

Life-history traits of invasive fish in small Mediterranean streams

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Abstract

We compared the life-history traits of native and invasive fish species from Catalan streams in order to identify the characters of successful invasive fish species. Most of the exotic fish species were characterized by large size, long longevity, late maturity, high fecundity, few spawnings per year, and short reproductive span, whereas Iberian native species exhibited predominantly the opposite suite of traits. Species native to the southeastern Pyrenees watershed were also significantly different from species native to the rest of the Iberian Peninsula but not native to this watershed. Iberian exotic species come predominantly from large river basins, whereas Catalan streams (and other small, coastal river basins) correspond to basins and streams of a smaller size and different hydrology, with differences in species composition and life-history traits of fish. The occurrence and spread of invasive species was not significantly related to life-history traits but to introduction date. The successful prediction of future invasive species is limited due to small differences in life-history and ecological traits between native and exotic species. Fecundity, age at maturity, water quality flexibility, tolerance to pollution and habitat seem the most discriminating life-history variables.

Introduction

Stream fish faunas are increasingly subject to alteration by introduction of non-native fishes. Successful establishment of non-native forms varies widely between geographic regions (38–77%), but is generally greater in areas that are either altered by man or initially poor in fish species (Ross 1991). Mediterranean streams have strong seasonal patterns of flow: low flow in the hot summer drought and flash floods during autumn and spring storms. Interannual variability in precipitation is high while lengthy periods of drought are common. As a consequence, the native fish fauna is depauperate and highly endemic (Doadrio et al. 1991). The natural variability in environmental conditions of many Iberian streams has been greatly reduced by water regu-

lation. In addition, industrial waste and sewage effluents cause water quality to deteriorate. These profound modifications to the fluvial systems of this region directly threaten the native fish fauna and favor the invasion of non-native species (Elvira 1995, 1998).

Introduced species have been successful in the Mediterranean-type climate of California in good part because the natural environment has been so altered. Free-flowing streams have increasingly been turned into reservoirs, regulated streams, and ditches (Moyle 1995). The failure of non-native species to become established despite repeated invasions is best attributed to their inability to adapt to the local hydrological regime (Minckley and Meffe 1987; Baltz and Moyle 1993). In contrast, native species are adapted to flooding regimes through a combination of

life-history strategies and physiological tolerances (Moyle et al. 1986). The factors that determine whether a species will be an invader or not include both the species and the habitat (Williamson and Fitter 1996). Here we concentrate on the characters of the species, basically life-history and ecological traits. We compare native and invasive species from Catalan streams in order to identify the characters of successful invasive fish species.

Materials and methods

The southeastern Pyrenees watershed is located in the northeast of Spain, has a surface area of 16,826 km² and includes nine river basins that flow into the Mediterranean Sea (Aparicio et al. 2000). From the north to the south, the river basins are Muga, Fluvià, Ter, Tordera, Besòs, Llobregat, Foix, Gaià, and Francolí. This watershed, limited by a larger river (Ebro) and the Pyrenees mountains, constitutes a biogeographical unit on the basis of its freshwater fishes (Doadrio 1988) and a management unit for Spanish water authorities. The Ter and Llobregat rivers are the largest in terms of length and discharge. They have a main peak flow in spring caused by snow melt and rain, and a secondary one in autumn due to rainfall. The other basins are short because they rise in littoral mountains and their valley slopes are relatively steep down to their mouths. They have the highest flow in autumn and a strong flow reduction in summer. River flows have been modified considerably by the construction of 10 large dams, and countless small dams and water diversion barriers (Aparicio et al. 2000).

Estimates of fish life-history traits were obtained from our own data (Vila-Gispert and Moreno-Amich 2000) and from literature sources specified in Table 1 (see also Vila-Gispert et al. 2002). Species considered were those listed in Doadrio (2001), excluding *Anguilla anguilla* due to their peculiar reproductive biology. Species were classified as native to the south-eastern Pyrenees watershed, species native to the rest of the Iberian Peninsula but not native to this watershed (hereafter referred to as Iberian exotic), and species not native to the Iberian Peninsula (hereafter referred to as foreign exotic). The results

not distinguishing between Iberian and foreign exotic were similar but less informative. In general, data about ecological variables were obtained from Doadrio (2001) and Oberdorff et al. (2002), date of introduction from Elvira and Almodóvar (2001), and distribution and occurrence of fish species from Aparicio et al. (2000) (Table 1). When no reliable data were found for a given variable, that cell in the species variable matrix was left blank and any calculations calling for the variable eliminated the species from the analysis. Whenever maturation and maximum length data were reported for the sexes separately, we used the estimates for females. In some instances, standard lengths (SL) were calculated from total lengths or fork lengths using published conversion equations.

