production.

The first two axes of the DCA of the fish assemblages, respectively, explained 32.5% and 6.7% of the total variation and suggested a quite different ordination of the reservoirs (Fig. 3). The first DCA axis distinguished the two reservoirs where we detected chub (*Squalius cephalus*), which dominated in Santa Fe, with several other introduced species (*Rutilus rutilus*, *Perca fluviatilis*) in Boadella reservoir. The second DCA axis is similar to the first PCA axis and also distinguished the two most oligotrophic reservoirs (Sant Antoni and Escales) that were dominated by native fish species considered intolerant to pollution and from cold water (mostly *Salmo trutta*, *Barbus haasi* and *Phoxinus phoxinus*). The most eutrophic (such as Foix and Sau) and the lower Ebro river reservoirs take rather central positions in the DCA biplot.

Direct gradient analysis: the relationship of fish assemblages with environmental variables

Of the environmental variables initially included in the CCA, only five were retained by the forward selection procedure (Fig. 4). The first two canonical axes, respectively, explained 24.6% and 11.7% of the variance in fish species data. The first axis was mainly associated with alkalinity, although this variable is also highly correlated with altitude ($r = -0.70$, $n = 14$, $P = 0.005$) and nutrient concentrations (see PCA discussed above). This first axis mostly distinguished the dystrophic Santa Fe reservoir, which was strongly dominated in number by chub and was the reservoir at highest altitude and with least conductivity and alkalinity. The second CCA axis distinguished eutrophic reservoirs (mostly Foix, Sau and Susqueda), with the highest values of chlorophyll and concentrations of ammonium and other nutrients. These eutrophic reservoirs were dominated by common carp (*Cyprinus carpio*), other species highlighted by the CCA such as eel (*Anguilla anguilla*) and goldfish (*Carassius auratus*) being less abundant. A partial CCA removing the effect of altitude (covariate) showed the same ordination of species and reservoirs with trophic state, confirming that part of this trophic gradient is not because of altitude (but because of cultural eutrophication).

The response curves of species abundance to altitude (Fig. 5) and trophic state (Fig. 6) confirm these patterns of species composition. The response for electrofishing data with altitude agrees with the DCA and shows native, cold water species (*S. trutta*, *B. haasi*, *Chondrostoma miegii* and *P. phoxinus*) peaking at higher altitudes (Fig. 5). The strong curve for *S. cephalus* is mostly because of the dystrophic Santa Fe reservoir. In contrast, common carp and eel peak at lower altitudes. The response to altitude for

