

Fish assemblage composition in relation to environmental gradients in Portuguese reservoirs

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Abstract – Patterns in fish taxa composition were examined in Portuguese reservoirs to assess whether distinct types of assemblages exist. Furthermore, the environmental variables most tightly associated with assemblage-level patterns were identified. Classification of the fish taxa-by-reservoirs matrix revealed four major groups. Groups were separated by means of canonical correspondence analysis according to (by decreasing correlation with canonical axis): air temperature, annual rainfall, surface elevation, trophic state, mean depth and reservoir placement within the basin. In addition to these variables, stocking practices and predation likely contributed to assemblage composition. Assemblages in group A were distinguished by the permanent presence of largemouth bass (*Micropterus salmoides*) and the absence of trout (*Salmo trutta* and/or *Oncorhynchus mykiss*), nase (*Chondrostoma* sp.) and barbel (*Barbus* sp.). Group B assemblages invariably included bass, barbel and nase, while pumpkinseed (*Lepomis gibbosus*) was frequent and trout was extremely rare. Assemblages in group C were also characterised by nase and barbel, but in contrast to group B, trout was frequent, whereas bass was rare and pumpkinseed was absent. Group D assemblages consisted exclusively of trout and chub (*Leuciscus* sp.). The relationships observed parallel patterns detected in natural lakes to a certain extent, despite the critical human influence and the probable instability of some of the patterns detected. © Ifremer/Elsevier, Paris

Fish assemblages / typology / native and exotic species / reservoirs / lakes / habitat / stocking / Portugal

Résumé – Structure des peuplements piscicoles en relation avec des gradients environnementaux dans des bassins de retenue portugais. La structure des peuplements piscicoles a été étudiée afin d'établir si des assemblages existaient et afin d'identifier les facteurs du milieu qui leur étaient les plus étroitement liés. La matrice de classification des taxons par réservoir révèle quatre grands groupes. Les groupes ont été séparés au moyen de l'analyse canonique des correspondances (par corrélation décroissante) selon la température de l'air, les précipitations annuelles, la surface maximale des plans d'eau, l'état trophique, la profondeur moyenne et la situation du plan d'eau dans le bassin hydrographique. En complément de ces variables, les pratiques de stockage et la prédation contribuent aussi à la composition de la structure ichtyologique. Les assemblages du groupe A sont distincts par la présence permanente du « black-bass » (*Micropterus salmoides*) et l'absence de truite (*Salmo trutta* et/ou *Oncorhynchus mykiss*), du hotu (*Chondrostoma* sp.) et du barbeau (*Barbus* sp.). Les assemblages du groupe B incluent invariablement le « black-bass », le barbeau et l'hotu, tandis que la perche-soleil (*Lepomis gibbosus*) est fréquente et la truite très rare. Les assemblages du groupe C sont aussi caractérisés par l'hotu, et le barbeau, mais à l'inverse du groupe B, la truite est fréquente, alors que le « black-bass » est rare et que la perche-soleil est absente. Les assemblages du groupe D consistent exclusivement en truites et chevaines (*Leuciscus* sp.). En dépit de l'influence humaine et de l'instabilité probable de certains assemblages observés, les relations mettent en évidence un certain parallélisme entre les assemblages lacustres. © Ifremer/Elsevier, Paris

Structure des peuplements / typologie / poissons d'eau douce / retenues d'eau / lacs / habitat / stockage / Portugal

1. INTRODUCTION

In Portugal, as in other areas, reservoirs represent a recent and widespread freshwater environment [9, 16,

51]. Since the 1940s, 61 reservoirs larger than 100 ha and numerous smaller ones have been built in the country. In addition, more are planned or already under construction, including the largest Portuguese reser-

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voir, Alqueva (25 000 ha at full pool level). In a region devoid of natural freshwater lakes and characterised by low fish species richness, reservoirs have offered new areas for native fish fauna to colonise and have stimulated the introduction of several exotic species, claimed to be better adapted to such 'lentic-lotic' environments [2, 8]. Moreover, although constructed mainly for either crop irrigation or hydropower generation, important recreational fisheries have been developed in these systems [5, 9, 10, 16].

From the mid-eighties onwards, fish surveys have been conducted in selected Portuguese reservoirs, but information has remained scattered, and to date, no effort has been made to detect patterns in fish assemblages and their possible environmental basis. Large-scale multi-lake studies have been used to assess the mechanisms important in structuring fish assemblages [34–37, 39, 46, 52–54]. The examination of among-lake variation in fish assemblage composition according to environmental gradients may help clarify the role of biotic and abiotic factors for community organisation, a major issue in aquatic ecology [37, 39]. Yet, and despite the world-wide spread of reservoirs, few observational studies (*sensu* [40]) have been conducted on the organisation of reservoir fish assemblages at larger spatial scales [7, 20]. Moreover, the detection of reservoir types based on fish associations might be extremely useful in fisheries management, not only to develop stratified approaches for monitoring, but also to elaborate management strategies appropriate for particular reservoir groups [7].

