Limnologica 34, 224–235 (2004)
http://www.elsevier.de/limno

LIMNOLOGICA

The organisation of fish assemblages in the regulated Lima basin, Northern Portugal

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Received: December 17, 2003 · Accepted: April 19, 2004

Abstract

In order to understand the structure of fish assemblages in the modified Lima basin (Northern Portugal), two distinct datasets concerning the presence and abundance of fish species were subjected to multivariate analysis. On the River Lima two types of flow modification are present within kilometres of one another: (a) a reduced and constant flow due to hypolimnetic release; and (b) an intense and irregular flow. A comparison of their influence on fish assemblages revealed a gradient of assemblage types from tributaries to main river sites. The latter were characterised by a strong dominance of cyprinids, particularly Iberian barbel *(Barbus bocagei)*. The former harboured two kinds of fish assemblages: those closer to the river mouth were dominated by the cyprinids Iberian chub *(Squalius carolitertii)* and Iberian nase *(Chondrostoma polylepis)*, which were also frequently present in the main river; while in those further upstream the predominant species was the brown trout *(Salmo trutta)*. Although explanatory variables such as distance from source, altitude, substrate coarseness and width were the primary correlates of fish assemblage composition, dam construction and flow regulation also had a significant effect upon assemblage structure, particularly by: i) reducing the importance of migratory species; ii) constraining the presence of trout in the regulated segments; and iii) simplifying the community, especially in the case of the constant and reduced flow regime.

Key words: River regulation – flow patterns – multivariate analysis – fish assemblages – River Lima – Portugal

Introduction

All over the world numerous studies have documented dramatic changes in the structure and diversity of fish assemblages as a result of human-induced habitat alterations (WARD & STANFORD 1979; PETTS 1988; COPP 1990; GEHRKE et al. 1995; JURAJDA 1995; PEŇÁZ et al. 1999). River regulation by dams is the greatest source of anthropogenic habitat alteration, with 77% of the total water discharge of the 139 largest river systems in North America and Europe currently affected (COWX & WELCOMME 1998). In most cases regulation distorts the natural flow regime and profoundly affects ecosystem functioning and the organisation of biotic communities

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0075-9511/04/34/03-224 $ 30.00/0

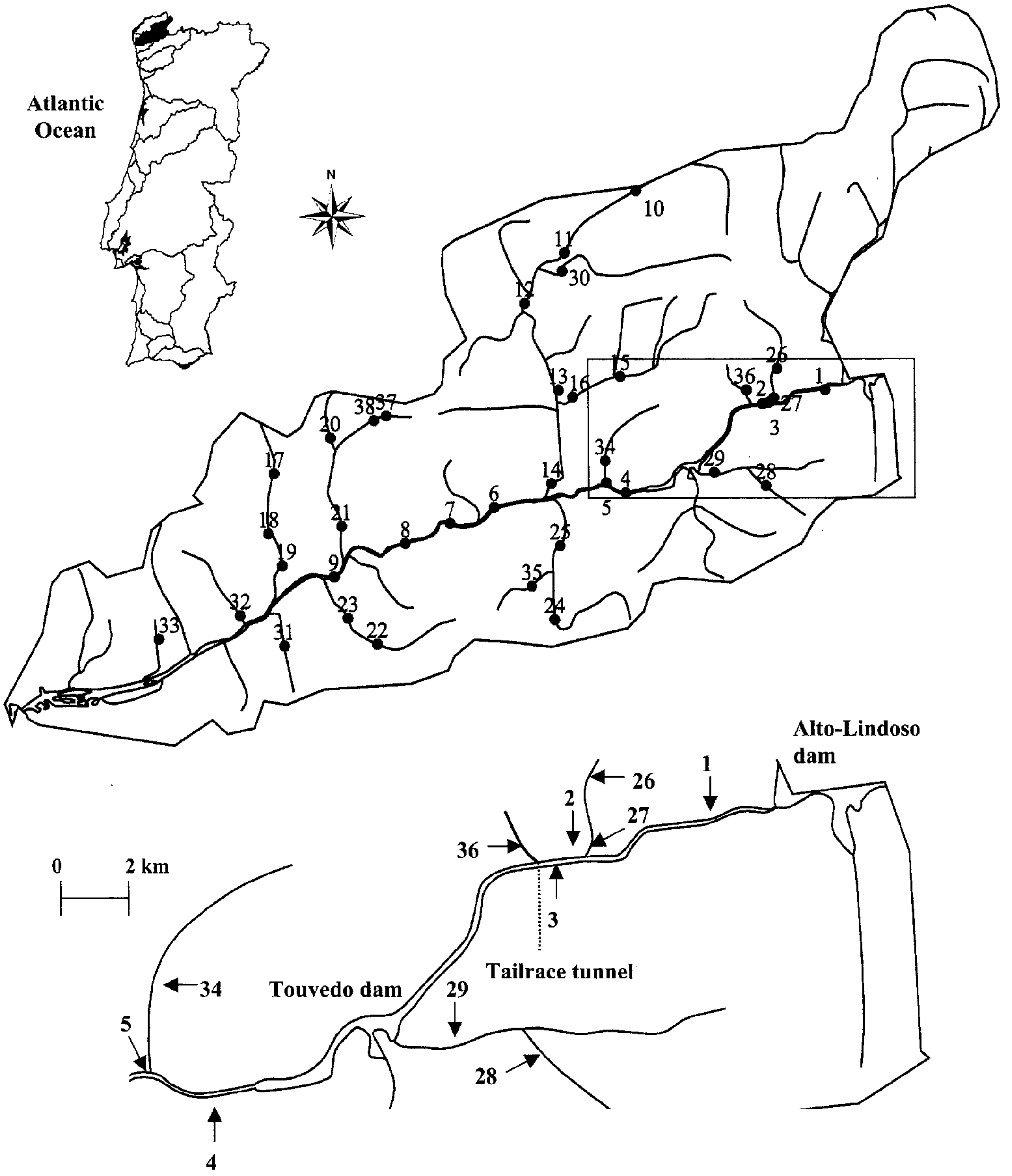

Fig. 1. Map showing the locations of the 38 sampling sites in the Lima basin. Site codes refer to Table 1.