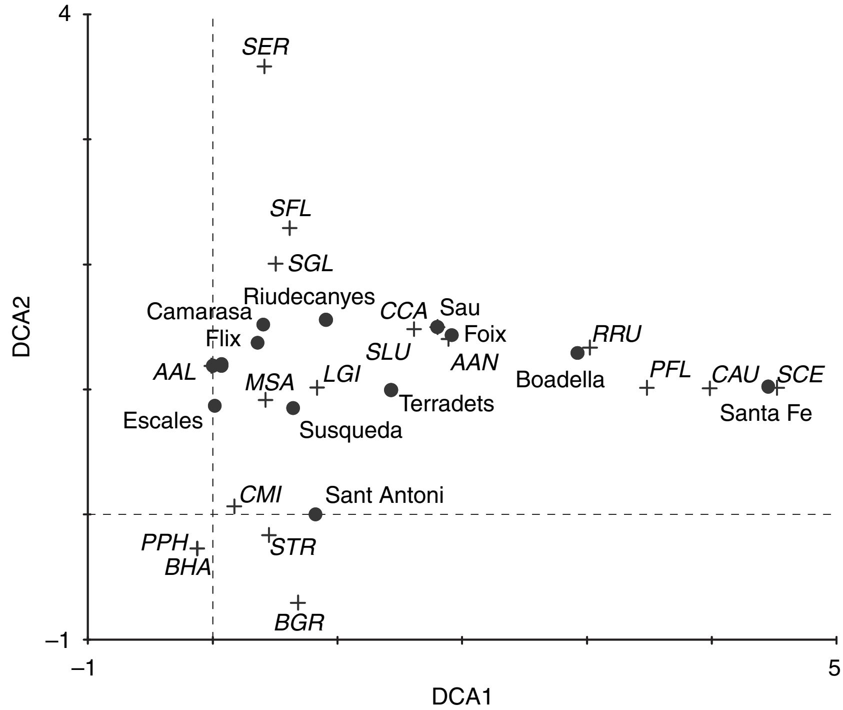

Fig. 3. Detrended correspondence analysis of electrofishing CPUE data for the reservoirs studied. Species (capital letters) and reservoir scores are labelled. Species codes are given in Table 2.

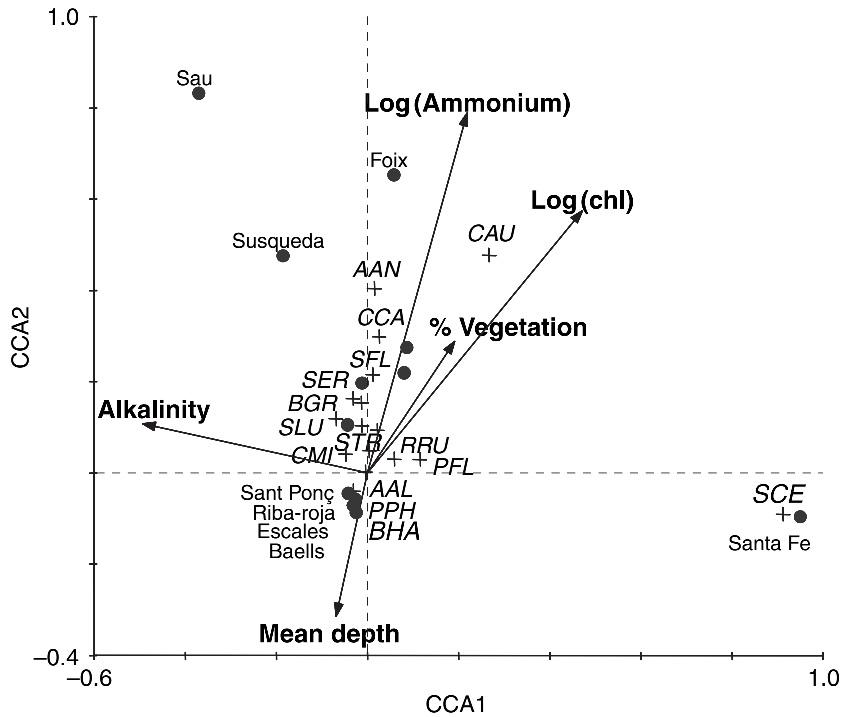

Fig. 4. Canonical correspondence analysis triplot of electrofishing CPUE and limnological variables assessed in the 14 reservoirs. See Table 2 for species codes. Limnological variables are represented by arrows. The length of the arrows is proportional to the importance of the variables and the directions of the arrows show their correlation with the axes.

gillnet data is similar but highlights a more limnetic zooplanktivore (*R. rutilus*) at lower altitudes (Fig. 5). In both figures, it is noteworthy that trout abundance peaks at the maximum altitude studied, in contrast to the other native species. The response of fish abundance to chlorophyll (Fig. 6, electrofishing data) and total nitrogen (Fig. 6, gillnet data) is in part inverse to the response to altitude but highlights the disproportionate abundance of common carp in the most eutrophic reservoirs. Roach (*R. rutilus*) displays a unimodal response to trophic state (Fig. 6), a pattern interestingly not observed for altitude. *S. cephalus* is a