Hence, the aim of the present study is to: (i) use survey data to develop a typology of Portuguese reservoirs based on fish assemblages; (ii) relate assemblages and corresponding reservoir groups to environmental variables; and (iii) contrast the patterns detected in this study with patterns observed in temperate natural lakes.

2. MATERIALS AND METHODS

2.1. Data type and origin

Information on reservoir fish assemblages used in this study was gathered from surveys conducted by the Instituto de Zoologia Augusto Nobre in northern reservoirs, and by Estação Florestal Nacional, Instituto Superior de Agronomia and Direcção Geral das Florestas in southern ones. With one exception, reservoirs were sampled between 1986 and 1997 (*table 1*). The usual sampling scheme used nylon multi-mesh trawls, or gill nets, which were set overnight in pelagic and benthic areas, and daylight electrofishing (direct current) from a boat in shallow littoral areas. In a few reservoirs, creel surveys were also carried out and in some shallow ones (average depth < 2 m) electrofishing was the only collection method used. In two reservoirs, data from fish collected during dry-outs are used. Each water-body was sampled 2 to 12 times

(average \pm SE = 3.5 ± 0.5), encompassing a maximum of two years. Two reservoirs had different collections separated by more than five years, which are analysed as distinct sampling units. The number of littoral electrofishing transects as well as the number of net-sets varied according to each reservoir's inundated area. Biological data used in this study are fish taxa presence/absence, as recommended for pattern analysis at larger spatial scales [32]. Species were merged by similarity in ecological requirements (mainly congeneric species) to increase the frequency of occurrence of each taxa. By doing this, species with low frequency of occurrence could be included in multivariate analysis without distorting results [11, 48]. Moreover, merging species into taxonomic groups can clarify global distribution patterns [55]. Despite the variable number of times each reservoir was sampled, no relationship was detected between number of species collected and number of sampling periods ($r = 0.28$, $P > 0.05$, $n = 37$).

Environmental data were obtained from the Instituto da Água [18, 19], and from topographical maps, and include the following variables, available for all reservoirs: surface elevation at full pool level, annual average rainfall, annual average air temperature, inundated area at full pool level, mean depth at full pool level, trophic status, distance from the dam to the source of the impounded river and distance from the dam to the sea. All the reservoirs studied connect upstream with impounded rivers, at least during periods of rainfall. On the contrary, downstream connectivity is largely prevented since most reservoirs do not have fish passes, and existing passes do not work properly [3]. The main reservoir utilisation (either hydropower generation or crop irrigation) and reservoir placement (either in a tributary stream or in a main river) were coded with binary dummy variables, as required by the analytical method used. The presence of a fish pass, the sampling year and the reservoir age were also noted for each reservoir. Reservoir trophic is based on chlorophyll-*a* concentration, Secchi disk transparency and phytoplankton structure [19]. Five categories were considered: 1) oligo-trophic, 2) oligo-mesotrophic, 3) meso-trophic, 4) meso-eutrophic and 5) eutrophic.

2.2. Analytical procedures

Two matrices were developed for analysis: fish taxa presence/absence by reservoirs and explanatory variables by reservoirs. Data from 35 reservoirs were used (*table 1, figure 1*). To assess if discrete types of assemblages existed in the reservoirs, the biological matrix was submitted to a hierarchical classification [24]. We used a flexible clustering method with Jaccard's index of similarity, as recommended for presence/absence data [24, 45]. An arbitrary cut off level was used, such that separate groups could be chosen. The analysis was performed and the resulting dendrogram displayed

Table I. Code, name, inundated area at full pool level, river basin and sampling year for the studied reservoirs.