(Davies et al. 1993; Poff et al. 1997). Nevertheless, the effects of regulation depend on the geographic location of the impoundment and the characteristics of both the river system and the way in which dams are operated, including the flow regime and its seasonal variability (Petts 1988).

Despite widespread flow regulation by dams over the last 50 years, insufficient attention has been paid to its effects on fish assemblages in the Iberian Peninsula (Casado et al. 1989; Camargo & Garcia de Jalon 1990; Garcia de Jalon et al. 1992; 1994; Almodóvar & Nicola 1999), particularly at the river basin level. However, regulation and the presence of dams are considered to be one of the main factors that are negatively affecting Iberian stream fish (Elvira 1996). It is therefore necessary to assess the extent of these effects on fish assemblages in order to be able to define proper mitigatory measures for Portuguese and Spanish River systems.

Portugal's rivers and streams are impounded by 166 large dams and more than 3,000 small weirs (1.5 to 15 m in height). The River Lima basin (Northern Portugal) is of particular interest to studies of the effects of regulation on fish assemblages, because it offers two different types of regulated flow patterns produced by dams placed only a few kilometres apart – in one case the water released is entirely hypolimnetic, but strongly reduced and with a constant flow, whereas in the other, the hydrograph of peaking tailwaters is intermittent and the water is released from a layer nearer the surface. Moreover, in the past decade there have been no studies on fish assemblages in the Lima basin (lotic segments) during and since the construction of the dams. Pre-regulation studies are also scarce (ROGADO 1992; VALENTE & ALEXANDRINO 1990; VALENTE et al. 1991). The present study is part of a larger one on the effects that river regulation is having on the biological communities of the River Lima basin (SANTOS et al. 2002; CORTES et al. 2002). Its main objectives were: (i) to study patterns in fish assemblage composition from streams with different characteristics; (ii) to analyse fish assemblages under different types of regulation; and (iii) to assess whether a flow that is minimum and stable (like that in the first case described above) and represents an attempt to achieve an in-stream ecological flow, has managed to maintain the existing assemblage structure effectively.

Study area

The River Lima rises in Spain's San Mamede mountains at an altitude of about 950 m, where it is fed by Antela Lake. It runs NE-SW for 68 kms through Spanish territory, about 3 kms more through Portuguese territory to the Alto Lindoso Dam and another 16.5 kms from there to the Touvedo Dam. By the time it reaches the Atlantic Ocean, its course has covered a total of 135 kms (Fig. 1).

The total catchment area is 2535 km^2, of which more than half is located in Spain. It is almost exclusively granitic and is characterized by a series of steep, narrow valleys with a relatively high run-off, due to an average annual rainfall of 1950 mm (more than 2800 mm at the headwaters). Downstream Touvedo Dam, the gradient is lower and homogeneous and the valleys become wider and dominated by alluvial materials. The headwaters of the tributaries are steeper and narrower, however. The riverbed is mainly composed of a mixture of boulders, pebbles and gravel. Riparian vegetation consists of English oak *(Quercus robur)*, common alder *(Alnus glutinosa)*, willow (*Salix* spp.) and poplar (*Populus* spp.).

River regulation began in 1992 with the construction of the Alto Lindoso Dam upstream and the Touvedo Dam immediately below it. Alto Lindoso is one of the key hydropower generators in Portugal, whereas Touvedo, which is smaller, acts as a tailwater reservoir, modulating the high flows released by its larger counterpart (250 m^3 s^{-1} at full load) and returning them to the river at no more than 100 m^3 s^{-1}. On the 16.5 km reach between the two dams, particular interest was paid to an upstream reach of about 7 km from the Alto Lindoso Dam to the outlet of the tailrace tunnel, which is fed by a constant hypolimnetic flow (0.5 m^3 s^{-1} from June-September and 2.0 m^3 s^{-1} from October-May) that the authorities set in order to fulfil minimal flow requirements (see Fig. 2 for a comparison of natural and modified regimes). Further downstream the remaining 9.5 kms have a much higher stream flow (due to the flow discharged by the above-mentioned tunnel) and are occupied by the Touvedo reservoir. By contrast, the main feature of the section downstream the Touvedo Dam is its irregular flow, precisely because the dam was designed to modulate the high flows from upstream (Fig. 2) by storing water for flash releases at times of day when demand is higher (the permanent minimum flow is set at 4.0 m^3 s^{-1}). The Touvedo Dam is equipped with the only fish lift in Portugal (SANTOS et al. 2002).

