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Fish fauna in Iberian Mediterranean river basins: biodiversity, introduced species and damming impacts

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ABSTRACT

1. A basin approximation was used to analyse distribution patterns of different components of biodiversity (taxonomic richness, endemism, taxonomic singularity, rarity) and conservation status of freshwater fish fauna in 27 Mediterranean Iberian rivers.

2. Basin area alone explained more than 80% of variation in native species richness. Larger basins featured not only a higher number of native species, but also more endemic and rare species and fewer diversified genera than smaller basins.

3. In contrast, smaller basins scored higher community conservation values, owing to their lower degree of invasion by introduced species.

4. The presence of dams was the most important factor determining the conservation status of fish communities, and it was also positively associated with the number of introduced species.

5. While the most important components of Iberian freshwater fish biodiversity are located in large basins, small unregulated basins feature better conserved fish communities.

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KEY WORDS: freshwater fish; river impoundment; fish conservation; biodiversity assessment; Iberian Peninsula

INTRODUCTION

In the context of the contemporary massive loss of biodiversity, freshwater ecosystems have frequently been cited as among the most altered and threatened by human activities (Mason, 1991; Dynesius and Nilsson, 1994; Saunders *et al.*, 2002). Though first approaches to decline and extinction phenomena were mostly centred on terrestrial organisms, conservation of freshwater fauna has received increasing attention in recent times (Richter *et al.*, 1997; Harding *et al.*, 1998; Ricciardi and Rasmussen, 1999). Understanding biodiversity distribution patterns is a central issue for scientists and managers concerned with the current extinction processes. Following the Theory of Island Biogeography (MacArthur and Wilson, 1969),

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naturally delimited areas, such as oceanic islands and isolated mountain-top ecosystems, have frequently been studied in the search for factors determining species richness (Cronk, 1997; Chown *et al.*, 1998). River basins are also ecological and geographical units with clear borders, often becoming true islands for the freshwater fauna they contain, and thus can be studied using an island biogeography approach (Sepkoski and Rex, 1974; Hugueny and L eveque, 1994).

Freshwater fish are not only the most diverse group of vertebrates, they also feature the greatest proportion of threatened species (Bruton, 1995; Leidy and Moyle, 1998; Duncan and Lockwood, 2001). The relatively limited space occupied by freshwater fish (i.e. river or lake basins) with very reduced ability for inter-basin movement (Hocutt and Wiley, 1986; Unmack, 2001), in contrast with the relatively free-moving marine fish, is at the root of the conservation problems of the former (Richter *et al.*, 1997). The decline of freshwater fish is a generalized phenomenon noticeable on global (Duncan and Lockwood, 2001; Cowx and Collares-Pereira, 2002), regional and local scales (Miller *et al.*, 1989; Crivelli, 1996; Moyle and Randall, 1998; L opez-Rojas and Bonilla-Rivero, 2000). The principal threats to freshwater fish are the deterioration or destruction of habitats, both by pollution and intense modifications (i.e. damming, channelizations), and the introduction of exotic species (Moyle, 1986; Allan and Flecker, 1993).

The native freshwater fish fauna of the Iberian Peninsula is characterized by a low number of families, with most of the species belonging to the family Cyprinidae, a high degree of diversification at the species level, and the greatest European percentage of endemism (Doadrio, 2001). As in other Mediterranean peninsulas, the Iberian fluvial network is complex, comprising a high number of independent river basins where the different species' populations are strongly isolated. Most Iberian rivers follow a typical Mediterranean cycle, with autumn–winter floods and strong summer droughts (Gasith and Resh, 1999). This important seasonal instability, coupled with a huge interannual variability in the precipitation regime (Blondel and Aronson, 1999), are key factors in the structure of freshwater communities (Prenda and Gallardo, 1996; Pires *et al.*, 1999; Magalh aes *et al.*, 2002).