Data for the following variables were used in the analyses: (1) maximum standard length reported in millimeters SL; (2) age at maturity (in months); (3) reproductive span (in months); (4) spawning type categorized as 1 (single spawning per year), 2 (from two to four spawnings per year), or 3 (more than four spawnings per year); (5) fecundity as the average number of vitellogenic oocytes of mature females in a single mature ovary or spawning event; (6) egg diameter (the average diameter of the largest oocytes in fully developed ovaries, to the nearest 0.01 mm); (7) longevity as the maximum age estimated (in years); (8) parental care following Winemiller (1989), quantified as $\sum x_i$ for $i = 1$ to 3 ($x_1 = 0$ if no special placement of zygotes, 1 if zygotes are placed in a special habitat (e.g. scattered on vegetation, or buried in gravel), and 2 if both zygotes and larvae are maintained in a nest; $x_2 = 0$ if no parental protection of zygotes and larvae, 1 if a brief period of protection by one sex (<1 month), 2 if a long period of protection by one sex (>1 month) or brief care by both sexes, and 4 if lengthy protection by both sexes; $x_3 = 0$ if no nutritional contribution to larvae (yolk sac material is not considered here), 2 if brief period of nutritional contribution to larvae (=brief gestation (<1 month) with nutritional contribution in viviparous forms), 4 if long period of nutritional contribution to larvae or embryos (=long gestation (1–2 months) with nutritional contribution), or 8 if extremely long gestation (>2 months)); (9) gregariousness referred to the adults was coded as a binary dummy variable (0 (no), 1 (yes); (10)

Table 1. Native, Iberian exotic, and foreign exotic fish species from the south-eastern Pyrenees watershed and reference sources of data.

Species	Code	Origin	References
<i>Aphanius iberus</i>	AIB	Native	Vargas and Sostoa (1997)
<i>Barbus haasi</i>	BHA	Native	Aparicio and Sostoa (1998)
<i>Barbus meridionalis</i>	BME	Native	Bruslé and Quignard (2001); Doadrio (2001)
<i>Chondrostoma arcasii</i>	CAR	Native	Rincón and Lobón-Cervía (1989)
<i>Gasterosteus gymnurus</i>	GGY	Native	Winemiller and Rose (1992)
<i>Salaria fluviatilis</i>	SFL	Native	Viñolas (1986); Sostoa (1990); Vila-Gispert and Moreno-Amich (2000)
<i>Salmo trutta</i>	STR	Native	Lobón-Cervía et al. (1986)
<i>Squalius cephalus</i>	SCE	Native	Casals (1985); Bruslé and Quignard (2001)
<i>Barbatula barbatula</i>	BBA	Iberian	Doadrio (2001)
<i>Barbus graellsii</i>	BGR	Iberian	Sostoa (1990); Miñano et al. (2000); Doadrio (2001)
<i>Chondrostoma miegii</i>	CMI	Iberian	Chappaz et al. (1989); Miñano et al. (2000)
<i>Cobitis calderoni</i>	COC	Iberian	Doadrio (2001)
<i>Cobitis paludica</i>	CPA	Iberian	Lobón-Cervía and Zabala (1984); Oliva-Paterna et al. (2002)
<i>Cottus gobio</i>	CGO	Iberian	Mann et al. (1984); Bruslé and Quignard (2001)
<i>Phoxinus phoxinus</i>	PPH	Iberian	Mills and Eloranta (1985)
<i>Alburnus alburnus</i>	AAL	Foreign	Mackay and Mann (1969)
<i>Ameiurus melas</i>	AME	Foreign	Winemiller and Rose (1992)
<i>Carassius auratus</i>	CAU	Foreign	Lelek (1980); Penaz and Kokes (1981); Bruslé and Quignard (2001); Doadrio (2001)
<i>Cyprinus carpio</i>	CCA	Foreign	Fernández-Delgado (1990)
<i>Esox lucius</i>	ELU	Foreign	Wright and Schoesmith (1988)
<i>Gambusia holbrooki</i>	GHO	Foreign	Fernández-Delgado (1989)
<i>Gobio gobio</i>	GGO	Foreign	Lobón-Cervía et al. (1991)
<i>Lepomis gibbosus</i>	LGI	Foreign	Crivelli and Mestre (1988); Vila-Gispert and Moreno-Amich (2000); Copp et al. (2002)
<i>Micropterus salmoides</i>	MSA	Foreign	Winemiller and Rose (1992)
<i>Perca fluviatilis</i>	PFL	Foreign	Mann (1978)
<i>Rutilus rutilus</i>	RRU	Foreign	Vila-Gispert and Moreno-Amich (2000)
<i>Salvelinus fontinalis</i>	SFO	Foreign	Winemiller and Rose (1992); Doadrio (2001)
<i>Sander lucioperca</i>	SLU	Foreign	Lehtonen et al. (1996); Bruslé and Quignard (2001)
<i>Scardinius erythrophthalmus</i>	SER	Foreign	Holcik (1967); Vila-Gispert and Moreno-Amich (2000)
<i>Tinca tinca</i>	TTI	Foreign	Pimpicka (1990)