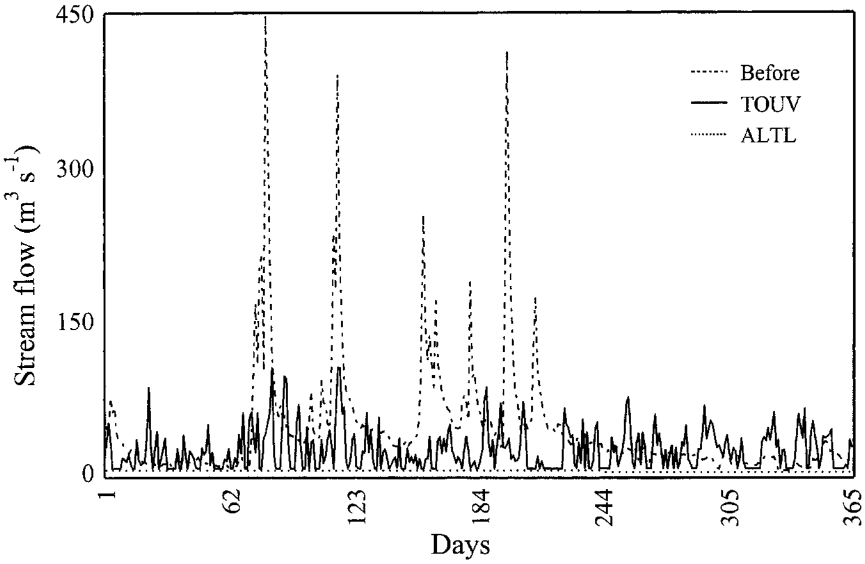

Fig. 2. Daily discharge (m^3 s^{-1}) for an average year before (1959/60) and after (1997/98) regulation. Downstream Alto Lindoso Dam (ALTL) the natural regime was replaced by an artificial sequence of flows of 0.5 m^3 s^{-1}, between June and September and 2.0 m^3 s^{-1} in the remaining period, whereas downstream Touvedo Dam (TOUV), an artificial sequence of flows varying between 4 m^3 s^{-1} (minimum instream flow) and 50 or 100 m^3 s^{-1} is the main feature, corresponding to one or two turbines operating.

Materials and Methods

Site selection

In order to assess overall patterns of the fish community structure, in the summer of 1998, a survey of fish assemblages was conducted in the Lima basin under base flow conditions at thirty-eight 100–200 metre-long sites on 1st–5th order streams along the River Lima and its tributaries. Sampling sites were selected on the basis of accessibility and were chosen to provide a broad spatial/environmental coverage of the Lima basin (Fig. 1, Table 1). Eight sites were sampled three more times, in the winter (January), spring (April) and autumn (October) of 1998. These sites – 1, 2, 5, 12, 24, 27, 29 and 36 – were established in order to evaluate the effect that the Alto Lindoso-Touvedo Dam system was having on the fish assemblages of the River Lima and were chosen to reflect the variety of physical conditions along the river.

The sampling sites were selected using a criterion of minimum evidence of human disturbance (flow regulation aside), such as major point-source pollution or agricultural run-off. River sources were also avoided so as to prevent comparisons between vastly different sites. In addition, no sites were chosen in the extensive brackish portion of the main river – i.e. downstream from site 9.

Table 1. Main characteristics of the studied sites. * Seasonal sampling.

Site	River	Order number	Altitude (m)	Mean slope (%)	Distance from source (km)	Width (m)	Depth (m)	Dominating substrate	No. of species
1*	Lima	4	190	2.4	44	20	0.8	BoulderRock	1
2*	Lima	4	65	0.1	50	25	0.7	BoulderRock	3
3	Lima	4	63	0.1	51	30	1.5	BoulderRock	4
4	Lima	4	25	0.2	62	60	3.0	Sand	6
5*	Lima	4	25	0.0	63	27	1.7	BoulderRock	4
6	Lima	5	10	0.0	72	70	1.8	Sand	5
7	Lima	5	10	0.0	76	75	1.9	Cobble	4
8	Lima	5	9	0.0	79	85	2.5	Fine	5
9	Lima	5	9	0.0	85	100	2.0	Fine	5
10	Vez	2	310	4.9	14	10	1.0	BoulderRock	2
11	Vez	3	105	1.5	20	16	0.5	BoulderRock	5
12*	Vez	3	65	0.5	25	26	0.8	BoulderRock	6
13	Vez	4	35	0.4	28	10	0.4	Cobble	5
14	Vez	4	25	0.2	38	22	0.9	Sand	6
15	Ázere	2	105	2.5	11	10	0.8	BoulderRock	4
16	Ázere	3	55	0.9	15	12	0.5	Cobble	5
17	Estorãos	2	35	1.1	5	2	0.3	Pebble	3
18	Estorãos	3	15	0.3	11	8	0.4	Sand	6
19	Estorãos	3	8	0.1	18	12	0.4	Sand	7
20	Labruja	2	120	3.7	6	5	0.7	BoulderRock	3
21	Labruja	2	15	0.4	13	9	0.6	Cobble	5
22	Trovela	2	90	6.1	8	10	0.4	BoulderRock	4
23	Trovela	3	25	0.7	11	7	0.7	Cobble	3
24*	Vade	2	135	7.2	5	8	0.3	BoulderRock	3
25	Vade	3	45	0.6	11	5	0.5	Cobble	4
26	Adrão	2	215	2.7	7	10	0.4	BoulderRock	4
27*	Adrão	3	65	7.8	10	6	0.4	BoulderRock	4
28	Froufe	1	460	11.0	4	4	0.4	BoulderRock	1
29*	Froufe	3	75	1.3	9	12	0.5	BoulderRock	5
30	Cabreiro	2	95	2.1	14	8	0.7	BoulderRock	4
31	Pontido	2	55	7.0	4	5	0.8	Sand	3
32	Lanheses	3	7	0.3	9	4	0.8	Sand	5
33	Nogueira	3	15	1.8	7	8	1.2	Fine	5
34	S. Jorge	2	45	1.0	8	3	0.4	Cobble	5
35	Fervença	1	230	12.3	5	4	0.4	BoulderRock	2
36*	Saramadigo	1	175	5.0	7	6	0.4	BoulderRock	2
37	Mestre	1	320	11.6	4	2	0.5	BoulderRock	1
38	Mestre	2	255	5.8	5	4	0.8	Cobble	2