Code	Name	Area (ha)	River basin	Sampling year
1	Alto Lindoso	1 072	Lima	1996
2	Touvedo	172	Lima	1997
3	Paradela	380	Cávado	1989
4	Alto Rabagão	2 212	Cávado	1989
5	Caniçada	689	Cávado	1989
6	Ermal	1 630	Ave	1989
7	Andorinhas	100	Ave	1989
8*	Azibo	410	Douro	1987/1994
9	Poio	10	Douro	1995
10	Miranda Douro	122	Douro	1986
11	Bemposta	430	Douro	1989
12	Régua	850	Douro	1986
13	Torrão	650	Douro	1989
14	Crestuma Lever	1 298	Douro	1989
15	Lagoa Comprida	83	Mondego	1994
16	Vale Rossim	37	Mondego	1994
17	Cabril	2 023	Tejo	1997
18	Belver	286	Tejo	1990
19	Coruche1	20	Tejo	1997
20	Coruche2	4	Tejo	1997
21	Coruche3	2	Tejo	1997
22	Magos	124	Tejo	1989–1990
23	Montargil	1 495	Tejo	1997
24	Maranhão	1 960	Tejo	1986
25	Gameiro	7	Tejo	1995
26	Divor	265	Tejo	1993
27	Monte Novo	277	Guadiana	1992–1993
28*	Pego Altar	655	Sado	1980/1991
29	Vale Gaio	550	Sado	1990–1992
30	Alvito	1 480	Sado	1992–1993
31	Revilheira1	2	Guadiana	1992
32	Revilheira2	1	Guadiana	1992
33	Tapada Grande	100	Guadiana	1992–1993
34	Tapada Pequena	20	Guadiana	1992–1993
35	Bravura	285	Odeóxere	1997

* Reservoirs with two different collections (in the 80's and 90's) are analysed as distinct sampling units.

with NTSYS [41]. Average number of species was also determined for each reservoir group.

Subsequently, the relationships between fish assemblages and explanatory variables were examined by submitting both matrices to canonical correspondence analysis (CCA) using CANOCO [47, 48]. CCA is an eigenvalue ordination specifically developed to relate multivariate ecological data matrices, and generates diagrams (biplots) that simultaneously display the similarities between reservoirs, based on their fish assemblages, and the relationships between the presence/absence of fish according to the supplied explanatory variables [50].

From all the explanatory variables initially considered, the best predictors (those retained for analysis) were selected by a forward selection procedure available in CANOCO, a multivariate extension of the stepwise regression method. A significance cut-off point of 0.10 was used [25]. The total variation in assemblage composition accounted for by the selected environmental variables was obtained by dividing the canonical eigenvalues of the CCA by the total inertia, i.e. the sum of all eigenvalues of a correspondence analysis of

the species matrix [50]. A Monte Carlo simulation test of both the first axis eigenvalue and trace (i.e. the sum of all canonical eigenvalues) was used to evaluate the statistical significance of the species-environment association [49].

3. RESULTS

In total, 24 species (14 native and 10 exotic) were recorded in the studied reservoirs (table II). Common carp, *Cyprinus carpio*, was the most frequent species encountered followed by largemouth bass, *Micropterus salmoides*, northern Iberian nase, *Chondrostoma polyploides*, northern Iberian barbel, *Barbus bocagei*, and pumpkinseed, *Lepomis gibbosus*. Tench, *Tinca tinca*, gudgeon, *Gobio gobio*, pike, *Esox lucius*, and the cichlid *Cichlasoma facetum* (all exotics) were rarely collected thus they were excluded from multivariate analysis to avoid distortion.

Hierarchical clustering of the 37 fish assemblages identified four groups of reservoirs (figure 2, table III). Group A included 10 reservoirs distinguished by fish

