

Fish Fauna in Iberian Mediterranean River Basins: Biodiversity, Introduced Species and Damming Impacts

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ABSTRACT

1. We used a basin approximation 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 less diversified genera than smaller ones.
3. In contrast, smaller basins scored higher community conservation values, due 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 ones feature better conserved fish communities.

INTRODUCTION

In the context of the contemporary massive loss of biodiversity, freshwater ecosystems have been frequently cited 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), naturally delimited areas, such as oceanic islands and isolated mountain top ecosystems, have been frequently 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 from an island biogeography approach (Sepkoski and Rex, 1974; Hugueny and Léveque, 1994).

Freshwater fishes are not only the most diverse group of vertebrates but also the one that features the greatest proportion of threatened species (Bruton, 1995; Leidy and Moyle, 1998; Duncan and Lockwood, 2001). The relatively limited space occupied by freshwater fishes (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 fishes, lays in the base

of the conservation problems of the former (Richter *et al.*, 1997). The decline of freshwater fishes is a generalised phenomenon noticeable on global (Duncan and Lockwood, 2001; Cowx and Collares-Pereira, 2002), regional and local (Miller *et al.*, 1989; Crivelli, 1996; Moyle and Randall, 1998; López-Rojas and Bonilla-Rivero, 2000) scales. The principal threats to freshwater fishes 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 characterised by a low number of families, 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; Magalhães *et al.*, 2002).

The Iberian freshwater fish fauna faces important conservation threats, with most native species suffering a progressive and generalised decline (Lobón-Cerviá *et al.*, 1989; Sostoa and Lobón-Cerviá, 1989; Elvira, 1995a; Perdices and

Doadrio, 1997, García-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 Almodóvar, 2001), many of them being piscivorous species, which is a trophic group almost completely absent in the original Iberian fauna. Concerning river alterations, the Spanish government approved in 2001 an ambitious National Hydrological Plan, which includes the construction of more than one hundred big dams and important inter-basin connections (MMA, 2002). In this situation, a comprehensive quantification of fish biodiversity and fish communities conservation status and their possible relation with environmental variables and river alterations should be developed as an important management tool for conservation.

This work reviews the distribution of biodiversity and conservation status of freshwater fish fauna in the southern Iberian peninsula on an individual basin basis, with two main objectives: 1) to search for patterns in the distribution of different biodiversity components (taxonomic richness, endemism, taxonomic singularity and rarity) among Iberian basins; and 2) to analyse the state of the invasion by introduced species, its relation with river damming, and its possible influence on native fish fauna.

METHODS

The distribution of freshwater fishes was compiled for twenty-seven 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). Only independent river basins were included in the analysis, with the exception of the river Tinto tributaries. The Tinto is a highly acidic river ($\text{pH} \approx 2.3$) due to the natural drainage of the south Iberian pyritic belt and mining activities, the latter of which have affected the river for around 5000 years (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 studied basins feature a Mediterranean climate, at least through most or all their surface, and are part of an 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 studied basins, among which 20 (87%) were endemic to the Iberian Peninsula. Four different approaches to native biodiversity were performed: i) taxonomic richness; ii) endemism; iii) taxonomic singularity; and iv) rarity (Ojeda *et al.*, 1995).

The numbers of native species, genera, and families, and introduced species were recorded for each basin. We also divided the number of native species by

the number of native genera in each basin to obtain a ratio species per genus for native fish. Species were considered native or introduced in the different basins according to Doadrio (2001). Native Iberian species which are known to have been translocated were considered introduced species in their new distribution areas. Some historical translocations could have remained unidentified, with introduced species being treated as native, but we consider this 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 10x10 Universal Transversal Mercator (UTM) quadrates 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.

Following Doadrio (2001), we treated the tench *Tinca tinca* as a native species, but, as it is currently a strongly managed species (and frequently restocked) and there is a poor knowledge of its original distribution, we did not include it in the calculations of endemism, rarity and taxonomic singularity indexes.

The fish community conservation status in each basin was assessed using an index inspired by the Conservation Value of Doadrio *et al.* (1991). We assigned a positive value 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 we used that value for calculations. A negative numeric value was also assigned to each introduced species according to their potential piscivory (cyprinids and small fishes, -1; predatory fishes not reaching 30 cm, -2; piscivorous species bigger than 30 cm, -3). The average conservation value (CVM) was calculated for each basin.