Field collections

Fish were collected during daylight using a generator-powered DC electrofisher (Electracatch International, SAREL model WFC7-HV) with 400 V and a constant 3-A average output to a 40-cm stainless steel anode system, moving upstream, usually in a zigzag direction in shallow areas (< 1 m) and from a rubber boat in deeper ones (>1 m) (GODINHO et al. 2000). Sampling duration was roughly proportional to site area, with an effort of 30 minutes per site. Though electrofishing is considered the least biased method of sampling stream fishes, it only works in shallow water conditions – up to ~2 m (COWX 1989). Consequently, deeper sites (i.e. deeper areas in the main river) may have been sampled with a relatively low level of efficacy (but see MIRANDA & SCHRAMM 2000). Fishing success (numbers collected per unit of effort) was not significantly related to either depth or width ($r = -0.10$ and -0.04 respectively, both $P > 0.10$, $n = 38$, author's unpublished data). Nevertheless, where particular species are concerned there may still have been sources of habitat-related bias in the collection method and this issue will be addressed in the discussion. After sampling, fish were identified by species, counted, measured (total length to the nearest 1.0 mm) and returned to the river.

Explanatory variables

Once the fish had been collected, several environmental variables were evaluated for each site, including watershed characteristics, instream physical habitat structure and physicochemical properties. Watershed characteristics included mean annual temperature and rainfall, altitude, mean slope and distance from source (the latter was obtained from 1:50000 topographical maps). A site's location on a tributary or the main river was coded with the binary dummy variable RIVER (TER BRAAK 1987). Instream physical habitat structure included mean and maximum depth, dominant substrate class (coarseness), number of different substrate classes (heterogeneity), water velocity and wetted width. Depth was determined at a number of random points (mean number = 25) within each site using a graduated dip-net pole and was then converted to the following classes: < 0.5, 0.5–1.0, 1.0–2.0, >2.0 m. The dominant substrate class (fine <0.05, sand 0.05–2, gravel 2–16, pebble 16–64, cobble 64–256, boulder/rock >256 mm) was subjectively estimated around a 0.5-m-radius circle at the same points; two variables were derived from the substrate observations – the dominant (more frequent) substrate class and the number of different substrate classes (heterogeneity). Water velocity was measured with a R. OTT instrument. Water velocity was the velocity at 0.6 of the total depth if the water was less than 80 cm deep, or the mean of the velocities at 0.2 and 0.8 of the total depth in deeper water. Wetted width was visually estimated and converted to the following classes: <5, 5–10, 10–20, 20–30, 30–50, 50–75, >75 m. Riparian vegetation and shelters (overhanging rocks and trees) were visually estimated as being absent, or some (<25), dense (<60) or heavy (>60%) bank cover. The physicochemical data collected included water temperature, pH, conductivity and dissolved oxygen, as measured with a WTW meter (MultiLine P4).

In addition, regulated sites (sites 1, 2, 3, 4 and 5) were coded with the binary dummy variable REGULATION. Due to the proximity of both dams, these sites were primarily influenced by regulated flows, whereas other regulated sites below Touvedo Dam (sites 6, 7, 8 and 9) were much less affected by Touvedo's variable and flashy discharges, as they were downstream from major free-flowing rivers.

Data analysis

Fish were allocated to size classes based on major breaks of size-frequency histograms for each species and then analysed with frequency of occurrence and relative abundance data. Canonical Correspondence Analysis (CCA) was then used to identify relationships between explanatory variables and biological data (TER BRAAK 1986; RODRIGUEZ & MAGNAN 1995).

Two matrices were developed: relative abundance of species size-classes by sampling sites (17 × 38), and explanatory variables (i.e. environmental + REGULATION) by sampling sites (18 × 38). The CPUE data were transformed into log $(x + 1)$ values to reduce the influence of extremely abundant species (TER BRAAK 1987). The software options were set for a forward selection procedure in order to test significance and remove collinear explanatory variables. From all the explanatory variables that were considered, the best predictors were selected with a significance cut-off point of 0.10 (MAGNAN et al. 1994).

In order to analyse the impact of river regulation in more depth, fish assemblages were compared at the eight seasonal sites that displayed different types of flow modification. Comparisons initially used Jaccard's similarity coefficients (JC) on species presence/absence (JACCARD 1908). This coefficient measures the taxonomic similarity of the assemblages as the proportion of species common to each pair of sites/total species. It ranges from 0, where two sites have no species in common, to 1, where species are always present at both sites. Results were clustered using the NTSYS-pc software (ROHLF 1990). A matrix of cophenetic values was constructed in order to assess the dendrogram/data fit. A matrix of species abundance (the sea lamprey was excluded from this analysis in advance, due to insufficient samples) by sampling sites in each sampling season was also constructed (6 × 32) and submitted to correspondence analysis (CA). Due to the absence of some size-classes on particular sampling occasions, species size-classes were combined for these analyses.

Results

In all, 4407 specimens belonging to 7 fish species were collected (Table 2). The number of species collected at each site ranged from 1 (at three sites) to 7 (at site 19) and was correlated with stream order (r = 0.53, $P < 0.01$, Spearman's correlation). Mean CPUE varied considerably between the more frequent species in the basin. The Iberian barbel *(Barbus bocagei)* was the most frequent and abundant species in the main river, followed by the remaining cyprinids, in decreasing order: Iberian chub *(Squalius carolitertii)*, Iberian red roach *(Chondrostoma arcasii)* and Iberian nase *(Chondrostoma polylepis)*, whereas brown trout *(Salmo trutta)* returned the highest frequency and abundance in the tributaries. The sea lam-

Table 2. Species codes and size-classes. Main river and tributaries frequency of occurrence (FO) and CPUE (mean ± SD and maximum value between brackets) for the species found in the Lima basin. Significance level for Mann-Whitney rank sum test, comparing CPUE between main river and tributaries is also given.