habitat was used to indicate habitat preferences of the adults along the longitudinal river gradient and was coded as 1 (upper), 2 (upper–middle), and 3 (lower); (11) trophic level was coded as 1 (herbivore/omnivore), 2 (invertivore), and 3 (piscivore); (12) coefficient of water quality flexibility (low values = narrow range of acceptable water quality) after Verneaux (1981) (see also Oberdorff et al. 2002); (13) coefficient of habitat flexibility (low values = narrow range of acceptable habitats) after Grandmottet (1983); and (14) tolerance coded as low (1) when species have a coefficient of water quality flexibility < 6 and a coefficient of habitat flexibility ≤ 0.1 , medium (2) when species have a coefficient of water quality flexibility = 6 or < 7 and a coefficient of habitat flexibility > 0.1 and < 0.3 , and high (3) when species have a coefficient of water quality flexibility ≥ 7 and a coefficient of habitat flexibility ≥ 0.3 .

Bivariate relationships were analyzed using Pearson's correlation coefficient for numerical variables. Differences among species origin (native, Iberian exotic and foreign exotic) in the mean of numerical variables were tested for significance using a one-way analysis of variance (ANOVA). Post-hoc comparisons of means were made with Games–Howell (GH) test. Maximum length, fecundity, age at maturity and spawning type were \log_{10} transformed for all analyses to improve linearity and homoscedasticity assumptions. For categorical variables such as gregariousness, tolerance, trophic level, and habitat, we used tests of independence (G -statistic) to test differences among species origin.

To explore patterns of association among variables and ordinate the species, principal component analysis (PCA) was performed on the 13 variables of the dataset containing 30 native and

introduced fish species from the southeastern Pyrenees watershed (Table 1). Kaiser–Meyer–Olkin’s measure of sampling adequacy was used to assess the usefulness of a PCA. KMO ranges from 0 to 1 and should be well above 0.5 if variables are very interdependent and a PCA is useful.

To test relationships between life-history and ecological traits and species origin, we performed discriminant function analysis (DFA) based on 11 variables. DFA derives canonical variables from the set of variables in a manner that maximizes multiple correlations of the original variables within groups. Stepwise DFA based on 11 variables was also performed. Correlations between the first two DFA axes and variables associated with invasive success (river length occupied in kilometers, proportional occurrence, percentage change in river length occupied, and date of introduction) were analyzed using Pearson’s correlation coefficient.

Because fecundity, age at maturity, egg diameter, and longevity are very dependent on fish size, differences among species origin subsets adjusted for maximum length were tested with analysis of covariance (ANCOVA). Homogeneity of regression coefficients (slopes) of the dependent-covariate relationship was tested with an ANCOVA design with the covariate-by-factor interaction. If the covariate-by-factor interaction was not significant (homogeneity of slopes), a standard ANCOVA was used to test significant differences in the y -intercept among populations (García-Berthou and Moreno-Amich 1993). All statistical analyses were performed with the SPSS for Windows 11.0.