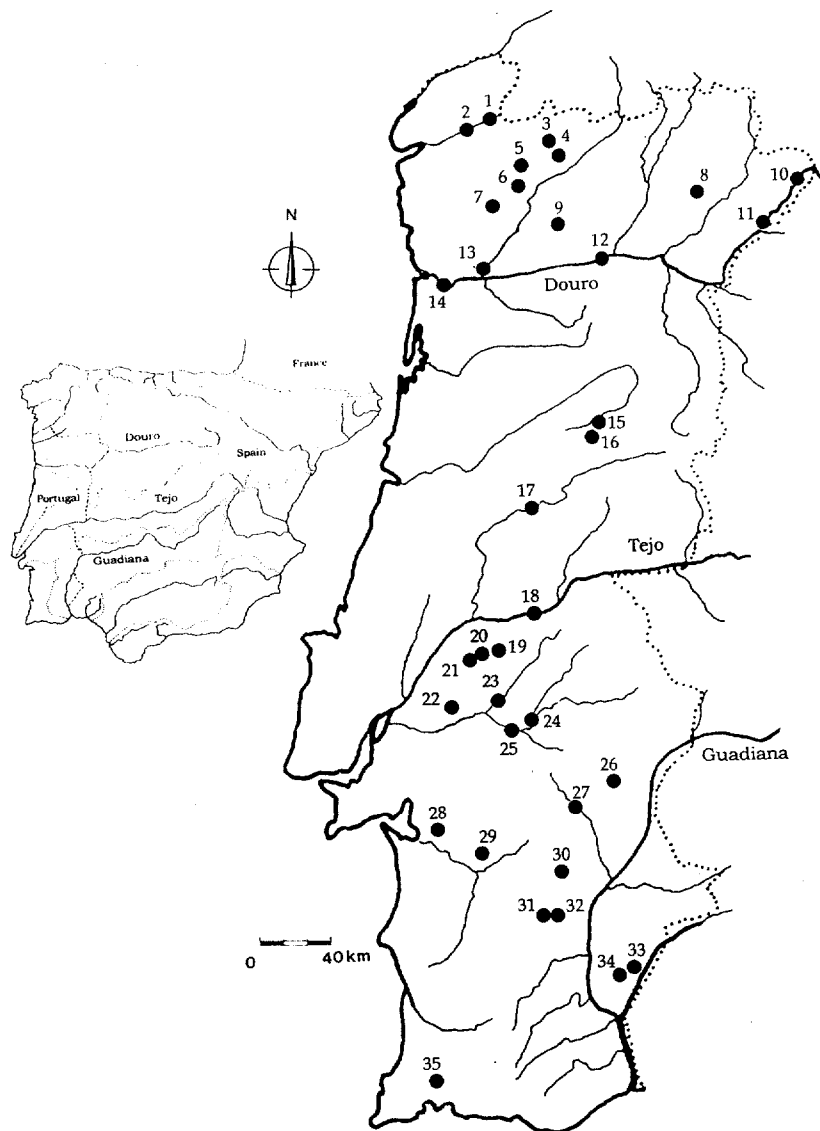


Figure 1. Location of the studied reservoirs. Only major rivers and streams are illustrated. Reservoir codes as in *table I*.

assemblages with bass always present, carp and pumpkinseed frequently occurring, and the absence of trout, nase and barbel. Group B contained 12 reservoirs and their fish assemblages were characterised by the permanent presence of barbel, nase and bass, the frequent occurrence of pumpkinseed, and the rare presence of trout (occurring in just one reservoir). In this group, pumpkinseed was absent from reservoir n° 28 when sampled in the early 1980s, but was present in the same reservoir's 1990s sample. Nase and barbel were also frequent in group C (12 reservoirs), but in contrast to group B, trout was frequent whereas bass was rare and pumpkinseed was absent. The Azibo reservoir, sampled in both 1987 and 1994, changed from group C to group B due to the introduction of bass (and of pike) and the disappearance of trout from collections.

Finally, group D included just three reservoirs with fish assemblages containing exclusively trout and chub. Average number of species was higher in groups B and C, and lower in groups A and D (*table III*).

From the 13 variables initially considered for inclusion in the CCA, only six were retained by the forward selection procedure, and accounted for 40 % of the total variation in species presence/absence (*table IV, figure 3a*). Neither sampling year nor reservoir age were selected as predictors. The first axis (22 % of total variation) was representative of a taxonomic gradient among the most common taxa – salmonids (trout), cyprinids (chub, nase, barbel, carp, goldfish), centrarchids (bass, pumpkinseed) – and was mainly associated with temperature, rainfall and elevation, although it also reflected the influence of average

Table II. Species collected in Portuguese reservoirs.

Species	Common name	Analysis group	Frequency of occurrence (%)
Native species			
Cyprinidae			
<i>Rutilus alburnoides</i>	Iberian roach	roach	5.4
<i>R. arcasi</i>	Iberian red roach	roach	13.5
<i>Leuciscus pyrenaicus</i>	Southern Iberian chub	chub	29.7
<i>L. carolitertii</i>	Northern Iberian chub	chub	29.7
<i>Barbus comiza</i>	Long snouted barbel	barbel	5.4
<i>B. microcephalus</i>	Short snouted barbel	barbel	2.7
<i>B. sclateri</i>	Southern Iberian barbel	barbel	2.7
<i>B. bocagei</i>	Northern Iberian barbel	barbel	56.8
<i>Chondrostoma tolylepis</i>	Northern Iberian nase	nase	59.5
<i>C. willkommi</i>	Southern Iberian nase	nase	5.4
Cobitidae			
<i>Cobitis paludica</i>	Southern Iberian loach	loach	10.8
<i>C. calderoni</i>	Northern Iberian loach	loach	5.4
Anguillidae			
<i>Anguilla anguilla</i>	eel	eel	24.3
Salmonidae			
<i>Salmo trutta</i>	brown trout	trout	32.4
Exotic species			
Cyprinidae			
<i>Cyprinus carpio</i>	carp	carp	70.3
<i>Carassius auratus</i>	goldfish	goldfish	32.4
<i>Tinca tinca</i>	tench	*	5.4
<i>Gobio gobio</i>	gudgeon	*	5.4
Poeciliidae			
<i>Gambusia holbrooki</i>	mosquitofish	mosquitofish	16.2
Centrarchidae			
<i>Lepomis gibbosus</i>	pumpkinseed	pumpkinseed	43.2
<i>Micropterus salmoides</i>	largemouth bass	largemouth bass	67.6
Cichlidae			
<i>Cichlasoma facetum</i>	cichlid	*	5.4
Esoxidae			
<i>Esox lucius</i>	pike	*	2.7
Salmonidae			
<i>Oncorhynchus mykiss</i>	rainbow trout	trout	13.5