Species	Code	Length class (mm)			Main river FO (%)	Tributaries FO (%)	Main river CPUE	Tributaries CPUE	*P*
		1	2	3					
Iberian barbel	Bb	<140	140–240	>240	88.9	37.5	25.8 ± 30.9 (83)	5.8 ± 13.8 (59)	<0.01
Iberian nase	Cp	<100	100–200	>200	55.6	43.8	8.2 ± 9.3 (23)	10.4 ± 18.5 (70)	
Iberian chub	Sc	<70	70–140	>140	77.8	62.5	17.1 ± 18.0 (52)	12.6 ± 17.6 (57)	
Iberian red roach	Ca	<60	>60		66.7	37.5	14.1 ± 18.0 (46)	10.0 ± 20.1 (84)	
Brown trout	St	<100	100–200	>200	22.2	87.5	0.4 ± 0.9 (2)	32.8 ± 25.9 (86)	<0.01
European eel	Aa	<200	>200		55.6	84.4	10.4 ± 13.8 (35)	8.7 ± 10.0 (38)	
Sea lamprey	Pm				22.2	6.3	0.4 ± 0.9 (2)	1.5 ± 7.5 (42)	

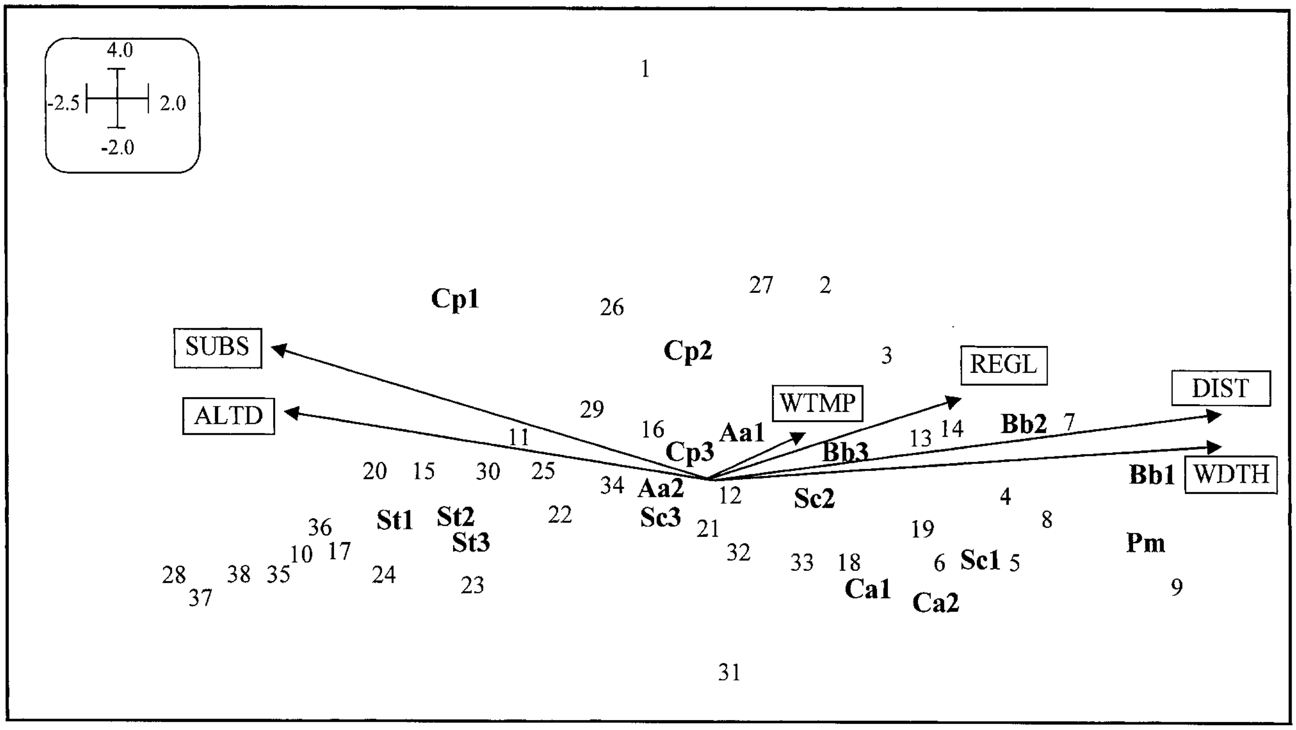

Fig. 3. Canonical correspondence analysis (CCA) diagram for the 17 species-size combinations and explanatory variables assessed at 38 sites in the Lima basin. Variable codes: SUBS = substrate coarseness, ALTD = altitude, WTMP = water temperature, REGL = REGULATION, DIST = distance from source, WDTH = wetted width. Eigenvalues were 0.29 for the first axis and 0.15 for the second axis. Site and species codes refer to Table 1 and 2, respectively.

Table 3. Summary statistics for the canonical correspondence analysis relating species to explanatory variables. Eigenvalues were 0.29 for the first axis and 0.15 for the second axis. * $P < 0.05$.

Explanatory variable	Code	Correlation with canonical axes	
		Axis 1	Axis 2
Width	WDTH	0.74*	0.12
Substrate coarseness	SUBS	–0.66*	0.50*
Water temperature	WTMP	0.13	0.18
Distance from source	DIST	0.74*	0.27
Altitude	ALTD	–0.64*	0.25
REGULATION	REGL	0.36*	0.32*

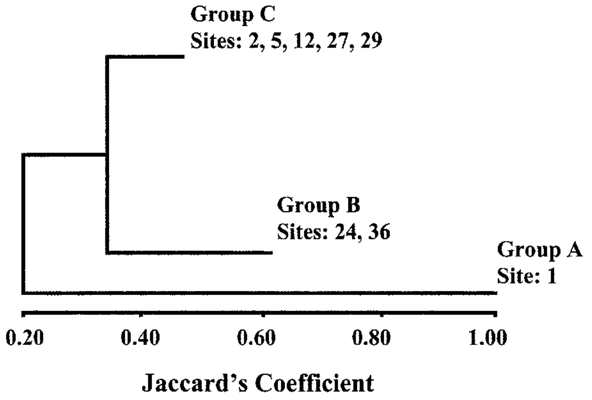

Fig. 4. Similarity (Jaccard's Coefficient) of fish assemblages as shown by cluster analysis on seasonal species presence. Site codes refer to Table 1.