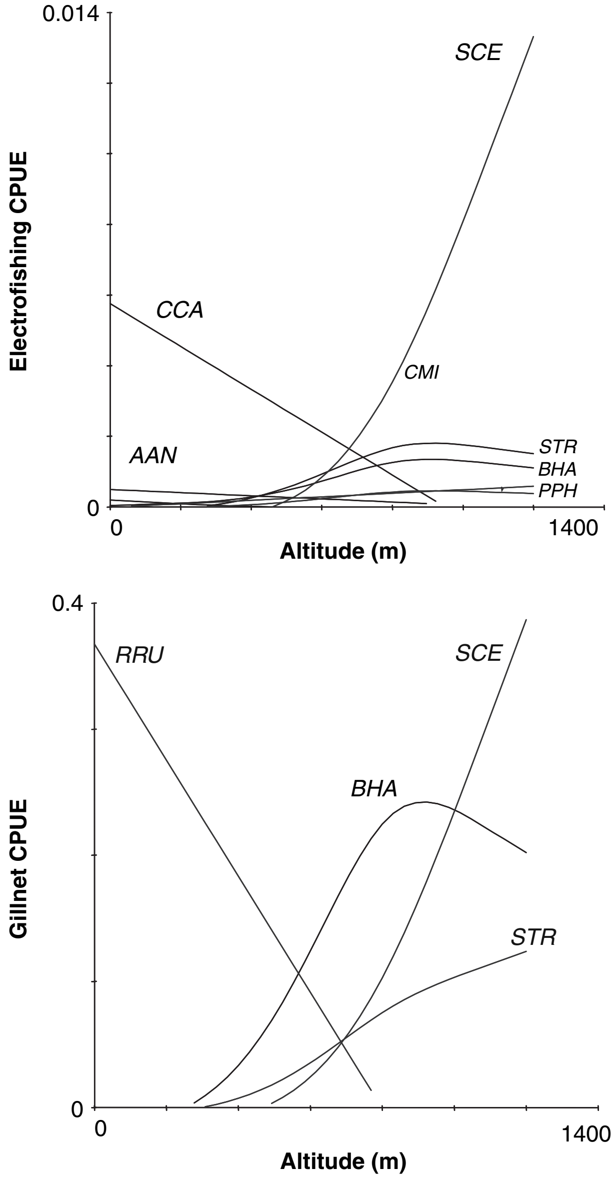

Fig. 5. Response curves of electrofishing (top) and gillnet (bottom) CPUE with altitude. The curves are the generalised additive models selected by the Akaike information criterion. See Table 2 for species codes.