* Species not included in the analysis.

depth and trophy. The second axis was much less informative (8 % of total variation), being primarily constrained by the reservoir placement within the basin. The association between environmental variables and fish assemblage composition was significant ($P < 0.001$, Monte Carlo simulation test with 1 000 permutations).

The four reservoir groups were successfully separated according to the selected environmental variables (table V, figure 3b). Reservoirs belonging to group D were clearly distinct from all others by having extremely low average annual temperature together with both high surface elevation and high rainfall. Reservoirs in group C were located at considerable lower altitudes, and were associated with warmer average temperatures and lower rainfall than group D. They had the highest mean depth of all groups and were located, as was group D, in central-northern Portugal. Reservoirs in group B were separated from reservoirs in group C by being located at lower elevations, and for having higher temperatures and lower rainfall. The

reservoirs of group B were largely located in southern Portugal, though three northern ones were included in this group. Group A included only lowland, shallow reservoirs that were located in the driest and warmest areas studied. They were situated in southern Portugal. Reservoirs from groups B and C were located much further from river sources than those from groups A and D.

4. DISCUSSION

Both native colonists and introduced non-native species were collected in the reservoirs. Nevertheless, three of the five most frequently encountered taxa were exotic, exposing the common practice of stocking with non-native fish [1, 8]. These exotic fish (carp, bass and pumpkinseed) are presently self-sustaining in the reservoirs but are considerably less frequent in riverine environments, underlying the importance of reservoirs for their successful establishment in Portugal [4, 8, 14, 28]. Elsewhere, fish introductions have invariably

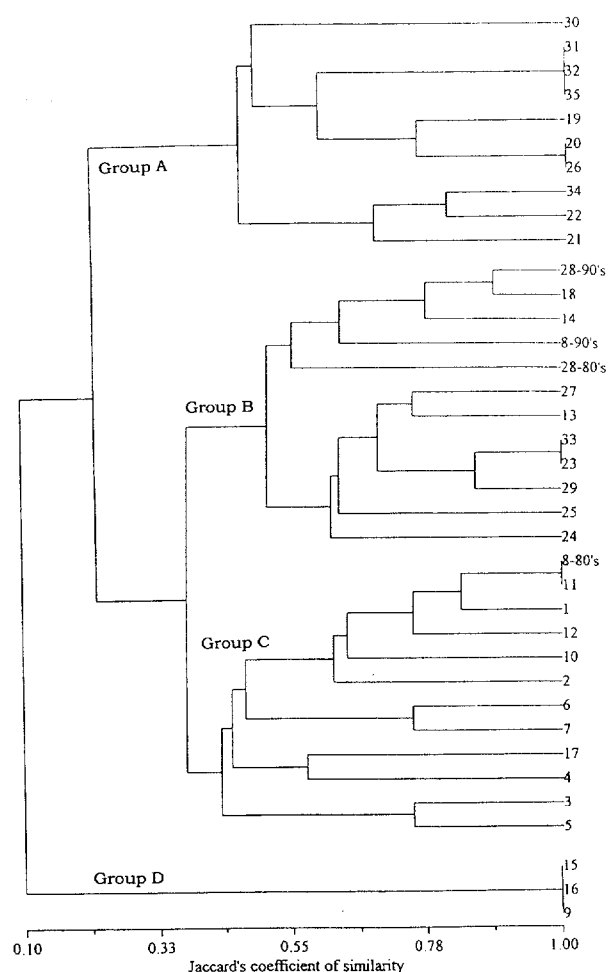


Figure 2. Cluster dendrogram summarising similarity among Portuguese reservoirs based on their fish assemblages. Reservoir codes as in *table 1*.

occurred following the building of reservoirs, and in Portugal, hatcheries have reared exotic fish (rainbow trout, largemouth bass and carp), since the 1950s until recently, for the general stocking of reservoirs [31, 51]. The pumpkinseed was introduced to Spain, and both naturally and with the help of anglers using it as live bait, expanded through common rivers (Tejo and Guadiana) to Portugal, where it was first collected in 1977 [1, 2, 12]. Consequently, many of the species occurring

Table III. Frequency of occurrence (%) of particular taxa in each reservoir group. Average number of species in each group is also given.