Table 4. Frequency of occurrence (%) for the species encountered in each group of cluster analysis on seasonal species presence. The mean number of species is also given.

Group	A	B	C
Species/sites	1	24, 36	2, 5, 12, 27, 29
Iberian barbel			80
Iberian nase	100		85
Iberian chub		25	90
Iberian red roach		13	35
Brown trout		100	50
European eel		100	95
Mean no. of species	1.0	2.4	4.4

Table 5. SD of sample scores for each site, obtained by CA on seasonal species abundance. Group and location (MR – main river; T – tributary) are also given.

Site	Group	Location	SD
1	A	MR	0.04
2	C	MR	0.10
5	C	MR	0.24
12	C	T	0.27
24	B	T	0.16
27	C	T	0.27
29	C	T	0.17
36	B	T	0.34

prey *(Petromyzon marinus)*, which is a vulnerable migratory species (SNPRCN 1991), was rarely found in the basin.

The results of the canonical correspondence analysis (CCA) of fish species composition and environmental variables are shown in Fig. 3. The explanatory variables accounted for 47% of the total variation in site-assemblage composition, with the first and second axes displaying 77% of that variation (Table 3). The first axis primarily revealed a gradient of fish assemblages composed mostly of trout, followed by a dominance of small cyprinids such as Iberian nase and Iberian chub, to assemblages characterised by Iberian barbel, in association with altitude, wetted width, distance from source and substrate coarseness. Nevertheless, the variable REGULATION was also selected as a significant correlate of assemblage composition, although it was partially correlated with some of the above variables. Site 1 was clearly separated from all the other sampled sites. The composition of fish assemblages and explanatory variables were significantly related ($P < 0.01$), as shown by a Monte Carlo simulation test with 199 permutations (Ter Braak 1987).

The autumn sample from site 1 was excluded from analysis due to the absence of fish. Cluster analysis identified three groups of sites (Fig. 4). Group A included all the samples from site 1 (receiving constant flow from the Alto Lindoso Dam), which was strongly separated from all the other 7 sites, largely on the basis of the presence of one single species, Iberian nase (Table 4). The fish assemblages in Group B (sites 24 and 36) were characterised by the presence of trout and European eel *(Anguilla anguilla)*, a low frequency of small-size cyprinids (Iberian chub and Iberian red roach) and the absence of larger cyprinids (Iberian barbel and Iberian nase), and included all the seasonal samples from two small, unregulated streams (order number 1–2). Finally, group C (sites 2, 5, 12, 27 and 29) included sites with richer fish assemblages, which were characterised by the frequent presence of Iberian barbel, Iberian chub, Iberian nase and European eel. Brown trout also occurred in 50% of the samples within this group, but was never collected at