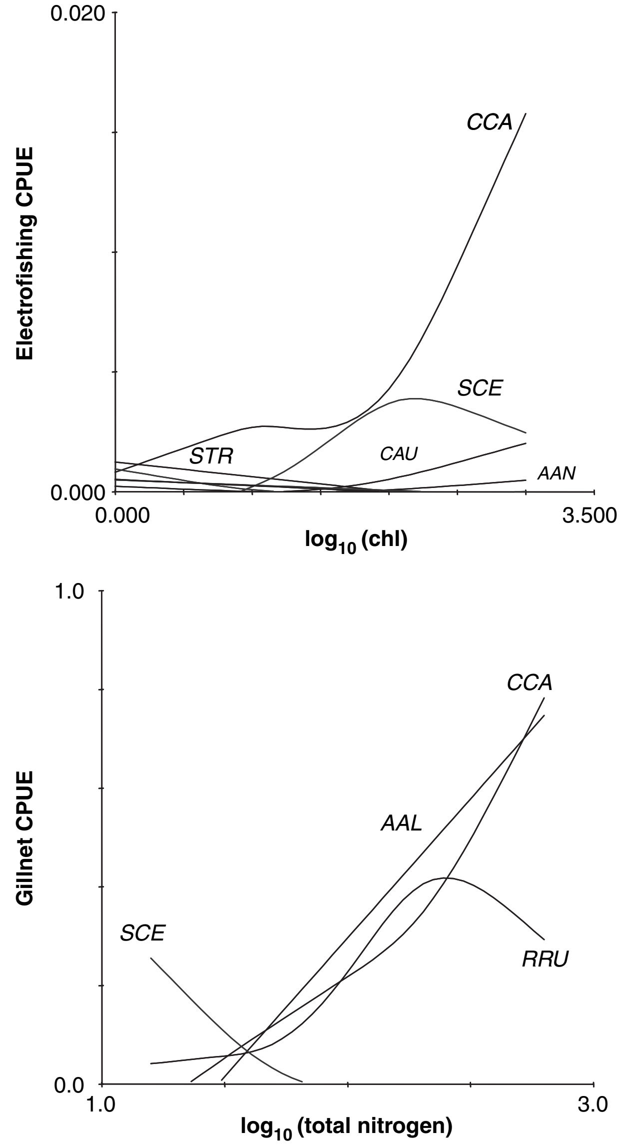

Fig. 6. Response curves of electrofishing CPUE with chlorophyll concentration (top) and gillnet CPUE with nitrogen concentration (top bottom). The curves are the generalised additive models selected by the Akaike information criterion. See Table 2 for species codes.

species rather intolerant to pollution but showed a unimodal response to chlorophyll (Fig. 6) because of the dystrophic Santa Fe reservoir (with high concentration of chlorophyll but usually low nutrient concentrations).

Even more convincing results are that the absolute abundances of common carp (present in the 14 reservoirs) are significantly related to total phosphorous concentration both for electrofishing/littoral and gillnet/limnetic samples, explaining about 40% of the variation (Figs 7 and 8). Very similar results were obtained for the relationship with chlorophyll concentration. Therefore, not only the relative abundance of common carp but also the absolute abundance increases with trophic state.

Diversity and richness measures

Despite the clear effects of trophic state on the fish assemblages, total fish species richness was not significantly related to the annual mean of total phosphorus (Fig. 9, $r = -0.36$, $n = 14$, $P = 0.20$). Similarly, the negative correlation of Shannon's diversity index with total P (Fig. 10) is very low and not significant for the littoral ($r = -0.13, n = 14, P = 0.66$) and the limnetic zone ($r = -0.10$, $n = 14$, $P = 0.73$).