Each basin was characterised by its surface (km²), the presence or absence of dams, the number of dams (ND), and the volume of water retained in reservoirs (RV; in Hm³). Data on basin surfaces and reservoir capacities were obtained from the Spanish Environmental Ministry web page (MMA, 2002). When necessary basin surfaces were estimated on basis of 1:50.000 maps. Numbers of dams were counted using 1:200.000 topographic maps. Climatic data from 251 stations in the different studied basins were compiled from Font (1983). Climatic variables included in the analysis were: mean temperature in

July, mean temperature in January (both °C), mean annual precipitation (mm) and intrannual precipitation variation coefficient.

Relationships among variables were studied using generalised linear models (GLM) and mean comparison tests (Student t). Variables concerning numbers of species, basin surface, number of dams and volume in reservoirs were logarithmically (base e) transformed (Chown *et al.*, 1998).

RESULTS

Native fish biodiversity

We detected a strong relationship between the number of native species and basin surface area (Figure 1), which accounted 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 indexes 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 *Anaacypris* or *Salaria*) tend to be present only in the largest basins.

We did not detect any statistical association between the climatic variables included in the analysis and any of the variables related with native freshwater fish biodiversity.

Introduced species and conservation status

As for native species, basin surface strongly influenced the number of introduced freshwater fish species, but in this case the presence of dams was also significant 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 index's variation 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, while in dammed ones this index is independent of basin area. Neither basin area, the number of dams, nor the volume in reservoirs had any significant influence on CVM once the presence of dams had been included in the model. However, a strong non-linear (power; $y = a \cdot x^b$) dependence of CVM on basin area could also be detected, accounting for 62% of the index's variance ($F = 36.9$; $p < 0.001$).

The number of introduced species in the studied basins does not seem to be influenced by native assemblages. In fact, both native and introduced species numbers 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 Mediterranean Iberian Peninsula.

DISCUSSION

Native fish biodiversity

Our results show that the most important components of freshwater fish biodiversity in the Iberian peninsula are confined to the biggest 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's development. While in the Tertiary Period the Iberian peninsula was occupied by endorheic basins, where most of the current fish species evolved, in the Quaternary Period 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 colonised later by a reduced number of species from the larger basins' assemblages. There are, however, certain species or genera that never colonised 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, increasing the probability of extinction (Taylor and Warren, 2001). In fact, local fish extinctions have been documented in some Iberian small basins (García-Berthou and Moreno-Amich, 2000; Clavero *et al.*, 2002), but, until the present, 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' distributions 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 fishes 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 endemic species numbers in river basins of the Northern Hemisphere. In the case of the studied basins, this pattern apparently points towards a recent colonisation of small basins by freshwater fishes. 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. com.). It is therefore possible that cryptic species which may have evolved in small basins, and which are morphologically indistinguishable from twin species in larger basins, presently remain undescribed.

Introduced species, dams and conservation status

Species introductions have been frequently cited as an important threat to native freshwater fauna, including amphibians and fishes (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 the native chichlids community (Kaufman, 1992), while in the western Mediterranean at least two cyprinid species are known to have disappeared following the introduction of the pikeperch *Sander lucioperca* (Crivelli, 1995). However, our results do not show any negative effect of introduced fishes on native fauna. In fact, introduced species richness follow a pattern similar to that observed for native ones, with increasing values in larger basins, being totally independent one of each other. Our analysis level, on a whole basin basis, might be responsible for this apparent innocuousness of introduced fish species, being unable to detect local impacts. Nevertheless, other works have shown the occurrence of local extinctions and strong declines in native species populations (García-Berthou and Moreno-Amich, 2000) and 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 fishes is a generalised phenomena in Iberian rivers, as a mean 32.4% of the fish species in the studied basins were introduced, while in the five largest basins the mean proportion rose to 52%. These values are clearly worse than those presented by Gido and Brown (1999) for 125 North American drainages, where the mean proportion of non native species was 14.2%. As shown in the results, the modification of river characteristics by damming has favoured the establishment of this introduced species in Iberian rivers (see also Corbacho and Sánchez, 2001). Most introduced species in Iberian freshwaters occupied lentic habitats in their native distributions, which 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 specialisation, such as piscivorous diets, has not evolved (Poff and Allan, 1995). In general, Iberian freshwater fishes 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 establish 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 was a certain critical size below which basins were hardly invaded and above which the level of invasion remained rather constant. This pattern could be related to the increasing stability of larger basins (see discussion above) that would allow the presence of introduced non-Mediterranean species. It is, however, very difficult 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). However, at local scales other works have shown the effects of dams on fish community integrity (i. e. Corbacho and Sánchez, 2000). Ruiz (1998) described the appearance of introduced species after a river impoundment in southern Spain in an area where the fish fauna before dam construction was 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 work at a basin scale could be explained primarily by the effects of river damming.