Results

Correlations between all pairwise combinations of life-history and ecological traits are given in Table 2. Most of the variables were correlated and the Kaiser–Meyer–Olkin’s measure of sampling adequacy (0.55) indicated the usefulness of a PCA, which explained 53% of the variation with two axes (Figure 1). As also seen with the factor loadings, the highest correlations were found between longevity, fecundity, maximum length, and age at maturity, which were positively intercorrelated and negatively related to

Table 2. Correlation matrix of life-history and ecological traits (Pearson’s correlation).

Variables	2	3	4	5	6	7	8	9	10	11	12	13
1. Age at maturity	-0.60*	0.59*	0.73*	0.58*	-0.10	-0.69*	0.21	-0.23	-0.14	0.01	0.09	-0.10
2. Spawning type	-	-0.45**	-0.59*	-0.64*	0.05	0.71*	-0.29	0.18	-0.15	-0.02	-0.41	-0.08
3. Fecundity		-	0.74*	0.82*	-0.04	-0.69*	0.21	-0.23	0.28	-0.14	0.54**	0.28
4. Maximum length			-	0.79*	-0.20	-0.60*	0.40**	-0.12	-0.01	0.15	0.37	0.05
5. Longevity				-	-0.23	-0.48**	-0.05	-0.08	0.29	0.18	0.41	0.14
6. Gregariousness					-	0.08	0.01	-0.36	0.21	-0.49*	0.01	0.20
7. Reproductive span						-	-0.27	0.38**	0.12	-0.09	-0.30	-0.10
8. Egg diameter							-	-0.09	-0.46**	0.17	-0.48	-0.51**
9. Parental care								-	0.20	0.29	-0.16	-0.17
10. Habitat									-	-0.15	0.64*	0.37
11. Trophic level										-	-0.35	-0.20
12. Coefficient of water quality flexibility											-	0.66*
13. Coefficient of habitat quality flexibility												-

Correlations were based on all available data for south-eastern Pyrenees watershed fish species (* $P < 0.05$; ** $P < 0.01$).

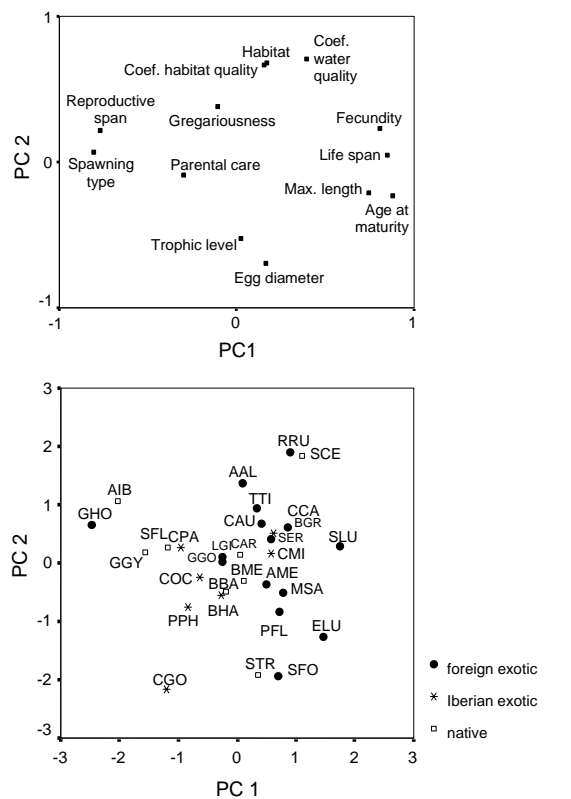


Figure 1. Principal component analysis of 13 life-history and ecological variables for native, Iberian exotic, and foreign exotic fish species from the southeastern Pyrenees watershed: (top) factor loadings of the variables, (bottom) species scores on the first two principal component axes. Species codes are given in Table 1. Symbols identify species origin.

reproductive span and spawning type. The first PCA axis identified a dominant gradient of life-history traits that contrasts species with large size, long longevity, late maturity, high fecundity, few spawning bouts per year, and short reproductive span (such as zander *Sander lucioperca*, largemouth bass *Micropterus salmoides*, and northern pike *Esox lucius*) with small species with short longevity, early maturity, low fecundity, multiple spawning bouts per year, and long reproductive span (such as mosquitofish *Gambusia holbrooki*, the Iberian toothcarp *Aphanius iberus*, and the freshwater blenny *Salaria fluviatilis*) (Figure 1). The second axis contrasts species with higher water and habitat quality flexibilities, small eggs, and of lower reaches on one end (mostly cyprinids) with species with low quality flexibilities, larger eggs, and of upper reaches on

the other (e.g., brown trout, brook trout, and bullhead *Cottus gobio*).