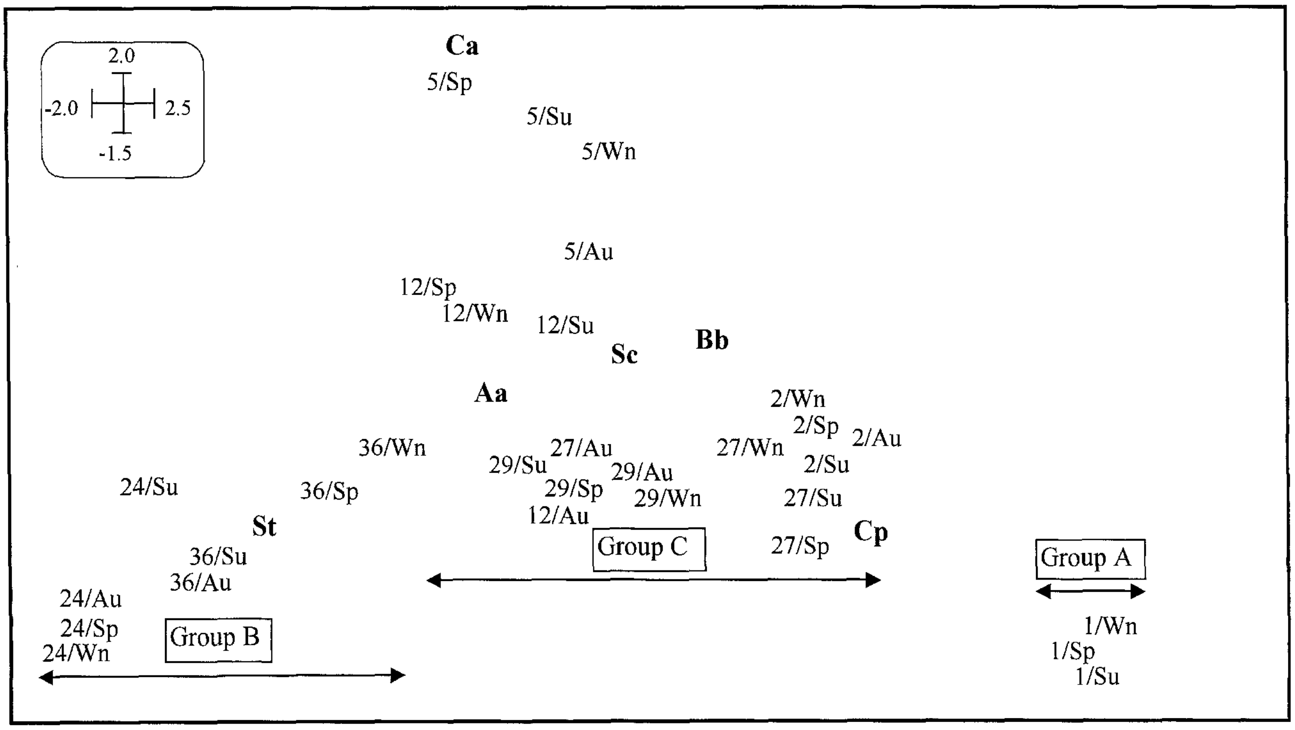

Fig. 5. Correspondence analysis (CA) diagram on seasonal species abundance. Season codes: Wn = winter, Sp = spring, Su = summer, Au = autumn. Eigenvalues were 0.33 for the first axis and 0.24 for the second axis. Site and species codes refer to Table 1 and 2, respectively.

the regulated sites (sites 2 and 5). The sites included in this group were medium-sized unregulated river sites and regulated main river sites (order number ≥ 3). Cophenetic values were highly correlated with site values ($r = 0.84$, $P < 0.05$), which suggested a good fit (little distortion) between the dendrogram and the data.

The CA that was performed at the same level with abundance data instead of presence/absence data yielded similar results, with the separation of the three groups of sites in accordance with the characteristic fish assemblage (Fig. 5). The regulated sites – particularly numbers 1 and 2 – displayed a lower (temporal) variation in assemblage composition than unregulated sites, as can be seen from the SD of sample scores for each site (Table 5).

Discussion

Fish species collected in this study included taxa that had previously been reported as occurring in the Lima basin (Valente & Alexandrino 1990). However, the migratory shads *Alosa alosa* and *Alosa fallax* that used to be common along the main river before regulation and impoundment were not found, though electrofishing could have been selective for these species, particularly at larger main river sites. Nevertheless, the use of gill nets (30 m × 2.5 m, with five positioned panels with mesh sizes of 32, 43, 50, 65 and 85 mm) at main river sites downstream from Touvedo Dam did not collect specimens from these species, thereby confirming our electrofishing results. Although the Atlantic salmon *(Salmo salar)* was not collected, it has been reported that it continues to occur, based on recent video recordings made at the Touvedo fish lift (Santos et al. 2002); however, it is extremely rare. Therefore, our results agree with the literature, where migratory species are frequently the first to decline following dam construction, due to a combination of factors, such as blockage of upstream and downstream movements, deterioration of water quality and loss of suitable habitat due to alteration of flow regimes (Ward & Stanford 1979; Petts 1988; Granado-Lorencio 1991; Nicola et al. 1996).

Generic patterns in the fish composition of the Lima basin were primarily associated with watershed features, particularly altitude and distance from source. Watershed features are frequently the major factors that shape fish assemblages on larger spatial scales, not only in temperate rivers (Kozel et al. 1989; Lyons 1989; Rahel & Hubert 1991) but also in Iberian ones (Godinho et al. 1997, 2000; Magalhães et al. 2002). However, the variable REGULATION also had an effect on assemblage patterns.

The most distinct fish patterns associated with regulation were found at site 1 (note its distinct position on the CCA biplot and its separation on the dendrogram). Similar results were found for the macroinvertebrate community, studied during the same period (CORTES et al. 2002). This site receives water directly from the bottom outlet of the Alto Lindoso Dam, which, due to its reservoir characteristics (mesotrophic with monomitic stratification) is richer in nutrients and organic matter, is thermally constant and is frequently deoxygenated (CORTES et al. 2002). This set of environmental conditions combined with an extremely low flow is likely to be detrimental to fish populations, particularly salmonids, which are intolerant to low oxygen concentrations (e.g. MOYLE & CECH 1996). Research carried out prior to river regulation (ROGADO 1992; VALENTE et al. 1991) in order to describe and study fish assemblages, mentioned the presence of brown trout and Atlantic salmon on this river reach. Currently, they have declined or are almost extinct (salmon). Similarly, cyprinid populations used to be locally abundant: in addition to Iberian nase, this reach used to harbour Iberian barbel, Iberian chub and Iberian red roach (VALENTE & ALEXANDRINO 1990). Presently, only the former was found. Different abilities to cope with conditions of the modified environment could have been determinant of the observed spatial patterns (BAIN et al. 1988). Indeed, it has been suggested that Iberian nase is more tolerant to river regulation than other Iberian cyprinids (GARCIA DE JALON et al. 1992). On the other hand, this species was frequently found in association with Iberian chub, particularly on the downstream reaches of tributaries. Similar patterns were observed in other small Iberian rivers, where intermittency is much more pronounced, and could also be supported by a lower predation risk, different food availabilities as well as biotic interactions (GODINHO et al. 1997, 2000).

Contrarily to Iberian nase, Iberian barbel was not encountered at site 1, although it occurred further downstream at sites 2 and 3. This could be due to an improvement in water quality as a result of an additional input from the upstream River Adrão (CORTES et al. 2002), therefore, providing more suitable conditions and increasing species richness. The effects of flow regulation on fish assemblages are most severe below dams, becoming less severe as tributary inflow and other physical processes ameliorate the dam's effects (BAIN et al. 1988; BROWN & FORD 2002). Nevertheless, the dominance of Iberian barbel in the main river (it was also the most frequent species collected by gill netting) is a common occurrence in other Iberian rivers, including some that are also influenced by regulation (GODINHO et al. 1997, 2000; CARMONA et al. 1999).

