

Life-history traits of non-native fishes in Iberian watersheds across several invasion stages: a first approach

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Abstract Freshwater ecosystems are seriously imperiled by the spread of non-native fishes thus establishing profiles of their life-history characteristics is an emerging tool for developing conservation and management strategies. We did a first approach to determine characteristics of successful and failed non-native fishes in a Mediterranean-climate area, the Iberian Peninsula, for three stages of the invasion process: establishment, spread and integration. Using general linear models, we established which characteristics are most important for success at each invasion stage. Prior invasion success was a good predictor for all the stages of the invasion process. Biological variables relevant for more than one invasion stage were maximum adult size and size of native range. Despite these common variables, all models produced a different set of variables

important for a successful invasion, demonstrating that successful invaders have a combination of biological traits that may favor success at all invasion stages. However, some differences were found in relation to published studies on fish invasions in other Mediterranean-climate areas, suggesting that characteristics of the recipient ecosystem are as relevant as the characteristics of the invading species.

Keywords Profiling alien fishes · Mediterranean region · Invasive species · Establishment · Spread · Integration

Introduction

Invasion of non-native fishes, a process with significant social and economic impacts (Lodge 1993; Pimentel et al. 2000; Pimentel 2005), is one of the main causes of the decline of native freshwater fishes worldwide. Indeed, biotic homogenization of freshwater fish faunas is a reality that has high ecological and economic costs (Cowx 1998, 2002; Welcomme 1998; Rahel 2000). The growing concern about the impacts of non-native fishes has led to an examination of the patterns and characteristics of both invaders and invasion process in order to improve our ability to predict the impact of new invaders (Kolar and Lodge 2001, 2002; Gido et al. 2004; Marchetti et al. 2004b, c).

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Invasive species profiling is one approach that identifies important characteristics of successful invaders (Rosecchi et al. 2001; Marchetti et al. 2004c; Vila-Gispert et al. 2005). However, distinct characteristics are important during different stages of the invasion process: transport, establishment, spread and integration (Moyle and Light 1996a). Thus, identifying life-history traits that are most relevant for success during different invasion stages is fundamental for understanding the invasion process and for predicting success of new or potential invaders.

Few studies of fish invasions have taken into account the different invasion stages. Kolar and Lodge (2002) found non-native fishes of the Great Lakes of North America had distinct life-history characteristics which determined success at each invasion stage. Marchetti et al. (2004b, c) reached a similar conclusion in Californian watersheds. In Catalonia (northeastern Iberian Peninsula) successfully established non-native fishes tend to have high longevity, high fecundity, and attain larger sizes than native fish species (Vila-Gispert et al. 2005), although the relative importance of these characteristics at different stages of the invasion process was not determined.

The study of characteristics of invasive fishes is complicated by the fact that most invaded waters have been highly altered by human activity, especially in Mediterranean climate regions where most rivers are impounded and/or diverted (e.g., Moyle 2002; Filipe et al. 2004). These habitat alterations increase the likelihood of the establishment and spread of non-native fishes (Moyle and Light 1996b; Marchetti et al. 2004a) and account for their abundance in many areas (Gehrke and Harris 2001; Marchetti and Moyle 2001; Filipe et al. 2004). In the Iberian Peninsula, the wide-scale damming of rivers (e.g., Elvira 1995; Collares-Pereira et al. 2000; Cowx and Collares-Pereira 2000) has led to the introduction of game fishes into reservoirs to promote recreational fisheries (Almaça 1995; Elvira 1998; Marta et al. 2001; Clavero and García-Berthou 2006). Moreover, the establishment of reproducing populations of these species is aided by the reduced environmental and hydrologic variability found in regulated rivers (Clavero et al. 2004). While recent research on fish in the Iberian Peninsula has demonstrated its usefulness as a study area for understanding aquatic

invasions (e.g., Alcaraz et al. 2005; Clavero and García-Berthou 2006), the studies so far have not included records of failed fish introductions and or incorporated records of new invasions. Here we expand on past studies by including both failed and new fish invaders and by taking a more thorough look at life-history features that are important in different stages of the invasion process in a clear defined geographical area, the Iberian Peninsula.

We first identified key life-history features for non-native fishes of the Iberian Peninsula. Then we addressed the following questions: (1) Are there differences in life-history characteristics of successful and failed invaders? (2) What traits are most important for the spread of successful non-native species? (3) Which characteristics enable non-native species to integrate into Iberian fish communities? (4) What is the importance of anthropogenic factors in enhancing invasions into Iberian watersheds?