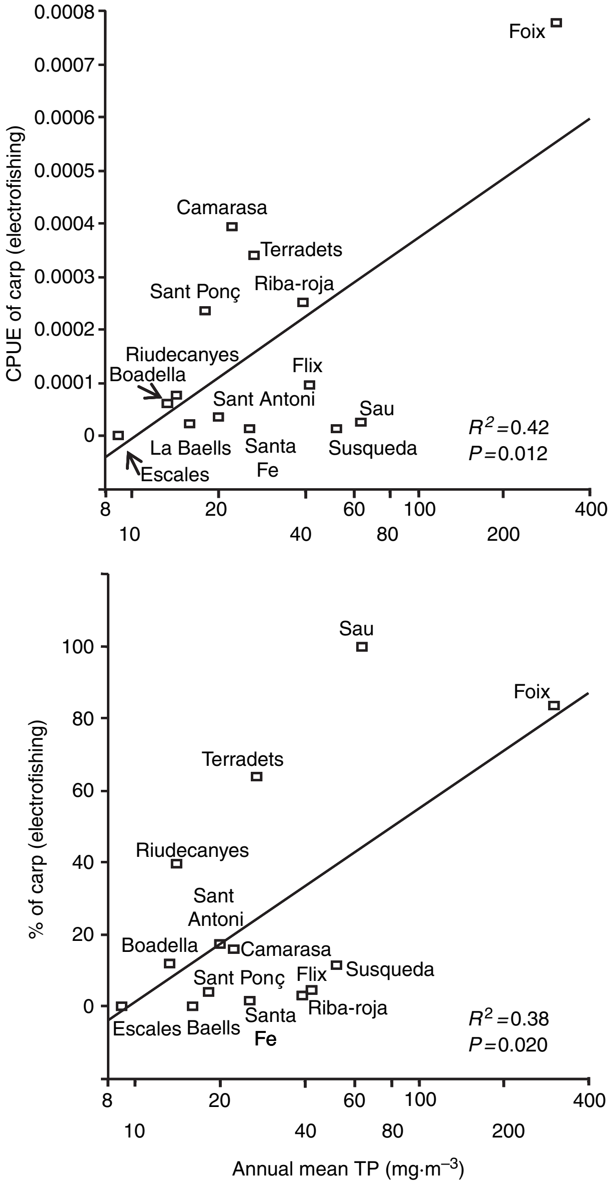

Fig. 7. Relationship of absolute (top) and relative (bottom) electrofishing CPUE of common carp with total phosphorous concentration. Linear regression analysis is also shown.

Discussion

Effects of trophic state on common carp abundance

Altitude and trophic state were the most important descriptors of variation of fish assemblages in Catalan reservoirs. Spatial changes in fish assemblage structure along the upstream–downstream physical gradient are well known (Schlosser 1982, 1990; Magalhães et al. 2002) and in most European rivers, 'trout', 'grayling', 'barbel' and 'bream' zones are recognised along the river continuum (Cowx & Welcomme 1998). In Iberian rivers, however, 'trout', 'barbel' and 'eel' zones are rather distinguished (Sostoa et al. 1990; Doadrio et al. 1991) because many central European species are not native to the Iberian Peninsula (García-Berthou & Moreno-Amich 2000; Vila-Gispert et al. 2002). This latter pattern was also observed in Catalan reservoirs, with brown trout and other native species in headwater reservoirs, common carp, eel and roach in the lowest altitude reservoirs and other species in middle reaches.

Altitude and trophic state of reservoirs are often correlated, as has been reported in Portuguese reservoirs (Godinho et al. 1998). After latitude, altitude has been suggested as the second most important natural factor controlling phytoplankton production in lakes and reservoirs worldwide (Brylinsky & Mann 1973). In general, the nutrient concentrations and productivity of freshwater ecosystems increase along the river continuum and downstream reservoirs should be expected to be more eutrophic. However, in our study, altitude was significantly related only to total N ($r = -0.62$, $n = 14$, $P = 0.018$) and not to total P ($r = -0.38$, $n = 14$, $P = 0.19$) or chlorophyll ($r = 0.014$, $n = 14$, $P = 0.96$). Moreover, multivariate analyses allowed separating the differential effects of altitude and trophic state. Most eutrophic reservoirs (that were of low altitude) were dominated by common carp (*C. carpio*) and secondarily other species such as goldfish (*C. auratus*) and, if passage is possible, eel (*A. anguilla*). In artificial and stressed ecosystems such as reservoirs the role of altitude probably mediates less the trophic level than in natural lakes or other aquatic ecosystems.

We found a strong, significant relationship of the absolute and relative abundances of common carp with trophic state both in the littoral and limnetic zones (independently with electrofishing and gillnet data). Lee & Jones (1991) also suggested that in most eutrophic U.S. reservoirs common carp dominated and this condition was difficult to reverse because of the well-known effects of carp of increased turbidity and decline of macrophytes (Crivelli 1983; Lougheed et al. 1998). The observed carp–trophic state relationship supports that the rest of patterns observed are not because of random variation in species composition but that the fish assemblage composition clearly reflects water quality, despite reservoirs being very fluctuant ecosystems. The fact that common carp was present in all reservoirs, is extremely tolerant to pollution and has been introduced many decades ago explains why such a relationship may be found and suggests that carp may be a good indicator of environmental degradation. Gido et al. (2000) have recently suggested that reservoir fish assemblages may be quite stable because their fish species are well adapted to stochastic events such as turbid inflows or fluctuations in water level.