Species origin affiliations are slightly apparent in the general pattern of ordination of species within regions in the plot of species scores on the first two PC axes (Figure 1). Foreign introduced species tended to score higher on PC1 than native and Iberian exotic species, whereas there are no clear differences on PC2 scores according to species origin. Most of foreign introduced species (such as zander, northern pike, largemouth bass, perch *Perca fluviatilis*, common carp *Cyprinus carpio*) combine large size, long longevity, late maturity, high fecundity, few spawning bouts per year, and short reproductive span. In contrast, most of the species with lowest PC1 (except mosquitofish), i.e. with the smallest size, shortest longevity, and lower fecundity among other features were native (such as the Iberian toothcarp, the blenny, and the three-spine stickleback *Gasterosteus gymnurus*) and the Iberian exotic species were intermediate.

Univariate comparisons in life-history and ecological traits among species origins revealed significant differences between native, Iberian exotic and foreign exotic species only in mean fecundity and coefficient of water quality flexibility (Table 3, Figure 2). A multivariate ANOVA was also significant (Wilks' lambda, $P = 0.036$). Post-hoc comparisons of means among species origin subsets identified significant differences in fecundity between native and foreign exotic species (GH test, $P = 0.027$) and between Iberian exotic and foreign exotic species (GH test, $P = 0.024$) but not between native and Iberian exotic. For categorical variables, tolerance and habitat frequencies depended on species origin (Table 4). Overall, 93% of the foreign exotic species were from lower habitats, whereas only 50% of the native and 43% of the Iberian exotic were found in lower habitats. Intermediate tolerance to pollution was displayed by 73% of the foreign exotic species but none of the native and Iberian exotic species.

DFA using species origin as the categorical response variable (Figure 3) confirmed this pattern of high fecundity (within-group correlation with the first DFA function = 0.38), long longevity (0.33), large size (0.31), lower habitat reaches (0.26), and few spawning bouts per year (-0.25) in association with foreign exotic species vs low fecundity, short longevity, small size, upper and middle habitat reaches, and multiple spawning

Table 3. Analyses of variance of life-history and ecological variables with species origin (native, Iberian exotic and foreign exotic): *F*-statistics, degrees of freedom (df), and *P*-values.

Variable	<i>F</i>	df	<i>P</i>
Longevity	3.05	2, 24	0.066
Fecundity	6.20	2, 27	0.006
Maximum length	3.14	2, 27	0.059
Spawning type	1.45	2, 26	0.291
Egg diameter	0.07	2, 26	0.932
Parental care	0.59	2, 27	0.559
Reproductive span	0.42	2, 27	0.660
Habitat	3.23	2, 27	0.055
Trophic level	0.34	2, 27	0.714
Coefficient of water quality flexibility	6.04	2, 12	0.015
Coefficient of habitat quality flexibility	0.79	2, 12	0.475

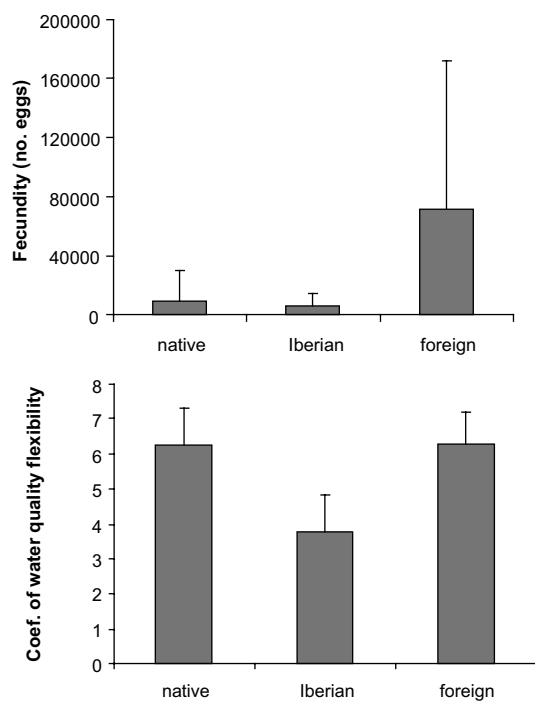


Figure 2. Means (+1 SE) of fecundity and coefficient of water quality flexibility by species origin (native, Iberian exotic and foreign exotic).