	Groups			
	A	B	C	D
Nase	0	100	100	0
Barbel	0	100	92	0
Chub	10	75	75	100
Roach	0	25	33	0
Trout	0	8	83	100
Carp	90	83	58	0
Goldfish	30	50	25	0
Loach	20	8	25	0
Largemouth bass	100	100	25	0
Pumpkinseed	70	75	0	0
Eel	10	33	33	0
Average number of species	3.2	7.1	5.3	2.0

Table IV. Summary statistics for the canonical correspondence analysis relating fish assemblages to environmental variables. Eigenvalues were 0.27 for the first axis and 0.10 for the second.

Environmental variables	Correlation with canonical axis	
	Axis 1	Axis 2
Temperature	-0.79*	0.12
Rainfall	0.77*	-0.05
Surface elevation	0.68*	0.22
Trophic category	-0.45*	-0.30
Mean depth	0.38*	-0.12
Distance to source	0.19	-0.52*

(* $P < 0.05$).

and assemblage patterns detected in this study are likely dependent upon fish introductions.

The most common native taxa collected in the reservoirs (barbel, nase and chub) are likewise the most frequent in Portuguese riverine systems, where they usually co-occur [4, 6, 14], except for the small sized minnows *Rutilus* sp., relatively frequent and abundant in many riverine stretches but scarce in reservoirs [4, 14]. Overall, few of the native species commonly found in Portuguese rivers were absent from the reservoirs, and these include mainly other small sized minnows like *Chondrostoma lusitanicum* and *Chondrostoma lemmingii*, as well as migratory species such as *Petromyzon*

Table V. Values of the environmental variables for each reservoir group.

	Group A	Group B	Group C	Group D
Average temperature (°C)	15–17	15–16	10–14	< 10
Average rainfall (mm) ± SE	630 ± 22	745 ± 73	1 462 ± 160	2 000 ± 410
Surface elevation (m) ± SE	111 ± 24	132 ± 51	391 ± 74	1 345 ± 179
Trophic category	meso-eutro	oligo-eutro	meso-eutro	oligo
Mean depth (m) ± SE	3.6 ± 1.3	11.2 ± 1.4	19.5 ± 3.8	12.2 ± 2.4
Distance to source (km) ± SE	5 ± 2	168 ± 90	268 ± 102	5 ± 3