The Iberian freshwater fish fauna faces important conservation threats, with most native species suffering a progressive and generalized decline (Lob on-Cervi a *et al.*, 1989; Sostoa and Lob on-Cervi a, 1989; Elvira, 1995a; Perdices and Doadrio, 1997; Garc a-Berthou and Moreno-Amich, 2000). Subsequently, more than 80% of Spanish species have been classified as vulnerable, endangered or critically endangered in accordance with IUCN criteria (Doadrio, 2001). Furthermore, this situation could become even worse in the future. Introduced species are widespread and expanding their ranges (Elvira, 1995b; Aparicio *et al.*, 2000; Elvira and Almod ovar, 2001), many of them being piscivorous species, which is a trophic group almost completely absent in the original Iberian fauna. Concerning river alterations, in 2001 the Spanish government approved an ambitious National Hydrological Plan, which includes the construction of more than 100 large dams and important inter-basin connections (MMA, 2004). In this situation, a comprehensive assessment of fish biodiversity and fish community conservation status and their possible relationship with environmental variables and river alterations should be carried out as an important management tool for conservation.

This work reviews the distribution of biodiversity and conservation status of freshwater fish fauna in individual river basins of the southern Iberian Peninsula. There were two main objectives: to search for patterns in the distribution of different biodiversity components (taxonomic richness, endemism, taxonomic singularity and rarity) among Iberian basins; and to analyse the state of the invasion by introduced species, its relationship with river damming, and its possible influence on native fish fauna.

METHODS

The distribution of freshwater fish was compiled for 27 river basins from the southern and central Iberian Peninsula using data from Doadrio (2001), Clavero *et al.* (2002) and the authors' own unpublished data

Table 1. Drainage area and number of native and introduced species in the 27 river basins included in this study

River	Area (km ²)	<i>N</i> native species	<i>N</i> introduced species
Tajo	81947	13	13
Guadiana	67040	12	10
Guadalquivir	54970	11	8
Júcar	22145	9	13
Segura	16164	5	8
Guadalete	3359.7	4	4
Guadalhorce	3157.7	4	3
Odiel	2308.2	6	3
Guadiaro	1504.7	3	2
Barbate	1290.1	4	3
Vélez	609.7	3	3
Corumbel*	197.4	4	4
Candón*	195	3	3
Nicoba*	180	3	2
Jarama*	172	1	2
Valverde*	106.5	3	1
Estero*	101	2	3
Jara	58.2	2	0
Hornueco*	49.7	3	0
Valle	42.8	1	0
Manzano*	33.6	3	0
Cachán*	33.4	2	0
Gallego*	33.1	1	0
Miel	14.2	2	0
Guadalmesi	13.6	1	0
Maraber	5.2	0	0
Lobo	3.7	0	0

* Rivers are tributaries of the River Tinto, but were considered independent basins owing to the extreme acidic water of the Tinto (see Methods section for details).

(Table 1). Only independent river basins were included in the analysis, with the exception of the River Tinto tributaries. The Tinto is a highly acidic river (pH 2.3) due to the natural drainage of the south Iberian pyritic belt and mining activities, the latter having affected the river for around 5000 yr (Amaral Zettler *et al.*, 2002). As a result, the Tinto has no animal life and acts as an axial barrier that isolates the remaining freshwater fish populations in its tributaries. All basins studied feature a Mediterranean climate, through most or all of their surface area, and are part of a homogeneous biogeographic unit (the south Iberian sector) as defined by Doadrio (1988) on the basis of freshwater fish distribution.

Only freshwater species *sensu stricto* were included in the analysis, with all diadromous species being excluded. Overall, 40 fish species were considered, 23 (57.5%) of them being native in the basins studied, among which 20 (87%) were endemic to the Iberian Peninsula. Four different evaluations of native biodiversity were made: (i) taxonomic richness; (ii) endemism; (iii) taxonomic singularity; and (iv) rarity (Ojeda *et al.*, 1995).

The numbers of native species, genera, families, and introduced species were recorded for each basin. In addition, the number of native species was divided by the number of native genera in each basin to obtain a ratio of species to genus for native fish. Species were considered native or introduced in the different basins according to Doadrio (2001). Native Iberian species that are known to have been translocated were considered as introduced in their new distribution areas. Some historical translocations could have remained unidentified, with introduced species being treated as native; but this is improbable, since it has not been detected through genetic analyses (Doadrio, 2001).

An index of endemism was calculated for each native species recorded, using the 11 main groups of river basins in the Iberian Peninsula defined by Vargas *et al.* (1998) to analyse the distribution patterns of freshwater fish and amphibians. The value of a species endemism index was defined as the inverse of the number of Iberian group of basins in which that species is present (data from Doadrio (2001)). An endemism index of 0.1 (lower than any other calculated value) was arbitrarily assigned to the few native species with wide European or Mediterranean distributions.