Spanish rivers feature more than one thousand big dams (at least 1 Hm³), with a rapid increase in the number of reservoirs since the 1950's (MMA, 1998). In spite of this, the recently approved National Hydrological Plan includes the construction of around one hundred new dams and huge inter-basin connections (MMA, 2002). In the light of the results shown here, the establishment of new reservoirs is an important threat to the native freshwater

fish fauna, through its promotion of the establishment of introduced species, most of which exhibit a high degree of invasiveness in these human created 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 an optimisation of water use, should be attempted by Mediterranean areas' governments.

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. It is therefore also important to preserve these water courses (Saunders *et al.*, 2002), since flow alterations would increase the probability of their invasion by introduced species.

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REFERENCES

- Allan J D, Flecker AS. 1993. Biodiversity conservation in running waters. *BioScience* **43**: 32-43.
- Amaral Zettler L A, Gómez F, Zettler E, Keenan BG, Amils R, Sogin ML. 2002. Eukariotic diversity in Spain's river of fire. *Nature* **417**: 137.
- Aparicio E, Vargas MJ, Olmo JM, de Sostoa A. 2000. Decline of native freshwater fishes in a Mediterranean watershed on the Iberian Peninsula: a quantitative assessment. *Environmental Biology of Fishes* **59**: 11-19.
- Blondel J, Aronson J. 1999. *Biology and wildlife of the Mediterranean Region*. Oxford University Press: Oxford.
- Bruton MN. 1995. Have fish had their chips? The dilemma of threatened fishes. *Environmental Biology of Fishes* **43**: 1-27.
- Carmona JA, Doadrio I, Márquez AL, Real R, Hugueny B, Vargas JM. 1999. Distribution patterns of indigenous freshwater fishes in the Tagus River basin, Spain. *Environmental Biology of Fishes* **54**: 371-387.
- Chown SL, Gremmen NJM, Gaston KJ. 1998. Ecological biogeography of southern islands: species-area relationships, human impacts and conservation. *American Naturalist* **152**: 562-575.

- Clavero M, Rebollo A, Valle J, Blanco F, Narváez M, Prenda J. 2002. Distribución y conservación de la ictiofauna continental en pequeñas cuencas costeras del Campo de Gibraltar. *Almoraima* **27**: 335-342.
- Coelho MM, Bogutskaya NG, Rodrigues JA, Collares-pereira MJ. 1998. *Leuciscus torgalensis* and *L. aradensis*, two new cyprinids for Portuguese fresh waters. *Journal of Fish Biology* **52**: 937-950.
- Corbacho C, Sánchez JM. 2001. Patterns of species richness and introduced species in native freshwater fish faunas of a Mediterranean-type basin: the Guadiana river (southwest Iberian Peninsula). *Regulated Rivers: Research and Management* **17**: 699-707.
- Cowx IG, Collares-Pereira MJ. 2002. Freshwater fish conservation: options for the future. In: Collares-Pereira MJ, Cowx IG, Coelho MM (eds.). *Conservation of freshwater fish: options for the future*. pp. 443-452. Fishing News Books, Blackwell Science: Oxford.
- Crivelli AJ. 1995. Are fish introductions a threat to endemic freshwater fishes in northern Mediterranean region?. *Biological Conservation* **72**: 311-319.
- Crivelli AJ. 1996. *The freshwater fish endemic to the northern Mediterranean region. An action plan for their conservation*. Tour du Valat Publication: Arles.
- Cronk QCB. 1997. Islands: stability, diversity, conservation. *Biodiversity and Conservation* **6**: 477-493.
- Doadrio I. 1988. Delimitation of areas in the Iberian peninsula on the basis of freshwater fishes. *Bonner Zoologische Beiträge* **39**: 113-128.