Materials and methods

We used basic information on freshwater fish species inhabiting Iberian drainages in Doadrio (2001), but information on new and failed invaders came from Elvira (2001), Elvira and Almodóvar (2001), Caiola and de Sostoa (2002), and unpublished data from personal experience (Table 1). A non-native fish species was considered successful when it was known to have reproduced in the wild. Species with single records in Iberian Peninsula (e.g., *Aphanius fasciatus*) or with wild populations only maintained by stocking programs (e.g., *Hucho hucho*) were considered to be unsuccessful introductions. The ten species variables of Marchetti et al. (2004c) were adopted for analysis: trophic status of adults, size of the species' native range, degree of parental care, maximum fecundity, maximum adult size, maximum lifespan, physiological tolerance, distance from nearest native source, prior invasion success and propagule pressure. An additional variable considered in our study was introduction effort, which measures the number of times that each species was introduced. The first eight variables have ecological or biological relevance and the last three are measures of human interest on the species. Attributes of non-native fish species of the Iberian Peninsula were based on Spillmann (1961), Lelek (1987), Banarescu (1999), Doadrio (2001) and

Table 1 Successful, failed and translocated fish species in the Iberian Peninsula, values for the 11 variables used in the analysis, and number of catchment groups where each species is established (see material and methods for detailed explanation of the variables and catchment grouping)

Species	Authority	Success	Adult trophic status	Size of native range	Parental care	Maximum fecundity	Maximum adult size	Maximum lifespan	Physiological tolerance	Distance to nearest native source	Prior invasion success	Propagate pressure	Introduction effort	Nr drainages groups	
Successful															
<i>Oncorhynchus mykiss</i>	(Walbaum)	1	I	3	2	2	4	3	2	4	71	4	3	13	
<i>Salvelinus fontinalis</i>	(Mitchell)	1	I	4	2	2	4	3	1	4	29	4	3	4	
<i>Exocoetidae</i>	Linnaeus	1	C	4	1	4	5	5	2	2	6	4	3	11	
<i>Abramis bjoerlna</i>	(Linnaeus)	1	I	4	1	5	3	4	3	2	2	1	1	4	
<i>Alburnus alburnus</i>	(Linnaeus)	1	I	4	1	4	3	3	3	2	1	1	2	7	
<i>Carassius auratus</i>	(Linnaeus)	1	D	4	1	5	3	4	4	4	47	1	2	13	
<i>Cyprinus carpio</i>	Linnaeus	1	D	4	1	5	5	4	4	3	93	1	2	15	
<i>Gobio lozanoi</i>	Doadrio & Madeira	1	I	1	1	3	2	3	3	2	2	3	2	10	
<i>Pseudorasbora parva</i>	(Temminck & Schlegel)	1	I	4	3	3	1	2	3	4	19	2	1	1	
<i>Rutilus rutilus</i>	(Linnaeus)	1	H	4	1	4	3	4	3	2	4	2	2	3	
<i>Scardinius erythrophthalmus</i>	(Linnaeus)	1	H	4	1	4	3	4	3	2	6	2	2	4	
<i>Cobitis bilineata</i>	Canestrini	1	I	2	1	3	2	3	3	2	0	1	1	2	
<i>Ameiurus melas</i>	(Rafinesque)	1	O	3	3	3	4	4	4	4	16	1	2	7	
<i>Silurus glanis</i>	Linnaeus	1	C	4	3	5	6	5	4	3	10	1	1	3	
<i>Fundulus heteroclitus</i>	(Linnaeus)	1	I	2	2	2	2	2	4	4	2	1	1	2	
<i>Gambusia holbrooki</i>	Girard	1	I	2	4	1	1	1	4	4	57	1	1	12	
<i>Poecilia reticulata</i>	Peters	1	O	2	4	1	1	1	3	4	33	1	1	1	
<i>Australoheros facetus</i>	(Jenyns)	1	O	3	3	3	3	4	4	4	1	1	1	4	
<i>Lepomis gibbosus</i>	(Linnaeus)	1	I	2	3	2	3	4	2	4	23	1	2	10	
<i>Micropterus salmoides</i>	(Lacepede)	1	C	3	3	4	4	4	3	4	44	4	3	15	
<i>Percu fluviatilis</i>	Linnaeus	1	C	4	1	5	4	5	2	2	7	1	1	2	
<i>Sander lucioperca</i>	(Linnaeus)	1	C	4	3	5	5	4	2	2	19	1	1	7	
Failed															
<i>Acipenser baerii</i>	Brandt	0	I	4	1	5	6	5	2	4	1	2	2	-	
<i>Hucho hucho</i>	(Linnaeus)	0	C	3	2	4	6	5	1	3	1	4	3	-	