bouts in association with native and Iberian exotic species. The second discriminant axis of DFA separated Iberian exotic species with late maturity (0.42) from native species with early maturity. DFA correctly predicted the origin status for 83% of the species. Stepwise DFA selected that fecundity was the most discriminating variable and was enough to significantly separate native, Iberian exotic and foreign exotic groups of species (Wilks' $\lambda = 0.75$; $F = 3.9$; $df = 2, 23$; $P = 0.03$).

Table 4. Tests of independence of categorical variables with species origin (native, Iberian exotic and foreign exotic): *G*-statistics, degrees of freedom (df), and *P*-values.

Variables	<i>G</i>	df	<i>P</i>
Tolerance	9.76	4	0.045
Habitat	9.92	4	0.042
Gregariousness	0.58	2	0.748
Trophic level	7.47	4	0.111

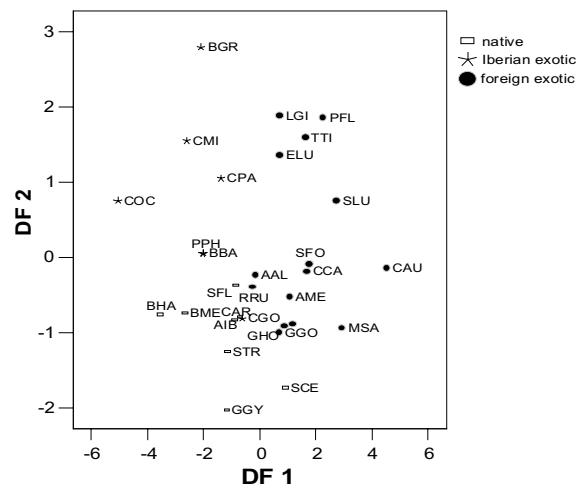


Figure 3. Species scores on the first two discriminant function (DFA) axes by species origin based on 13 life-history and ecological variables. Species code as in Table 1.

ANCOVA analyses showed that the slopes of the relationships between fecundity, age at maturity, egg diameter, and longevity with maximum length (covariate) did not significantly vary among species origins. The intercepts or adjusted means varied significantly ($F = 3.84$; $df = 23, 2$; $P = 0.04$) only for age at maturity (Figure 4).

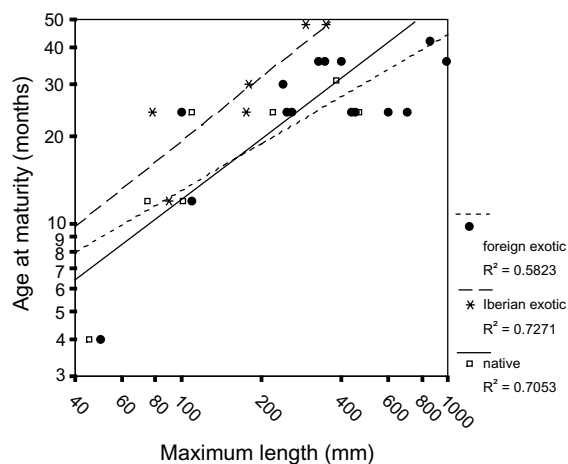


Figure 4. Relationship of age at maturity with the maximum fish size by species origin affiliations (native, Iberian exotic and foreign exotic). The age at maturity and maximum length were \log_{10} transformed.

For a given length, Iberian exotic fish have a higher age at maturity.

Pearson's correlations between the first two DFA axes and variables associated with invasive success (river length occupied in km, proportional occurrence, percentage change in river length occupied, and date of introduction) are summarized in Table 5. The two discriminant functions were not correlated with any invasive success variable, whereas the proportional occurrence of species and river length occupied were negatively correlated with the date of introduction.