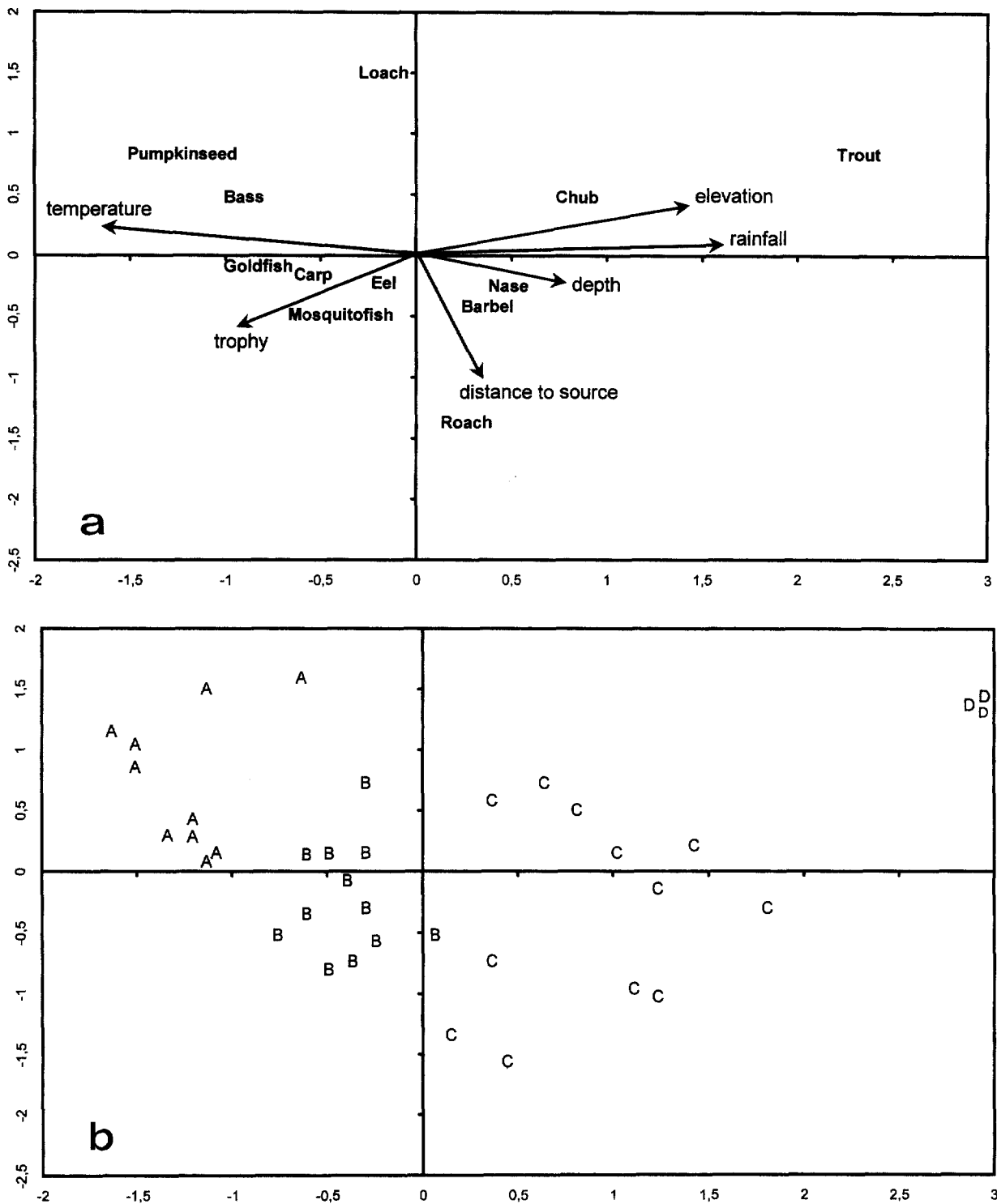


Figure 3. (a) Canonical correspondence analysis biplot for fish taxa and environmental variables assessed in 37 reservoirs. Species scores are labelled. Environmental variables are represented by arrows that roughly point towards the factor direction of maximum variation. The length of an arrow is relative to the importance of that variable in assemblage ordination. (b) Reservoir scores, labelled with respective group affiliation (A, B, C and D, according to figure 2) on the same axis.

marinus, *Alosa alosa* and *Alosa fallax*, whose migrations have been blocked by dams. Nonetheless, the relative abundance of all the native species encountered is considerably lower in reservoirs than in rivers ([4, 14, 34] and F. Godinho, unpubl. data) clearly revealing the disruptive effect reservoirs have on native communities.

Temperature was the main environmental variable associated with assemblage composition and we detected a taxonomic change (salmonids-cyprinids-centrarchids) in relation to this factor. Annual average air temperature separated groups C-D (temperature < 15 °C, coldwater assemblages with trout and rarely with centrarchids) from groups A-B (temperature > 15 °C, warmwater assemblages without trout and with centrarchids). Though other habitat variables affect the presence of temperate freshwater fish, available temperatures, by means of particular taxa physiological tolerance to this factor, are usually one of the primary constraints of distribution at larger spatial scales [27, 42]. Trouts are particularly sensitive to warm temperatures, and the native brown trout is naturally missing from all southern Portugal, being confined to high elevations in the central part of the country (J. Oliveira, pers. comm.).

The stocking rationale of the inland Portuguese fisheries management authority may, however, also have contributed to the relevance of temperature as it consisted of separate stocking of trout (in the north) and bass (in the south). Additionally, pumpkinseed has entered Portugal via southern basins (Tejo and Guadiana). Nevertheless, the failed introduction of trout in a few warmer group B reservoirs appears to strengthen the role of temperature in dictating trout presence and assemblage structure. On the other hand, the widespread establishment of introduced carp in group C reservoirs suggests that some of these systems may be amenable to colonisation by other warmwater species, like bass (already established in 3 reservoirs after being introduced by anglers) and pumpkinseed. Supporting this hypothesis are: (i) the common presence of bass in reservoirs located in the upper Spanish portion of the northern River Douro, where it has been massively introduced by the Spanish authorities [6, 23]; and (ii) the occurrence of pumpkinseed in some reservoirs also located in the upper River Douro [6]. Consequently, the Portuguese stocking rationale (largemouth bass) and dispersal paths (pumpkinseed) may have critically influenced the absence of centrarchids from type C assemblages.