Table 1 Continued

Species	Authority	Success	Adult trophic status	Size of native range	Parental care	Maximum fecundity	Maximum adult size	Maximum lifespan	Physiological tolerance	Distance to nearest native source	Prior invasion success	Propagule pressure	Introduction effort	Nr drainages groups
<i>Oncorhynchus kisutch</i>	(Walbaum)	0	I	2	2	3	4	2	1	4	4	2	1	-
<i>Abramis brama</i>	(Linnaeus)	0	I	4	1	5	4	4	3	2	1	1	2	-
<i>Alburnoides bipunctatus</i>	(Bloch)	0	I	4	1	3	2	3	3	2	0	1	2	-
<i>Ctenopharyngodon idella</i>	(Steindachner)	0	H	4	1	5	5	4	2	4	54	3	1	-
<i>Leuciscus idus</i>	(Linnaeus)	0	I	4	1	5	4	4	3	2	4	1	2	-
<i>Misgurnus anguillicaudatus</i>	(Cantor)	0	I	4	1	3	3	4	4	4	1	1	1	-
<i>Ictalurus punctatus</i>	(Rafinesque)	0	C	3	3	3	5	4	3	4	11	2	1	-
<i>Aphanius fasciatus</i>	(Valenciennes)	0	I	3	3	2	1	3	4	2	0	1	1	-
<i>Astronotus ocellatus</i>	(Agassiz)	0	I	4	3	3	4	4	4	4	2	1	1	-
<i>Pygocentrus nattereri</i>	Kner	0	C	4	3	3	3	3	4	4	0	1	2	-
<i>Piaractus brachipomus</i>	(Cuvier)	0	C	4	3	5	5	5	4	4	0	1	2	-
Translocated														
<i>Salmo trutta</i>	Linnaeus	-	I	4	2	4	4	4	2	1	31	4	3	-
<i>Chondrostoma arcasii</i>	(Steindachner)	-	D	3	1	3	2	3	3	1	0	3	3	-
<i>Chondrostoma miegii</i>	Steindachner	-	H	1	1	3	3	3	3	1	0	1	1	-
<i>Chondrostoma polylepis</i>	Steindachner	-	H	2	1	3	3	4	3	1	0	3	3	-
<i>Phoxinus phoxinus</i>	(Linnaeus)	-	O	4	1	2	2	3	2	1	1	3	2	-
<i>Squalius alburnoides</i>	(Steindachner)	-	I	3	1	3	2	3	3	1	0	3	3	-
<i>Squalius pyrenaicus</i>	(Gunther)	-	I	3	1	3	3	3	3	1	0	1	1	-
<i>Tinca tinca</i>	(Linnaeus)	-	O	4	1	5	4	4	4	1	16	2	2	-
<i>Cobitis paludica</i>	(De Buen)	-	I	3	1	3	2	3	4	1	0	1	2	-
<i>Barbatula barbatula</i>	(Linnaeus)	-	I	4	1	3	3	3	2	1	1	1	1	-

See Sect. "Materials and methods" for detailed explanation of the variables and catchment grouping

Moyle (2002) and additionally from recent publications on fish life-history [e.g., Loubens and Panfili (2001) for *Piaractus brachipomus*]. Categorical and ordinal measures were used for all variables (except prior invasion success), due to the lack of reliable continuous quantitative data for the majority of the species.

Adult trophic status

Variable assigned according to the main food items (>50% of adult diet): carnivore (C), omnivore (O), herbivore (H), invertivore (I) and detritivore (D). This variable was considered in the analysis as a dummy variable because it is a nominal variable (Zar 1999).

Size of native range

Because of imprecise information on the native ranges of many species, we used a four-scale categorization for size of native range based on likely occurrence: 1-range occupies < 5% of one zoogeographic sub-region, i.e., local endemics (e.g., *Chondrostoma miegii*); 2-range occupies 5–50% of one zoogeographic sub-region (e.g., *Lepomis gibbosus*); 3-range occupies >50% of one zoogeographic sub-region (e.g., *Ictalurus punctatus*); 4-range occupies more than one zoogeographic sub-region (e.g., *Phoxinus phoxinus*). Species that occupy more than one zoogeographic sub-region but with a very restricted distribution in each sub-region (<5%) were scored as “3” (e.g., *A. fasciatus*).

Parental care

Categories follow Marchetti et al. (2004c): 1-open substrate spawners with no parental care; 2-brood hiders, fish that hide eggs but show no additional care; 3-guarders, guard their embryos and/or larvae; 4-bearers, fish that carry their embryos with them.

Maximum fecundity

The maximum number of eggs per female under natural conditions: 1-<100 eggs; 2-100–1,000 eggs; 3-1,000–10,000 eggs; 4-10,000–1,00,000 eggs; 5->1,00,000 eggs.

Maximum adult size

The maximum length individuals are known to achieve in the wild. Categories were preferred over direct numerical estimates because measurement methods are variable. All categories represent measurements of total length: 1-<10 cm; 2-11–20 cm; 3-21–40 cm; 4-41–80 cm; 5-81–160 cm; 6->160 cm.

Maximum lifespan

Variable defined as the maximum known age of large individuals in wild populations living under natural conditions: 1-≤2 years; 2-3–4 years; 3-5–8 years; 4-9–16 years; 5->16 years.