Taxonomic singularity of each native species was defined as the inverse of the number of native congeneric species inhabiting the Iberian Peninsula (data from Doadrio (2001)).

Each native species' rarity was numerically estimated as the inverse of the number of 10×10 Universal Transverse Mercator (UTM) grid squares occupied by that species in Spain (Doadrio, 2001). An average value of endemism (END), taxonomic singularity (TS) and rarity (RAR) was calculated for each basin.

Tench *Tinca tinca* was treated as a native species (Doadrio, 2001), but, as it is currently a heavily managed species (and frequently re-stocked) and its original distribution is poorly known, it was not included in the calculations of endemism, rarity and taxonomic singularity indices.

The fish community conservation status in each basin was assessed using an index inspired by the Conservation Value of Doadrio *et al.* (1991). A positive value was assigned to each native species according to its IUCN threatened categories proposed by Doadrio (2001): Critically endangered, 4; Endangered, 3; Vulnerable, 2; Lower risk, 1. Whenever a protection category was proposed for a species' population in a certain basin that value was used for calculations. A negative numeric value was also assigned to each introduced species according to its potential piscivory: cyprinids and small fishes, -1; predatory fish not reaching 30 cm, -2; piscivorous species larger than 30 cm, -3. The average conservation value (CVm) was calculated for each basin.

Each basin was characterized by its surface area (km^2), the presence or absence of dams, the number of dams, and the volume of water retained in reservoirs. Data on surface areas and reservoir capacities were obtained from the Spanish Environmental Ministry web page (MMA, 2004). Where necessary, basin surface areas were estimated from 1:50 000 maps. Numbers of dams were counted using 1:200 000 topographic maps. Climatic data from 251 stations were compiled from Font (1983), and comprised mean temperature ($^{\circ}\text{C}$) in July and in January, mean annual precipitation (mm) and intra-annual precipitation variation coefficient.

Relationships among variables were studied using generalized linear models (GLMs) and mean comparison tests (Student's *t*). The data concerning numbers of species, basin surface area, number of dams, and volume in reservoirs were logarithmically (base *e*) transformed (Chown *et al.*, 1998).

RESULTS

Native fish biodiversity

A strong relationship was detected between the number of native species and basin surface area (Figure 1), accounting for 82% of the variation in native species richness. The level of intrageneric diversity seems to be one of the causes of the higher native species richness in larger basins (Figure 2).

Basin area was also an important factor explaining variations in endemism, rarity and taxonomic singularity values (Table 2). The analysis of these indices showed that smaller basins usually feature widely distributed species belonging to the most diversified genera (e.g. *Barbus*, *Squalius* and *Chondrostoma*) in the Iberian Peninsula. Endemic species present in a single basin (e.g. *Aneacypris hispanica*, *Barbus microcephalus*), with very restricted distributions (e.g. *Cobitis vettonica*) and/or with high taxonomic singularity (e.g. genera *Aneacypris* or *Salaria*) tend to be present only in the largest basins.

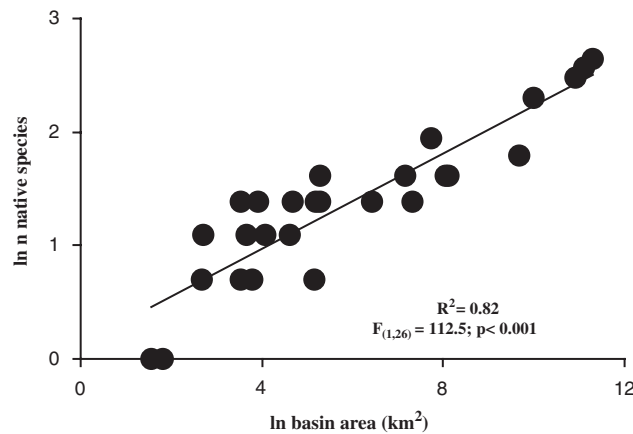


Figure 1. Relationship between native freshwater fish species richness and basin area for 27 river basins.