Our results agree with the classification of brown trout and minnow as intolerant and bleak as a tolerant

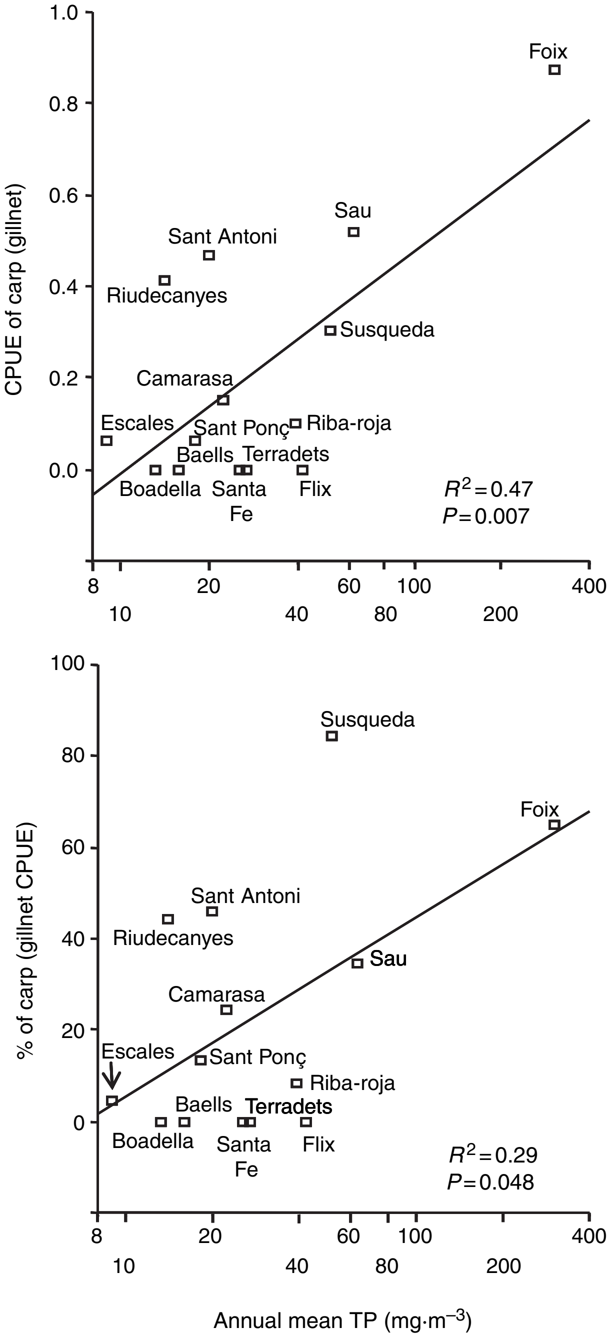

Fig. 8. Relationship of absolute (top) and relative (bottom) gillnet CPUE of common carp with total phosphorous concentration. Linear regression analysis is also shown.

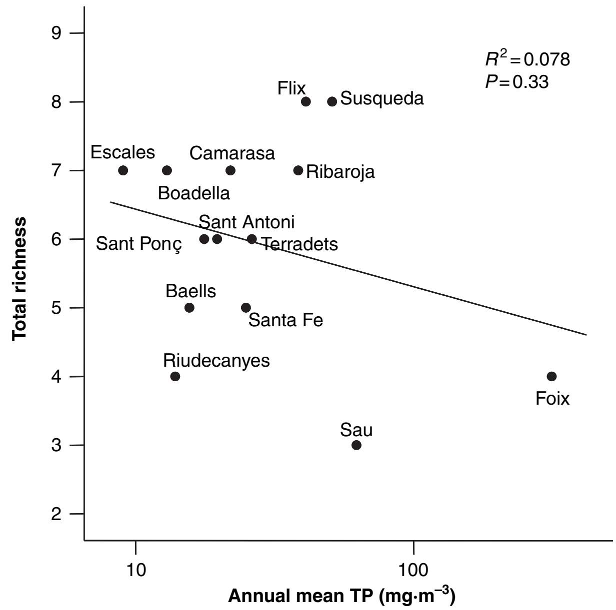

Fig. 9. Relationship between total species richness (total number of fish species detected) and the annual mean concentration of total phosphorous (log scale). Linear regression analysis is also shown.