Other variables strongly associated with the taxonomic gradient and the corresponding separation of assemblage types were rainfall and elevation. In fact, these variables, in association with temperature, may represent a powerful composite factor influencing the overall habitat supplied by each reservoir. In addition, these variables underlie the latitudinal position of a reservoir in Portugal, since southern regions are warmer, dryer and low-elevated whereas central-northern areas are cooler, wetter and high-elevated. How-

ever, since both rainfall and elevation were strongly correlated with temperature ($r = -0.90$, $P < 0.01$ and $r = -0.87$, $P < 0.01$, respectively) it is not possible to isolate the separate influence of these variables upon assemblage composition.

Besides the warmwater/coldwater separation, assemblages were further divided into: simple (with few species, groups A and D) or complex (with many species, groups B and C). First, the different reservoir's positioning in relation to river headwaters may have influenced the number of native species present. In temperate rivers, several studies have documented a positive relationship between native fish species richness and distance to source (or other correlated variables such as catchment area), due to an increase in habitat heterogeneity (e.g. [26, 29, 30, 44]). Hence, native species initially retained in reservoirs from groups A-D (closer to river sources) during impoundment could have been less than in reservoirs from groups B-C. In support of this deduction, the number of native species collected in the reservoirs was related with the dam distance to the source of impounded river ($r = 0.756$, $P < 0.01$, $n = 37$).

Nase and barbel were particularly influential in the simple-complex separation, being present in groups B (warmwater-complex) and C (coldwater-complex) and absent in groups A (warmwater-simple) and D (coldwater-simple). These cyprinids are potamodromous (sensu [15]), needing lotic spawning and nursery habitats [14, 38, 43]. Therefore, the ability to move upstream in impounded rivers should be critical for their persistence in reservoirs. Some of the environmental variables selected in the CCA, likely related to fish movements, may elucidate the differences between groups of reservoir. Reservoirs from group D are at extremely high altitudes (Lagoa Comprida and Vale Rossim are located at altitudes > 1 400 m above sea level) in the headwaters of mountain streams. Such streams may present difficulties for the upstream movements of cyprinids as a consequence of their high gradients [27]. In turn, reservoirs of group A should severely constrain upstream movements due to their reduced connectivity. This reservoirs are located in the driest sampled areas, where rivers are naturally intermittent, being additionally very close to river sources, where intermittency is more pronounced [33].

Interspecific interactions between native cyprinids and exotic species (particularly the piscivorous largemouth bass) might also have contributed to the almost complete absence of native cyprinids from reservoirs in group A [13]. Native minnows have evolved without the presence of a specialist piscivorous fish (sensu [21]) and may be particularly naïve when confronted with introduced predators, such as the largemouth bass [13, 17]. Although bass occurred also in reservoirs from group B, distinct environmental characteristics may explain the contrasting presence of native cyprinids. Prey vulnerability varies with habitat conditions, and in reservoirs, high vulnerability has been related to shallow systems with low impounded water volumes [39]. In these small systems, predators and prey are

concentrated, resulting in high prey conspicuity and vulnerability [22]. Reservoirs from group A may have induced high prey vulnerability due to their morphometry (in addition to being the shallowest systems, these reservoirs had also small inundated areas, average inundated area \pm SE = 220 \pm 144 ha) whereas deeper (and larger, average inundated area \pm SE = 695 \pm 171 ha) reservoirs from group B may have induced much lower prey vulnerability.

Studies in lakes (i.e. natural systems) have demonstrated that small sets of explanatory variables (usually piscivory, some environmental variables such as depth and temperature, and zoogeographical factors) suffice to account for considerable portions of the variation in assemblage structure along intermediate-large spatial scales [34–37, 52–54]. Despite the artificiality of the systems, the present study detected patterns in reservoirs somewhat similar to those noticed in

temperate lakes. A Centrarchidae/Salmonidae separation, according primarily to temperature (but also to elevation, rainfall, depth and trophic conditions), and a simple-assemblage/complex-assemblage separation, according to the reservoir's relative position in the basin (likely influencing both the initial number of native colonisers and longitudinal connectivity) and predation from introduced piscivorous fish (as mediated by reservoir morphometry). However, some of the trends observed in this study were strongly influenced by human practices and possibly have low persistence. For example, the Azibo assemblage has changed from group C to group B between the first and the second sampling period, after the introduction and establishment of a large pike (introduced from Spanish stocks by anglers) and largemouth bass (also introduced by anglers) populations, and the vanishing of trout.

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