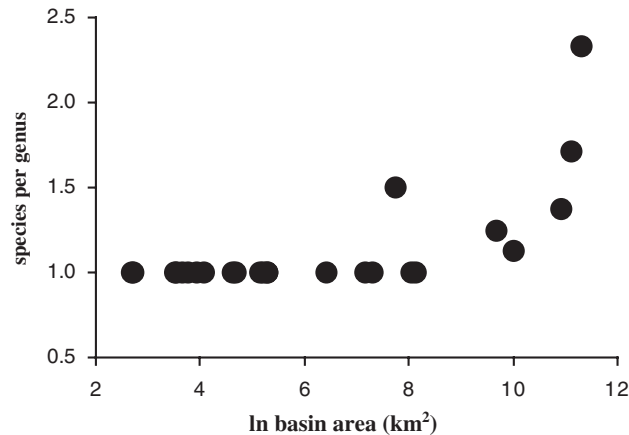


Figure 2. Ratio of number of species per genus for native fish as a function of basin area.

No statistical associations were detected between the climatic variables included in the analysis and any of the variables related to native freshwater fish biodiversity.

Introduced species and conservation status

As for native species, basin surface area strongly influenced the number of introduced freshwater fish species, but in this case the presence of dams was also significant in the model, which explained more than 90% of the variation in number of introduced species (Table 3).

The GLM using CVM as a dependent variable included as explanatory variables the presence of dams and the interaction of this variable and basin area, accounting for 73% of the variation in the index among basins (Table 3). The relationship between CVM and basin area is clearly influenced by the presence of dams (Figure 3). In basins without dams, CVM decreases with increasing surface area, whereas in dammed basins this index is independent of basin area. The basin area, the number of dams, and the volume in reservoirs had no significant influence on CVM once the presence of dams had been included in the model.

Table 2. Results from the regression models of the effect of river basin area on different measurements of native freshwater fish biodiversity

		D.f.	F-value	p	R ²	Variable	D.f.
Number of native species	Model	1	112.5	<0.001	0.82	Intercept	1
	Error	25				Basin area	1
	Total	26					
Mean endemism (END)	Model	1	23.3	<0.001	0.50	Intercept	1
	Error	23				Basin area	1
	Total	24					
Mean taxonomic singularity (TS)	Model	1	12.8	<0.01	0.36	Intercept	1
	Error	23				Basin area	1
	Total	24					
Mean rarity (RAR)	Model	1	10.9	<0.01	0.32	Intercept	1
	Error	23				Basin area	1
	Total	24					

Table 3. Results from a generalized linear model of the effects of basin area and damming on the number of introduced fish species, and the calculated conservation value of the fish community

		D.f.	F-value	p	Adjusted R ²	Variable	D.f.	F-value	p
Number of introduced species	Model	2	119.3	<0.001	0.91	Intercept	1	4.4	<0.05
	Error	22				Basin area	1	66.1	<0.001
	Total	24				Dams	1	18.8	<0.001
Mean conservation value (CVm)	Model	3	22.3	<0.001	0.73	Intercept	1	24.5	<0.001
	Error	21				Dams	1	20.4	<0.001
	Total	24				Dams*Basin area	2	4.8	<0.05

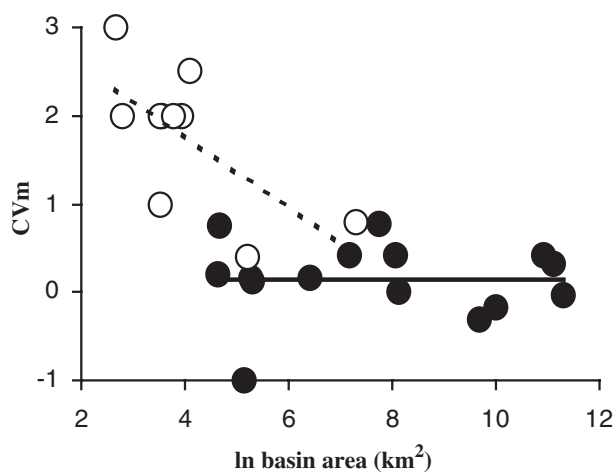


Figure 3. Mean conservation value (CVm) of the fish community as a function of basin area. Regression lines are presented separately for dammed basins (filled circles, solid lines) and undammed basins (empty circles, dotted lines).

However, a strong non-linear (power; $y = ax^b$) dependence of CVm on basin area could also be detected, accounting for 62% of the variance in the index ($F=36.9$; $p<0.001$).