species (Oberdorff et al. 2002) but question the classification of chub as a tolerant species, and suggest that *B. haasi* and *C. miegii* (Iberian endemics without previous published information) should be considered as intolerant species. Eel, goldfish and particularly common carp [species previously classified as without adequate information by Oberdorff et al. (2002)] should be regarded as tolerant species. We did not find significant evidence of variation in abundance with environmental degradation for the other fish species recorded.

The effects of reservoir age

In the few comparative studies of fish in European reservoirs (Kubečka 1993; Argillier et al. 2002; Irz et al. 2002b), age has been pointed out as an important factor, second to the altitudinal gradient, in the description of fish assemblages. For French reservoirs, water quality data were not available but it was suggested that eutrophication probably increased with age, affecting fish assemblages that were dominated by bleak and pikeperch in older reservoirs (Argillier et al. 2002; Irz et al. 2002b). Kubečka (1993) suggested five successional stages in the fish assemblages of Central and Eastern European reservoirs, from a brief initial period with riverine species (specially, salmonids) and pike (*Esox lucius*), followed by a perch (*P. fluviatilis*) increase and ending with cyprinid domination. A succession from salmonids to percids and later cyprinids is general of European lakes along productivity gradients (Persson 1991).

However, age was not highlighted in our analyses as a primary factor governing fish assemblages, despite that trophic state has also been related to age in Spanish reservoirs (Margalef 1983). In fact, reservoir age was not significantly related to total P (r = 0.19, n = 14, P = 0.51) or to total N (r = −0.04, n = 14, P = 0.89). We believe that this is because Catalan reservoirs were uniformly older (mean = 57 years, range = 28–88, Table 1) than French reservoirs