Physiological tolerance

This variable represents tolerance to changes in water quality (usually temperature, dissolved oxygen, turbidity and salinity) or extreme conditions in water quality: 1-intolerant, fishes with low tolerance to change or extremes in water quality (e.g., *Oncorhynchus kisutch*); 2-moderately tolerant fishes capable of living in water with moderate variability in water quality (e.g., *Perca fluviatilis*); 3-tolerant fishes capable of living in waters in which water quality often reaches their limits of physiological tolerance for short periods (e.g., *Micropterus salmoides*); 4-extremely tolerant fishes capable of living in systems with poor water quality (e.g., *Ameiurus melas*).

Distance from nearest native source

Categories were used because exact distances are not known: 1-within Iberian Peninsula; 2-Western Europe to the Danube River (excluded); 3-Central and Eastern Europe from the Danube eastwards; 4-Intercontinental.

Prior invasion success

The number of countries worldwide in which each species has been introduced and successfully established was based on FAO Inland Water Resources and Aquaculture Service database (<http://www>).

fao.org/figis/servlet/static?dom=root&xml=Introsp/introsp_search.xml). The number of countries was transformed using the function $\text{Ln}(x + 1)$ prior to analysis to rectify violations of homoscedasticity and normality.

Propagule pressure

This is the number of fish used in unsuccessful introductions and the number of fish used to establish the first self sustaining population in successful introductions: 1-<100 individuals, usually released by fishermen or aquarists; 2-100–1,000 individuals, usually escapees from aquaculture operations; 3-1,000–10,000 individuals, usually released by water transfers and stocking programs for forage species; 4->10,000 individuals released by stocking programs, mainly for recreational fisheries. These four categories were used because actual numbers are often rough estimates based on historical records, or were determined by the authors based on the most likely scenarios for the introduction. It was assumed that illegal unrecorded introductions by anglers (e.g., *Silurus glanis*) or aquarists (e.g., *Australoheros facetus*) were < 100 individuals. For some of the native fishes that have established outside of their native range through water transfers, an estimated propagule was considered to be 100–1,000 fish.

Introduction effort

Variable that accounts for the number of introductions in Iberian freshwaters: 1-one introduction event (e.g., *Pseudorasbora parva*); 2-several introductions by aquaculture escapees, aquarists or fishermen (e.g., *Acipenser baerii*); 3-repeated introductions by government agencies (e.g., *O. mykiss*).

Establishment

A binary response variable was defined to examine successful establishment by comparing successful with unsuccessful fish invaders. Native species established outside their native range (translocations) were not included in the establishment analysis because no reliable data are available on numbers of successful or unsuccessful translocations.

Spread

This variable was the number of isolated catchment groups in the Iberian Peninsula invaded by a species where invasion was most likely the result of an introduction rather than natural spread from an adjoining catchment. Fifteen catchment groups were considered in the study area and defined by the composition of the native fish fauna, where endemic species indicated isolation (Fig. 1). Catchment groups were used (rather than area or some similar variable) in order to characterize the extent to which the species had spread while recognizing that exact extent of spread was rarely known, in part because many species are still expanding their ranges. This variable was transformed using the function $\text{Ln}(x + 1)$ following Marchetti et al. (2004c).

Integration

Variable defined as the average value of species distribution and abundance per catchment group for Iberian Peninsula, categorized in the following way: 1-species present in low numbers and at one or two localities; 2-species locally common but with a very limited distribution; 3-species fairly common in the catchment but not abundant; 4-species widespread but not necessary abundant everywhere; 5-species widespread and abundant everywhere. This

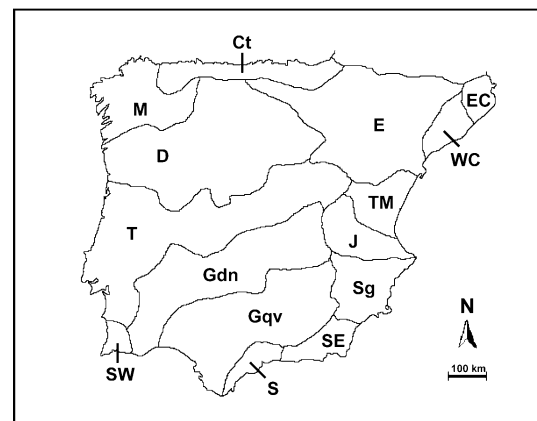


Fig. 1 Map of Iberian Peninsula with 15 catchment groups considered in the dispersion analysis: EC and WC east and western Catalanian drainages, E Ebro, TM Turia and Mijares, J Júcar, Sg Segura, SE southeastern drainages, S southern drainages, Gqv Guadalquivir, Gdn Gadiana, SW Southwestern drainages, T Tejo, D Douro, M Minho, Ct Cantabrian drainages

information was based on Doadrio (2001) and authors' personal knowledge of Portuguese and Spanish watersheds.