Fish assemblages from unregulated tributaries were characterised by the dominance of brown trout. Although a certain confinement of trout to the tributaries would naturally be expected, regulation should have contributed to this pattern by altering the aquatic environments in the main river and causing a depletion of dissolved oxygen on the water (CORTES et al. 2002). According to surveys undertaken on the main river before dam construction, brown trout was frequent on the upstream reach that is now receiving the constant flow (ROGADO 1992; VALENTE & ALEXANDRINO 1990; VALENTE 1993). Our results support some studies (CAMARGO & GARCIA DE JALON 1990; ALMODÓVAR & NICOLA 1999), but not others where trout has persisted following regulation (GARCIA DE JALON et al. 1988; CASADO et al. 1989; GARCIA DE JALON et al. 1994), or have even increased in abundance (MCKINNEY et al. 2001). However, the physical stability provided by constant hypolimnetic releases and reduced discharge variability, has not been beneficial for fish populations, particularly brown trout, because the water quality has seriously deteriorated.

The relationship between the three groups of sites, obtained by cluster analysis and confirmed by CA, as a measure of the degree of regulation, and species richness (Table 4) seems to be consistent with the intermediate disturbance hypothesis (CONNELL 1978). The hypothesis contends that low species richness is maintained by environmental stability at one extreme, or high disturbance at the other, with maximum richness occurring at some intermediate frequency of disturbance. The small unregulated streams (group B) are highly variable systems (SANTOS et al., in press), where low species richness seemed to be maintained by the frequency of disturbance, rather than by environmental stability. On the other hand, the stabilization of flow regimes at site 1 (group A) and the consequent reduced frequency of disturbances, along with a degradation of water quality, appeared to have significantly lowered the richness in local fish assemblages. Moreover, increased stability may disrupt environmentally cued cycles of reproduction and recruitment (WARD & STANFORD 1983). Contrarilly, fish assemblages at group C were found to contain most species. In addition to medium-sized unregulated streams, where riparian vegetation is often found to play an important role in the ecological structure and functioning (SCHIEMER et al. 1995; BARRELA & PETRERE 2003), this group also contained two main river sites: one, downstream site 1, but under more "unstable" conditions, since it receives an additional water input from a 3rd order upstream tributary, and other, downstream Touvedo Dam, directly influenced by short-term flow fluctuations. Because natural environmental instability plays a critical role in shaping assemblage structure (CONNEL 1978), artificially increased environmental instability should also affect assemblage structure. Appart from the absence of brown trout, our analyses did not show clear differences in the fish assemblages between these two sites and the formers. However, some authors suggested that besides the level of disturbance, habitat patchiness must also be considered when analysing fish assemblage composition (ALMODÓVAR & NICOLA 1999;

PEŇÁZ et al. 1999; TAYLOR et al. 2001). The maintenance of habitat heterogeneity certainly explains the high resilience of fish assemblages subjected to the unpredictable flow fluctuations. Substrate coarseness was one of the main parameters structuring fish assemblages (Table 1, Fig. 3). The importance of this variable has been highlighted elsewhere (SHELDON & MEFFE 1995; GODINHO et al. 2000), since it is essential by providing protection against widespread mammals (such as *Luttra luttra*) and birds (such as *Alcedo atthis* and *Ardea cineria*) and also by preventing fish from being washed away due to sudden discharges (HEGGENES 1988; LOBÓN-CERVIÁ 1996).

The artificial-induced stability at group A was also supported by a lower temporal variation in assemblage composition, compared to the other groups of sites (Table 5). Natural disturbances occur on a range of spatial and temporal scales, and the responses of natural assemblages to them depend on disturbance size, intensity and frequency (CONNELL & KEOUGH 1985). The artificial disturbances caused by a permanent constant hypolimnetic flow, did not impose a temporal scale of disturbance within the natural range experienced by stream fishes, which would certainly increase assemblage complexity (CONNEL 1978). On the other hand, in spite of the short-term flow fluctuations from Touvedo Dam, fish assemblages seemed to be able to cope with the new regime. Indeed, the pre-regulation community, which was largely dominated by cyprinids – Iberian barbel, Iberian nase and Iberian chub – along with brown trout and sea lamprey (VALENTE & ALEXANDRINO 1990), was similar to that observed in this study, although salmonids and shads have disappeared and sea lamprey was rarely observed. These results also parallel those obtained for the macroinvertebrate community and, besides the important role of undisturbed substrata, they could be linked to a lesser degradation of the water quality from the Touvedo reservoir, which, contrarily to Alto Lindoso reservoir, is derived from a more superficial layer, suffering from less oxygen depletion (CORTES et al. 2002). Therefore, WARD & STANFORD's (1983) contention that short-term flow fluctuations result in decline and extirpation of stream biota, was not totally supported by our results; although some of the anadromous species have seriously declined, most of the cyprinid species were able to adapt in the modified environment.

This work illustrated the effects of multiple factors on fish assemblages. In the studied basin, assemblages reflected the influence not only of large-scale watershed features, but also of anthropogenic actions derived from the building of dams and the subsequent flow regulation. The most obvious effects of regulation were the decrease or even disappearance of brown trout and migratory species from regulated segments. In the Lima basin, the deterioration in water quality appeared to be more detrimental to fish assemblages than the effects of unpredictable and variable discharges. Finally, this study expands on research of naturally disturbed rivers by providing results on an extreme case of artificial stability that appeared to reduce assemblage complexity and therefore, failed as an attempt to achieve an adequate ecological flow, being necessary to look for other, more appropriate mitigation measures.

Acknowledgements

The authors wish to thank C.P.P.E. (Companhia Portuguesa de Produção de Electricidade) for supplying data on river discharge measurements. Thanks are also due to António Albuquerque, Ricardo Diogo and Paulo Pinheiro for their valuable technical assistance. Lastly, thanks are also extended to Dr Richard Rogers, who reviewed the original manuscript. J.M. Santos was supported by a PhD grant from Fundação para a Ciência e Tecnologia (F.C.T.).

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