The number of introduced species in the basins studied does not seem to be influenced by native assemblages. In fact, numbers of both native and introduced species increased in parallel with basin area, but no significant statistical relationship between the two variables was found once the effect of area had been eliminated. Abiotic factors related to river damming, and not biotic relationships with native fauna, would then be influential in the establishment of introduced species in the Mediterranean Iberian Peninsula.

DISCUSSION

Native fish biodiversity

These results show that the most important components of freshwater fish biodiversity in the Iberian Peninsula are confined to the largest basins, a situation that might be explained by the interaction of several factors. The first and perhaps most important factor is the geological history of each basin. In the Tertiary, when most of the present fish species evolved, the Iberian Peninsula was occupied by endorheic basins, whereas in the Quaternary these areas became fluvial basins, drained by the main Iberian rivers (Vargas *et al.*, 1998; Doadrio, 2001). Smaller river basins that did not emerge from endorheic basins were probably colonized later by a reduced number of species from the larger basins' assemblages. There are, however, certain species or genera that never colonized small basins, being exclusive to those which drain the ancient endorheic areas where they evolved.

The greater energy supply, buffer effects from catastrophic events (the most important in the area being summer drought), and habitat heterogeneity in large basins are also important factors maintaining biodiversity and a low extinction risk among fish populations. This is especially important in fluctuating environments, such as those of Mediterranean areas (Gasith and Resh, 1999), since variations in the flow regime and drought periods are much more intense in smaller basins, thus increasing the probability of extinction (Taylor and Warren, 2001). In fact, local fish extinctions have been documented in some small Iberian basins (García-Berthou and Moreno-Amich, 2000; Clavero *et al.*, 2002), but, until now, not in the larger ones. Exclusion of certain species by competition is also less intense in large basins, encouraging the presence of congeneric species (Figure 2). Carmona *et al.* (1999) proved the existence of at least three different geographical communities (chorotypes) within the Tajo river basin, the largest considered in this study, using fish species' distribution data. These chorotypes were mainly defined by the presence of different congeneric species belonging to the genera *Chondrostoma*, *Squalius*, *Barbus* and *Cobitis*.

It is noticeable from the results presented here that the important isolation suffered by Iberian fish in the great number of independent river basins has not led to local speciation. In fact, endemic species seem to be restricted to the larger basins that also hold the richest fish faunas. This agrees with the observations made by Oberdorff *et al.* (1999), who found that overall species richness was a strong predictor of the number of endemic species in river basins of the Northern Hemisphere. In the case of the basins studied, this pattern apparently points towards a recent colonization of small basins by freshwater fish. However, fish biodiversity has not been completely catalogued in the Iberian Peninsula (Doadrio, 2001), and new species are being described at a high rate in recent times. In fact, four new species have been described since 1997 (Doadrio and Perdices, 1997; Coelho *et al.*, 1998; Doadrio *et al.*, 2002), and this trend will continue in the future (Doadrio, 2001; Ignacio Doadrio pers. comm.). Therefore, it is possible that cryptic species which may have evolved in small basins, and which are morphologically indistinguishable from twin species in larger basins, at present remain undescribed.

Introduced species, dams and conservation status

Species introductions have frequently been cited as an important threat to native freshwater fauna, including amphibians and fish (Miller *et al.*, 1989). The introduction of the Nile perch (*Lates niloticus*) in Lake Victoria caused the most dramatic recorded episode of vertebrate species extinction among a native cichlid community (Kaufman, 1992), and in the western Mediterranean there are at least two cyprinid species known to have disappeared following the introduction of the pikeperch *Sander lucioperca* (Crivelli, 1995). However, the results of this study do not show any negative effect of introduced fish species on native fauna. In fact, the richness of introduced species follows a pattern similar to that observed for native species, with increasing values in larger basins and totally independent of each other. Analysis at the level of a whole basin might be responsible for the inability to detect local impacts of introduced fish species. Nevertheless, other studies have shown the occurrence of local extinctions and strong declines in native species populations (García-Berthou and Moreno-Amich, 2000) and of decreasing distribution areas of native species (Aparicio *et al.*, 2000), both related to introduced species establishment and expansion in the Iberian Peninsula.