Data analysis followed the methodology of Marchetti et al. (2004c) because of limitations of the data set, which had a relatively small number of fish species relative to the number of variables. In Iberian Peninsula, the low number of non-native fish species, relative to other regions, limits statistical approaches, but this is balanced by the large amount of information available for each species. Our first analysis (the full model) used all eleven variables in order to assess which variables might be most important for each invasion stage. Our second analysis (the reduced model) used a subset of eight biological variables, excluding the three independent variables of human interest (prior invasion success, propagule pressure and introduction effort) in order to assess the importance of non-anthropogenic factors.

We performed a logistic regression analysis between the response variable (success/non-success) and the 11 independent variables considered (full model), followed by a reduced set of variables (8 independent variables of biological information). Kendall's tau-b correlation coefficient (Siegel and Castellan 1988) was used prior to the logistic regression analysis to assess highly correlated variables ($r > 0.70$), following Filipe et al. (2002) and Marchetti et al. (2004c). We excluded variables with high correlations with other variables as well as variables that had the least reliable data (and therefore less explanatory power). A manual forward selection procedure was followed with a probability of entry of < 0.15 and removal of > 0.20 of each variable (Hosmer and Lemeshow 2000; Tabachnick and Fidell 2001). The variables were manually inserted in the model according to the Wald's test and the model improvement (Goodness of Fit). To assess the fit of the logistic regression model, a classification table was used (Tabachnick and Fidell 2001).

The spread and integration stages were analyzed using multiple regression models only with the successful non-natives. The dependent variable for the spread stage was the number of invaded catchment groups, and for the integration stage was the average species abundance and distribution in Iberian Peninsula. For each stage, two models were generated, one with the full set of independent variables and another with variables related to fish biology.

Before starting the selection of variables for multiple regression models, we performed a correlation analysis using Kendall's tau-b coefficient to identify highly correlated variables ($r > 0.70$). Variables were excluded in order to minimize correlations among variables; in case of ties in the number of correlations, the variable with more reliable data was included. A manual forward selection procedure was applied to the variables with a probability of entry of F to enter of < 0.15 and to exclude of > 0.20 (Marchetti et al. 2004c).

Results

For Iberian Peninsula catchments, we found records of 35 non-native fish species and translocations of ten indigenous taxa. Concerning the 35 non-native fishes, 22 were successful and 13 were failed introductions (Table 1). Only adult size and prior invasion success appeared to influence non-native fish establishment (Fig. 2 and Table 1, respectively). The Kendall's tau-b correlation coefficient showed no highly significant correlations ($r > 0.70$) either in the data set with all non-native fish (establishment stage) or in the set with only successful non-natives (spread and integration stage).

The logistic regression model containing all 11 independent variables (full model) showed that for non-native fish establishment, adult maximum size, distance to nearest range, and prior invasion success were important predictors (Table 2). The latter variable was strongly and positively associated with successful establishment. The overall percentage of correct classification in the model was 80%. The reduced model was marginally significant; maximum adult size was the only biological feature that seemed to be important to species establishment, with an overall percentage of correct classification of 66% (Table 2).

The full multiple regression model for the spread stage explained 50% of the data variability and included size of native range, parental care, adult maximum size and prior invasion success (Table 3). This model suggested that spread in the Iberian Peninsula is positively associated with small native range, low degree of parental care, large adult size, and higher prior invasion success. The reduced model

Fig. 2 Percentage of successful (*grey area*) and unsuccessful (*blank area*) fish introductions for each variable subcategory. Numbers on top of the bars represent the number of successful and failed invaders respectively. Categories for each variable are explained in Sect. "Methods", but higher values for each category represent higher variable values. For example, under native range, 1 represents a small native range, while 4 represents a very large native range. For adult trophic categories, C is carnivore, O is omnivore, H is herbivore, I is invertivore and D is detritivore