- Doadrio I (ed.). 2001. *Atlas y libro rojo de los peces continentales de España*.
Ministerio de Medio Ambiente: Madrid.
- Doadrio I, Elvira B, Bernat Y. 1991. *Peces continentales españoles. Inventario y clasificación de zonas fluviales*. ICONA, Ministerio de Agricultura, Pesca y Alimentación: Madrid.
- Doadrio I, Perdices A. 1997. Taxonomic study of the Iberian *Cobitis* (Osteichthyes, Cobitidae) with description of a new species. *Zoological Journal of the Linnean Society* **119**: 51-67.
- Doadrio I, Carmona JA, Fernández-Delgado C. 2002. Morphometric study of the Iberian *Aphanius* (Actinopterygii, Cyprinodontiformes), with description of a new species. *Folia Zoologica* **51**: 67-79.
- Duncan JR, Lockwood JL. 2001. Extinction in a field of bullets: a search for causes in the decline of the world's freshwater fishes. *Biological Conservation* **102**: 97-105.
- Dynesius M, Nilsson C. 1994. Fragmentation and flow regulation of river systems in the northern 3rd of the world. *Science* **266**: 753-762.
- Elvira B. 1995a. Conservation status of endemic freshwater fish in Spain. *Biological Conservation* **72**: 129-136.
- Elvira B. 1995b. Native and exotic freshwater fishes in Spanish river basins. *Freshwater Biology* **33**: 103-108.
- Elvira B, Almodovar A. 2001. Freshwater fish introductions in Spain: facts and figures at the beginning of the 21st century. *Journal of Fish Biology* **59**: 323-331.

- Font I. 1983. *Atlas climático de España*. Instituto Nacional de Meteorología: Madrid.
- García-Berthou E, Moreno-Amich R. 2000. Introduction of exotic fish into a Mediterranean lake over a 90-year period. *Archiv für Hydrobiologie* **149**: 271-284.
- Gasith A, Resh VH. 1999. Streams in Mediterranean climate regions - Abiotic influences and biotic responses to predictable seasonal events. *Annual Review of Ecology and Systematics* **30**: 51-81.
- Gido KB, Brown JH. 1999. Invasion of North American drainages by alien fish species. *Freshwater Biology* **42**: 387-399.
- Harding JS, Benfield EF, Bolstad PV, Helfman GS, Jones III EBD. 1998. Stream biodiversity: the ghost of land use past. *Proc. Nat. Acad. Sci. U.S.A.* **95**: 14843-14847.
- Herbold B, Moyle PB. 1986. Introduced species and vacant niches. *American Naturalist* **128**: 751-760.
- Hocutt CH, Wiley EO. 1986. *The zoogeography of North American freshwater fishes*. John Wiley and Sons Ltd.: Chichester.
- Hugueny B, Lèveque C. 1994. Freshwater fish zoogeography in west Africa: faunal similarities between river basins. *Environmental Biology of Fishes* **39**: 365-380.
- Kauffman L. 1992. Catastrophic changes in species-rich freshwater ecosystems: the lessons of Lake Victoria. *BioScience* **42**: 846-858.

- Leidy RA, Moyle PB. 1998. Conservation status of the world's freshwater fish fauna: an overview. In: Fielder PL, Karieva PM (eds.). *Conservation Biology: for the coming decade, 2nd edn.* pp. 187-227. Chapman and Hall: New York.
- Lobón-Cerviá J, Elvira B, Rincón PA. 1989. Historical changes in the fish fauna of the River Duero basin. In: Petts GE (ed.). *Historical change of large alluvial rivers: western Europe.* pp. 221-232. John Wiley and Sons Ltd.: Chichester.
- López-Rojas H, Bonilla-Rivero A. 2000. Anthropogenically induced fish diversity reduction in Lake Valencia Basin, Venezuela. *Biodiversity and Conservation* **9**: 757-765.
- MacArthur RH, Wilson EO. 1967. *The theory of island biogeography.* Princeton University Press: Princeton.
- Magalhães MF, Beja P, Canas C, Collares-pereira MJ. 2002. Functional heterogeneity of dry-season fish refugia across a Mediterranean catchment: the role of habitat and predation. *Freshwater Biology* **47**: 1919-1934.
- Mason CF. 1991. *Biology of freshwater pollution.* Longman Scientific and Technical: New York.
- MMA. 1998. *Libro blanco del agua en España.* Ministerio de Medio Ambiente: Madrid.
- MMA. 2002. http://www.mma.es/rec_hid/plan_hidro/index.htm
- Miller RR, Williams JD, Williams JE. 1989. Extinction of North American fishes during the past century. *Fisheries* **14**: 22-38.