The invasion by introduced fish is a widespread phenomenon in Iberian rivers: on average, 32.4% of the fish species in the basins studied were introduced, and in the five largest basins the mean proportion rose to 52%. These values are clearly higher than those presented by Guido and Brown (1999) for 125 North American drainages, where the mean proportion of non-native species was 14.2%. The results here show that the modification of river characteristics by damming has favoured the establishment of introduced species in Iberian rivers (see also Corbacho and Sánchez (2001)). Most occupied lentic habitats in their native distributions, and such habitats are scarce in Mediterranean areas (Elvira and Almodóvar, 2001). Mediterranean rivers undergo enormous intra- and inter-annual flow variations, becoming extremely unpredictable ecosystems (Gasith and Resh, 1999). In this environment, strong habitat or trophic specialization (such as piscivorous diets) has not evolved (Poff and Allan, 1995). In general, Iberian freshwater fish are habitat generalists very well adapted to survive in constantly changing environments (Magalhães *et al.*, 2002). Reservoirs provide the stable lentic habitats in which introduced species, many of them predatory, can develop thriving populations. It is also commonly assumed that introduced species can more easily become established in altered ecosystems (Herbold and Moyle, 1986; Ross, 1991; Ross *et al.*, 2001), such as those created by reservoirs.

Since the presence of dams in a basin, and basin area, are not independent variables (see Figure 3), the influence of dams on the CVM index could be reflecting the effect of basin area. In fact, the negative power dependence of the index on basin area can be interpreted as if there is a certain critical size below which basins are scarcely invaded and above which the level of invasion remains rather constant. This pattern could be related to the increasing stability of larger basins (see discussion above), which would allow the presence of introduced non-Mediterranean species. It is very difficult, however, to analyse separately the effect of basin area and dam construction, since medium- or large-sized basins without dams are extremely scarce in the Iberian Peninsula (see below). Other studies have shown the effects of dams on fish community integrity at local scales (e.g. Corbacho and Sánchez, 2000). Ruiz (1998) described the appearance of introduced species after impoundment of a river in southern Spain in an area where the fish fauna before dam construction had been composed exclusively of native species. Prenda *et al.* (2002) also showed that fish communities in southern Iberian reservoirs were mainly composed of introduced species, being clearly more affected by invasions than fluvial ecosystems in similar areas. From this evidence, we consider that the patterns of fish community conservation status detected in this study at a basin scale can be explained primarily by the effects of river damming.

Spanish rivers feature more than 1000 large dams (at least 1 hm³), with a rapid increase in the number of reservoirs since the 1950s (MMA, 1998). In spite of this, the recently approved National Hydrological Plan includes the construction of around 100 new dams and huge inter-basin connections (MMA, 2004). In the

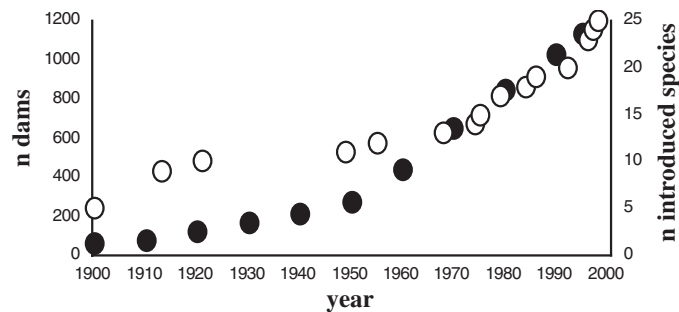


Figure 4. Cumulative numbers of dams (filled circles) and introduced fish species (empty circles) during the 20th century. Data from MMA (1998: dams) and Elvira and Almodóvar (2001: introduced species).

light of the results shown here, the establishment of new reservoirs is an important threat to the native freshwater fish fauna, through promoting the establishment of introduced species, most of which exhibit a high degree of invasiveness in these artificial ecosystems. Following the empirical demonstration in this study of a statistically significant association, it is suggested that there is a causal relationship between the parallel increases of dams and number of introduced species recorded in Spain during the 20th century (Figure 4). Assuming that conservation of biodiversity is an important assignment, different management strategies of hydrological resources, based on optimizing water use, should be attempted by governments in Mediterranean areas.

As the main sources of freshwater fish biodiversity in the Iberian Peninsula are the large river basins, special efforts should be made to conserve their unique fauna. Nevertheless, though smaller basins feature fewer and less distinct species, small undammed basins are, so far, the only ones that maintain pristine fish communities. Therefore, it is also important to preserve these watercourses (Saunders *et al.*, 2002), since flow alterations would increase the probability of their invasion by introduced species.

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