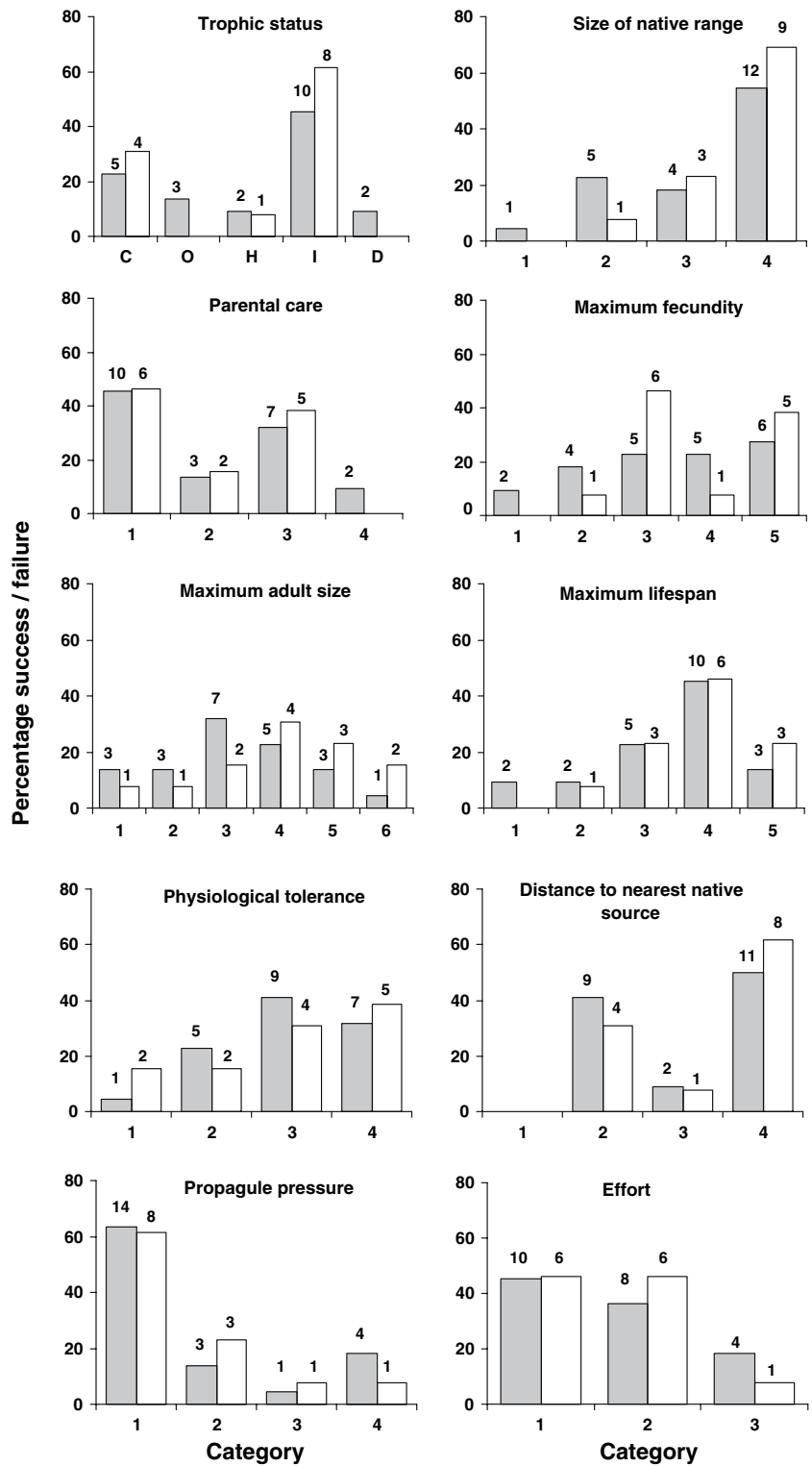


Table 2 Logistic regression models (full and reduced—see Sect. “Materials and methods”) for factors associated with the establishment of non-natives in the Iberian Peninsula, showing regression coefficients (*B*), standard error (SE), Wald test and *P* values

Model	Variable	<i>B</i>	SE	Wald	<i>P</i> -value
Full $G = 27.09$, $P = 0.03$	Adult maximum size	-0.82	0.45	3.27	0.07
	Distance to nearest range	-0.93	0.54	2.99	0.08
	Prior invasion success	1.52	0.56	7.40	0.01
	Constant	3.64	1.92	3.60	0.06
Reduced $G = 35.41$, $P = 0.11$	Adult maximum size	-0.41	0.27	2.28	0.13
	Constant	2.01	1.07	3.50	0.06

G represents Goodness of Fit of the model

Table 3 Multiple regression models (full and reduced—see Sect. “Materials and methods”) for factors associated with the successful spread of non-native species (number of catchments) showing regression coefficients (*B*), standard error (SE), *P* values and percentage of explained variance from the model (R^2)

Model	Variable	<i>B</i>	SE	<i>P</i> -value
Full $R^2 = 49.6\%$, $F = 4.18$	Size of native range	-0.35	0.15	0.04
	Parental care	-0.26	0.13	0.06
	Adult maximum size	0.23	0.10	0.04
	Prior invasion success	0.31	0.10	0.01
	Constant	2.03	0.55	<0.01
Reduced $R^2 = 39\%$, $F = 3.84$	Detritivore	0.98	0.44	0.04
	Size of native range	-0.32	0.16	0.06
	Adult maximum size	0.27	0.11	0.02
	Constant	1.91	0.44	<0.01

F is a measure of the overall fit

for spread accounted for 39% of the variability in the biological data and indicated that non-natives with large adults and a detritivore feeding strategy are widespread in Iberian Peninsula while non-natives with a large native range seemed less widespread (Table 3).