- Moyle PB. 1986. Fish introductions into North America: patterns and ecological impact. In: Mooney HA, Drake JA (eds.). *Ecology of biological invasions of North America and Hawaii* pp. 27-43. Springer-Verlag: Berlin.
- Moyle PB, Randall PJ. 1998. Evaluating the biotic integrity of watersheds in the Sierra Nevada, California. *Conservation Biology* **12**: 1318-1326.
- Oberdorff T, Lek S, Guèguan JF. 1999. Patterns of endemism in riverine fish of the Northern Hemisphere. *Ecology Letters* **2**: 75-81.
- Ojeda F, Arroyo J, Marañón, T. 1995. Biodiversity components and conservation of Mediterranean heathlands in southern Spain. *Biological Conservation* **72**: 61-72.
- Perdices A, Doadrio I. 1997. Threatened fishes of the world: *Cobitis paludica* (De Buen, 1930) (Cobitidae). *Environmental Biology of Fishes* **49**: 360.
- Pires AM, Cowx IG, Coelho MM. 1999. Seasonal changes in fish community structure in the middle reaches of the Guadiana basin, Portugal. *Journal of Fish Biology* **54**: 235-249.
- Poff NL, Allan JD. 1995. Functional organization of stream fish assemblages in relation to hydrologic variability. *Ecology* **76**: 606-627.
- Prenda J, Gallardo A. 1996. Self-purification, temporal variability and the macroinvertebrate community in small lowland Mediterranean streams receiving crude domestic sewage effluents. *Archiv für Hydrobiologie* **136**: 159-170.
- Prenda J, Clavero M, Blanco F, Rebollo A. 2002. Consecuencias ecológicas de la creación de embalses en el ámbito mediterráneo: el caso de los peces. In:

- Moral L (coord.) *Actas del III Congreso Ibérico de Gestión y Planificación del Agua*. pp: 497-503. Sevilla.
- Ricciardi A, Rasmussen JB. 1999. Extinction rates of North American freshwater fauna. *Conservation Biology* **13**: 1220-1222.
- Richter BD, Braun DP, Mendelson MA, Master LL. 1997. Threats to imperiled freshwater fauna. *Conservation Biology* **11**: 1081-1093.
- Ross ST. 1991. Mechanisms structuring streamfish assemblages: are there lessons from introduced species?. *Environmental Biology of Fishes* **30**: 359-368.
- Ross RM, Lellis W, Bennet RM, Johnson C. 2001. Landscape determinants of nonindigenous fish invasions. *Biological Invasions* **3**: 347-361.
- Ruiz AR. 1998. Fish species composition before and after construction of a reservoir on the Guadalete River (SW Spain). *Archiv für Hydrobiologie*. **142**: 353-369
- Saunders DL, Meeuwig JJ, Vincent CJ. 2002. Freshwater protected areas: strategies for conservation. *Conservation Biology* **16**: 30-41.
- Sepkoski JJ, Rex MA. 1974. Distribution of freshwater mussels: coastal rivers as biogeographic islands. *Syst. Zool.* **23**: 165-188.
- Sostoa A, Lobón-Cerviá J. 1989. Fish and fisheries of the river Ebro: actual state and recent history. In: Petts GE (ed.). *Historical change of large alluvial rivers: western Europe*. pp. 233-247. John Wiley and Sons Ltd.: Chichester.

Taylor CM, Warren Jr. ML. 2001. Dynamics in species composition of stream fish assemblages: environmental variability and nested subsets. *Ecology* **82**: 2320-2330.

Unmack PJ. 2001. Biogeography of Australian freshwater fishes. *Journal of Biogeography* **28**: 1053-1089.

Vargas JM, Real R, Guerrero JC. 1998. Biogeographical regions of the Iberian peninsula based on freshwater fish and amphibian distributions. *Ecography* **21**: 371-382.