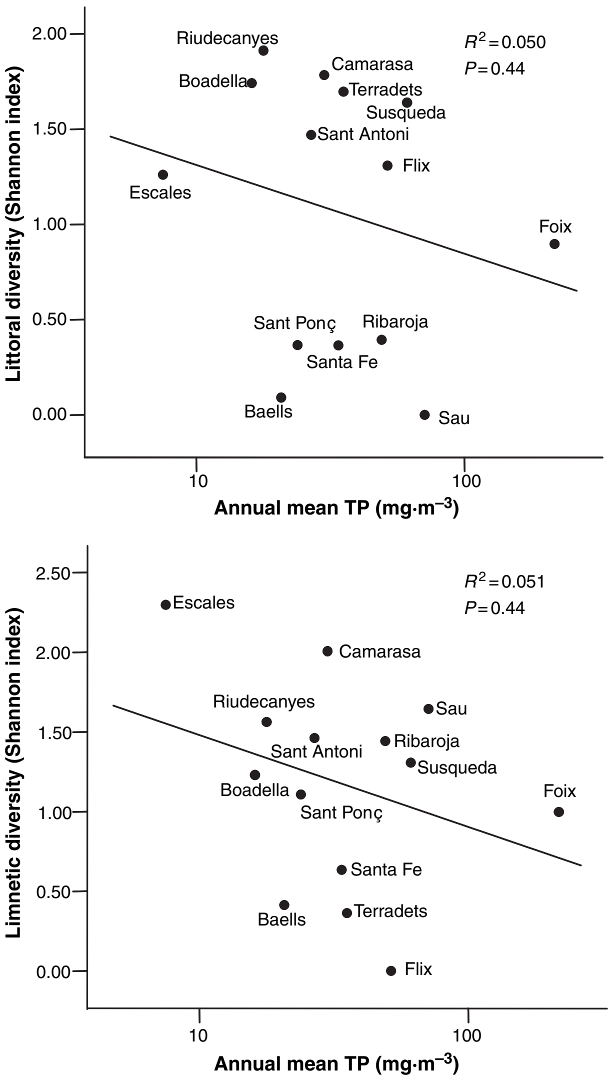

Fig. 10. Relationship between Shannon's diversity index ($\log_2$) in the littoral (electrofishing captures, top) and limnetic (gillnet captures, bottom) zones with the annual mean concentration of total phosphorous (log scale). Linear regression analysis is also shown.

(mean = 35, range = 4–71). The transition in fish assemblages from the filling period to the cyprinid domination took no more than 10 years in the few reservoirs were it has been studied (Kubečka 1993), explaining the relative unimportance of age in our study. Therefore, small effects of age should probably be expected in reservoirs older than 10 years as filling but more long-term data, particularly in new or refilled reservoirs, are needed to understand the historical dynamics of reservoir fish populations and its relationship with water quality.

Richness and diversity of fish assemblages

Although we observed clear effects of water quality on the fish species composition of the reservoirs studied, there was no significant effect of water quality on overall fish richness or diversity (Figs 9 and 10). Fish richness was low (maximum of eight species detected per reservoir) and most of the species were introduced. French reservoirs below 1500 m of altitude had 9.1 species on average whereas in Catalan reservoirs the mean was of 5.9 species. Given the relatively low fish richness of Mediterranean (Moyle & Marchetti 1999) and European (Gassner et al. 2003) freshwater ecosystems and the biotic homogenisation characteristic of reservoirs (Rahel 2002), fish richness should probably not be expected to covary with water quality. Another indication of this fact is that despite the clear altitudinal effects on water quality and fish assemblages, fish richness was not significantly related to altitude either ($r = -0.37$, $n = 14$, $P = 0.19$), as was also observed in French reservoirs below 1500 m of altitude (Irz et al. 2002b, 2004). Similarly to richness, Shannon's index of diversity (Fig. 10) or evenness (not shown) for the littoral and the limnetic fish assemblage did not depend on altitude or total P either. Other authors have shown that species composition and other fish community attributes rather than Shannon's index respond better to environmental degradation (Angermeier & Schlosser 1987) and thus a response of fish richness and diversity to variation in water quality should not be taken for granted in freshwater ecosystems.

Resumen

1. La relación entre la calidad del agua y las comunidades de peces está poco documentada en los embalses europeos, a pesar de tener gran importancia para su gestión y monitorización.
2. Se muestreó la comunidad de peces de 14 embalses españoles mediante pesca eléctrica desde embarcación en la zona litoral y con redes agalleras de luz múltiple en la zona limnética. Simultáneamente se recopilaron datos de ocho descriptores físicos y se midieron veinte características de calidad del agua de estos embalses.
3. Análisis multivariante (métodos de ordenación y modelos generalizados aditivos) mostró que la altitud y el estado trófico (indicado por la clorofila o concentraciones de nutrientes) explican, de forma independiente, la mayor parte de variación de las comunidades de peces de estos embalses. Los embalses más eutróficos están dominados por carpa (*Cyprinus carpio*) mientras que en los embalses oligotróficos son más abundantes otras especies intolerantes a la contaminación, principalmente nativas (como la trucha, *Salmo trutta*).
4. Las abundancias absoluta y relativa de la carpa están fuertemente relacionadas con el estado trófico de los embalses y un 40% de su variación se explica por la concentración de fósforo total. A pesar de los claros cambios en la composición de especies, no se halló efecto significativo de la calidad del agua en la riqueza o diversidad de peces, lo que sugiere que en estas comunidades con baja riqueza la composición de especies es mejor indicador de la eutrofización antrópica que la diversidad de peces.

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