The integration of non-natives into local fish communities was conditioned by feeding strategy, size of native range, physiological tolerance and prior invasion success. Size of a non-native’s native range and an omnivorous feeding strategy seemed to reduce integration into established fish assemblages, while physiological tolerance and prior invasion success predicted a better integration into fish communities (Table 4). This model explained 47% of variability and the reduced model accounted for 33% of the variability (Table 4). The reduced multiple regression model was associated positively with physiological tolerance and negatively with size of native range and omnivory.

Discussion

We found few characteristics related to success and failure that were common across all invasion stages, indicating that successful non-native fishes have combinations of characteristics that determine success in each invasion stage. Prior invasion success was common to the three invasion stages but none of the biological features was related to success in all stages. The most common biological variables associated with success were size of native range and adult maximum size, which were present in more than one invasion stage in six models (Table 5). Presumably, the combination of inter-related features was responsible for success in establishment, spread and integration of non-native fishes into the Iberian fish communities. Fortunately, Iberian Peninsula did not have as many successful non-native fishes ($N = 22$) as other similar sized regions of the globe [e.g., California, $N = 49$ (Marchetti et al. 2004c);

Table 4 Multiple regression models (full and reduced—see Sect. “Materials and methods”) for factors associated with the successful integration of non-native species (average abun-dance and distribution) showing regression coefficients (B), standard error (SE), P values and percentage of explained variance from the model (R^2)

Model	Variable	B	SE	P -value
Full $R^2 = 46.7\%$, $F = 3.72$	Omnivore	-0.87	0.39	0.04
	Size of native range	-0.28	0.14	0.06
	Physiological tolerance	0.35	0.15	0.04
	Prior invasion success	0.21	0.10	0.05
	Constant	1.26	0.71	0.10
Reduced $R^2 = 32.7\%$, $F = 2.91$	Omnivore	-0.86	0.42	0.06
	Size of native range	-0.25	0.15	0.11
	Physiological tolerance	0.33	0.17	0.06
	Constant	1.71	0.74	0.03

F is a measure of the overall fit

Table 5 Occurrence of explanatory variables in the full and reduced models for establishment, spread and integration stages for Iberian Peninsula non-native fish species

Variable	Establishment		Spread		Integration	
	Full	Reduced	Full	Reduced	Full	Reduced
Omnivore					-	-
Detritivore				+		
Size of native range			-	-	-	-
Parental care			-			
Adult maximum size	-	-	+	+		
Physiological tolerance					+	+
Distance to nearest range	-					
Prior invasion success	+		+		+	

Italy, $N = 39$ (Copp et al. 2005)] but this constrained our model building, specifically in spread and integration stages. Despite this limitation, the variability explained by our model was similar to that explained in Marchetti et al. (2004c) for California. Our approach followed that of Marchetti et al. (2004a, b, c) in which we conducted our study within a well defined natural geographic unit and then interpreted the results based on personal knowledge of the distribution and biology of the fishes, complemented with an extensive literature search. Unfortunately, the rate of introductions is increasing (Elvira and Almodóvar 2001; Clavero and García-Berthou 2006) so our models should be useful for predicting spread and possible impact. Ironically, as more species are introduced and invade, more sophisticated statistical approaches become possible.

Are there differences in life-history characteristics of successful and failed invaders?

The successful establishment of non-native fishes in Iberian watersheds was positively related to their shorter distance to the nearest native region, small adult size, and prior invasion success. Small-sized species with native ranges close to the Iberian Peninsula and that had previous invasion success were most likely to become established. For fish invasions into California watershed, only prior invasion success was common with our results for the Iberian Peninsula (Marchetti et al. 2004c). Vila-Gispert et al. (2005) found a similar pattern for Catalan streams and suggested that regional environmental conditions (highly seasonal variation in hydrologic regime) prevented non-native fishes (mostly

large in size, with short spawning seasons) from becoming established, in contrast to the native species which are generally small in size and have multiple spawning events. Rosecchi et al. (2001) found the same life-history features for recent successful invaders in the Camargue (southern France). Most of the non-native fishes that have become established in the Iberian Peninsula were originally from other European regions and North America and have been successfully introduced elsewhere (Table 1). In Portugal and Spain, recreational fisheries increased in the last 20 years (Collares-Pereira et al. 2000; Marta et al. 2001) and introduction of fishes to support fisheries have been a major source of new fish invasions (Elvira and Almodóvar 2001; Alcaraz et al. 2005) as they are worldwide (Cowx 1998; Welcomme 1998; Cambray 2003, Moyle and Marchetti 2006).

What traits are most important for the spread of successful non-native species?