Table 1. Drainage area and number of native and introduced species in the 27 river basins included in this study. Marked rivers (*) are tributaries of the Tinto river, but were considered independent basins due to the extreme acidic water of the Tinto (see methods for details).

RIVER	AREA (km²)	N native species	N 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
JARRAMA*	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
GUADALMESÍ	13,6	1	0
MARABER	5,2	0	0
LOBO	3,7	0	0

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

		d.f.	F-value	<i>p</i>	<i>R</i> ²	Variable	d.f.
<i>Number of native species</i>	Model	1	112.5	<0.001	0.82	Intercept	1
	Error	25				Basin area	1
	Total	26					
<i>Mean Endemicity (END)</i>	Model	1	23.3	<0.001	0.50	Intercept	1
	Error	23				Basin area	1
	Total	24					
<i>Mean Taxonomic Singularity (TS)</i>	Model	1	12.8	<0.01	0.36	Intercept	1
	Error	23				Basin area	1
	Total	24					
<i>Mean Rarity (RAR)</i>	Model	1	10.9	<0.01	0.32	Intercept	1
	Error	23				Basin area	1
	Total	24					

Table 3. Results from a GLM 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	<i>p</i>	<i>adj. R</i> ²	Variable	d.f.	F-value	<i>p</i>
<i>Number of introduced species</i>	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
<i>Mean Conservation Value (CVm)</i>	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 CAPTIONS

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 fishes as a function of basin area.

Figure 3. Mean Conservation Value (CV_m) of the fish community as a function of basin area. Regression lines are presented separately for dammed (closed circles, solid lines) and undammed (open circles, dotted lines) basins.

Figure 4. Accumulative numbers of dams (close circles) and introduced fish species (open circles) during the 20th century. Data from MMA (1998) (dams) and Elvira and Almodóvar (2001) (introduced species).