Bigger adult size together with low parental care, small size of native range, high prior invasion success and a detritivorous feeding strategy are features that permit a species to spread in Iberian catchments. Prior invasion success and large size are surely linked to repeated introductions of game fishes throughout the Iberian Peninsula (e.g., *M. salmoides*). On other hand, having characteristics of native fishes such as low parental care is likely to enhance species spread. Most of the native freshwater fishes are open substrate spawners or brood hiders (Doadrio 2001); therefore having one of these “local” features is presumably advantageous to non-native fishes as well. Likewise, Moyle and Marchetti (2006) found that long lifespan (correlated with adult maximum size) and coming from a nearby regional source (correlated with parental care), enhanced the spread of non-natives in California watersheds. Species with a wider native range did not seem to have an advantage during the spread stage in the Iberian Peninsula, a result consistent with California invasion patterns (Moyle and Marchetti 2006). This might be linked to adaptations to environmental conditions present in only limited regions of the world similar to those of the Iberian Peninsula or to recent colonization of Iberian freshwaters by species with wider native distribution that did not spread yet (e.g., *S. glanis*). Curiously, *Cyprinus carpio*, the oldest

Iberian introduction (17th century) exhibits almost all features of a successful spread species: detritivory, large size, low parental care and high prior invasion success but also has a wide native range.

Which characteristics enable non-native species to integrate into Iberian fish communities?

During the integration phase, prior invasion success and high physiological tolerance seemed to confer advantages to non-native species, while being omnivorous and having a wide native range appeared to be disadvantageous. *G. holbrooki* is a good example of a fully integrated species in the Iberian watersheds: it is an insectivorous species, successfully introduced in 57 countries, which has a high physiological tolerance and a relatively small native range. High physiological tolerance, especially for high temperature and low dissolved oxygen, is presumably important due to the highly seasonal and long-term variability of Iberian streams (e.g., Bernardo et al. 2003; Magalhães et al. 2003). Most Iberian fish species are insectivorous (e.g., Magalhães 1993; Valladolid and Przybylski 1996) while omnivory is not a common feeding strategy (Doadrio 2001). Prior invasion success seems to be linked to recent invaders commonly used in recreational fisheries in other European countries (García-Berthou et al. 2005; Clavero and García-Berthou 2006) or other human uses (e.g., mosquito control). The full model of the integration stage for the Iberian Peninsula is the model that had the most life-history features in common with the integration stage for California watersheds, with similar flow regimes (Moyle and Marchetti 2006). Of the five characteristics important for Californian fishes, three were common to the present study: a specific feeding strategy (not being omnivorous), physiological tolerance and prior invasion success.

What is the importance of anthropogenic factors in enhancing invasions into Iberian watersheds?

Prior invasion success was the only human interest variable that predicted invasion success at all stages of the process. In fact eight out of 22 species were introduced successfully for fisheries. The *H. hucho* was the only one of 13 failed non-natives that is a sport fish that has been continuously stocked by

regional governments (Doadrio 2001). This result was similar with the findings of Marchetti et al. (2004c), reflecting the importance of fishes with high value to humans (recreational fisheries). Indeed, biological features that appeared in our results such as adult maximum size are undoubtedly related to value in fisheries. Generally, recreational fisheries in the Iberian Peninsula are more intense in lake-like environments such as reservoirs (Marta et al. 2001). Impoundment also aids non-native fish establishment, spread and integration by reducing hydrological variability below the dams, preventing seasonal floods and reducing the impact of droughts, both selecting against non-natives (Baltz and Moyle 1993; Moyle and Light 1996a, b). In the Iberian Peninsula the increased incidence of river impoundment (Collares-Pereira et al. 2000) is likely to reinforce the already clear association between dams and non-natives (Elvira 1995, 1998; Elvira et al. 1998; Clavero et al. 2004; Filipe et al. 2004).

Conclusions

This study confirmed the difficulty of coming up with universal traits that may favor non-native fishes due to the idiosyncratic nature of so many introduction attempts. Nevertheless the similarity between our results and those of Moyle and Marchetti (2006) for California introductions suggests that some generalities can be made, at least for regions with similar climatic regimes:

- Prior invasion success can predict future invasion success, although this is due to humans knowledge in matching desirable fish biological traits to suitable habitats;
- Non-native fishes from nearby areas are more likely to succeed than those from more distant areas, because of the greater likelihood of being adapted to local natural flow and temperature regimes. Notwithstanding it is curious that so many of the successful species (9/22) are native to North America;
- Successful invaders have traits that promote success at all stages of the invasion process but the combination of traits can vary widely. These traits may also differ among geographic regions;
- For some widely-distributed species (e.g., *C. carpio*, *Salmo trutta*) invasion success presum-

ably results from each species capacity to adapt to new situations (phenotypic plasticity) rather than to specific life-history attributes (Rosecchi et al. 2001; Sakai et al. 2001; Alcaraz et al. 2005).

Thus analyzing traits of species which have invaded several regions worldwide, and then adjusting these analyses to the native fauna and specific environmental characteristics of each region, seems likely to result in models which can predict trends and patterns of world fish invasions. The patterns found here are also sufficient to make predictions as to which proposed introductions (e.g., for fishing) are likely to become widespread in Iberian Peninsula, but harm to native organisms is harder to predict, therefore the precautionary principle should apply to new introductions: “do no harm”.

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