FIGURE 1

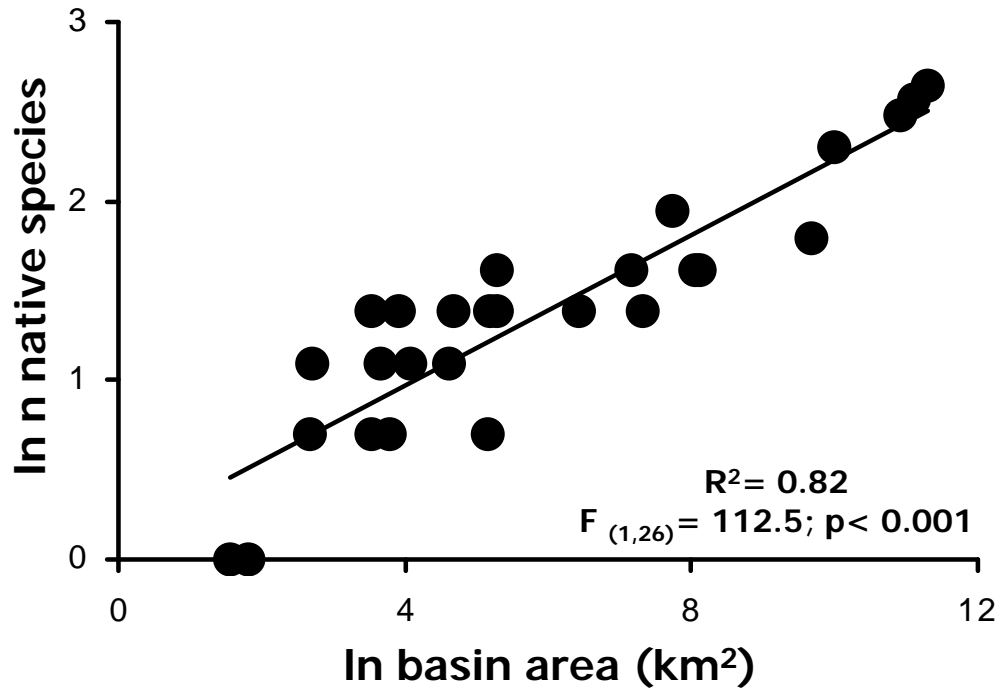


FIGURE 2

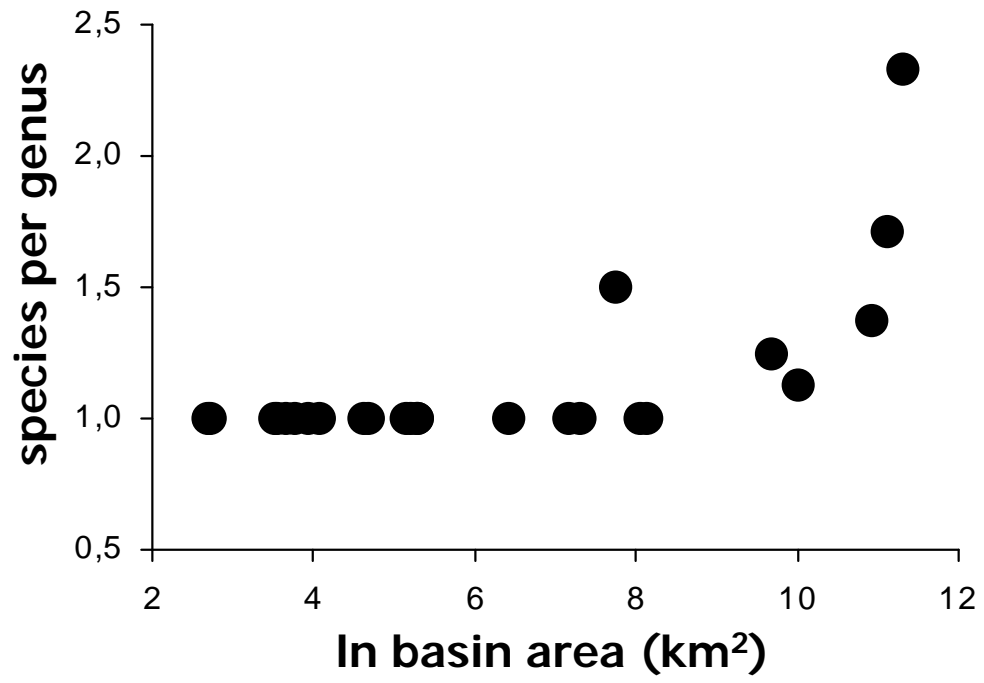


FIGURE 3

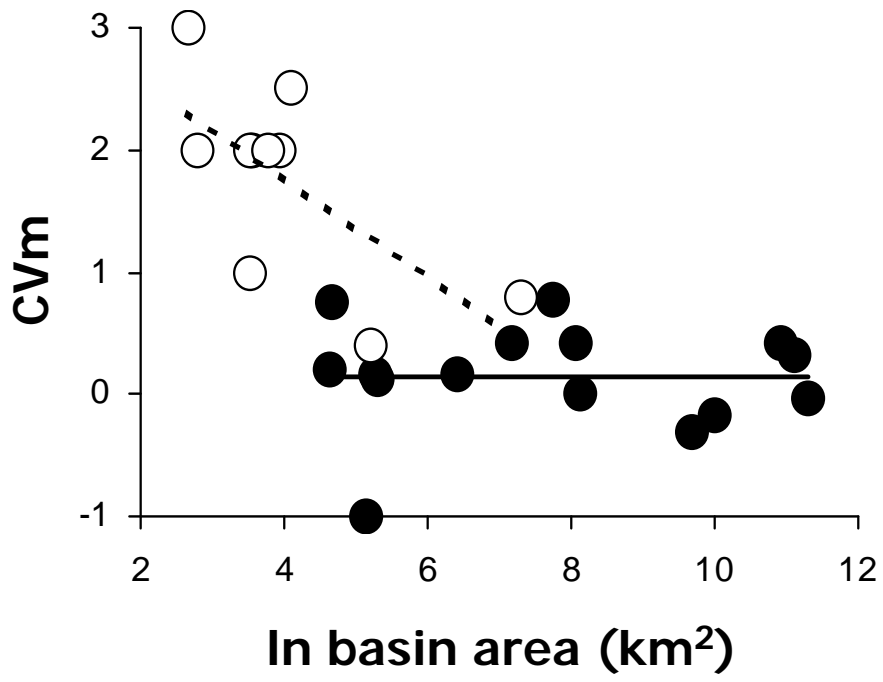


FIGURE 4