Discussion

Differences between native and exotic species characteristics were already apparent in the gen-

eral pattern of ordination of species in the plot of species scores on the first two PC axes (Figure 1). Most of the foreign exotic species were located near one endpoint of the first axis of PCA, having large size, long longevity, late maturity, high fecundity, few spawnings per year, and short reproductive span, whereas Iberian exotic and native species exhibited predominantly the opposite suite of traits. The suite of life-history traits of foreign exotic species corresponds well to periodic life-history strategy defined by Winemiller (1989) and Winemiller and Rose (1992) which maximizes age-specific fecundity at the expense of optimizing turn-over time (turn-over times are lengthened by delayed maturation) and juvenile survivorship (see also Vila-Gispert and Moreno-Amich 2000, Vila-Gispert et al. 2002). Several authors (Cohen 1967; Boyce 1979; Baltz 1984) predict maximization of fecundity in response to predictable, seasonal environment variation. Environmental conditions of most Catalan streams have been altered by both pollution and the construction of dams which reduces strong flow variability and stabilizes downstream flows. As a consequence, most of the foreign exotic species that have successfully invaded Catalan streams come from seasonal habitats (central European and southeastern North American streams) that are more hydrologically stable. In contrast, native and Iberian exotic species were characterized by small size, short longevity, early maturity, low fecundity, multiple spawnings per year, and long reproductive span. Relative to foreign exotic species, native and Iberian exotic species displayed a more opportunistic life-history strategy (Winemiller 1989; Winemiller and Rose 1992) which enhances the intrinsic rate of population increase and consequently, the fitness of individuals in populations that frequently

Table 5. Correlation matrix (Pearson's correlation) of the first two axes of DFA and variables associated with invasive success (river length occupied in kilometers, proportional occurrence, percentage change in river length occupied, and date of introduction).

Variable	3	4	5	6
1. DFA 1	-0.01	-0.18	0.08	0.19
2. DFA 2	-0.03	0.08	0.10	-0.45
3. River length	-	0.90**	-0.14	-0.96**
4. Proportional occurrence		-	-0.24	-0.98**
5. Percentage change in river length			-	0.34
6. Date of introduction				-

River length was log-transformed (* $P < 0.05$; ** $P < 0.01$).

colonize habitats over small spatial scales following disturbances.

DFA showed a trend of higher fecundity, longer longevity, larger size, lower reaches and fewer spawning bouts in association with foreign exotic species. In contrast, lower fecundity, shorter longevity, smaller size, upper reaches, and more spawning bouts were associated with Iberian exotic and native species. The highest proportion of native and Iberian exotic fishes in Catalan streams are found in headwaters and upper reaches of streams (Aparicio et al. 2000; Doadrio 2001), whereas most of the foreign exotic species are found in the middle and lower reaches. As pointed out by Minckley and Meffe (1987) and Moyle (1995), natural flooding provides the most evidence for slowing or precluding establishment of foreign exotic species. Headwater streams and upper reaches of Catalan streams experience strong seasonal patterns of flow: low flows in summer that restrict aquatic habitats to small isolated pools, and high flows in winter and spring. These environmental conditions prevent the invasion of large foreign exotic species more adapted to lentic habitats, whereas native and Iberian exotic species more adapted to strong seasonal patterns of flow could survive due to its lower sizes and to multiple spawnings that prevent the loss of all offspring after flood disturbances. In contrast, foreign exotic species successfully invade middle and lower reaches of Catalan streams where the effects of flow regulation are stronger. DFA also separated Iberian exotic species with late maturity from native ones with early maturity. Iberian exotic species come from large streams where the impacts of floods were lesser than in small Catalan streams. As a result, early maturity in species from Catalan streams maximizes the intrinsic rate of population increase after flood disturbances.

Invasive success measured as the river length occupied in kilometers, proportional occurrence, and percentage change in river length occupied was not correlated with any discriminant function axes, so it seemed that life-history and ecological traits could not be used to explain differences in invasive success. In contrast, the proportional occurrence of species and the river length occupied were negatively correlated with date of introduction of species, suggesting that introduction date is an important explanatory

variable and that species more recently introduced will extend its distribution.

Surprisingly, native species were similarly distant in life-history traits from Iberian than from foreign exotic species (Figures 3 and 4). Iberian exotic species come predominantly from large river basins such as Guadalquivir (602 km), Guadiana (778 km), Duero (775 km), Tajo (940 km), and Ebro (928 km), whereas Catalan streams (excluding Ebro river) correspond to basins and streams of smaller size and different hydrology, due to the short distance from the mountains to the coastline (maximum length 167 km). These spatial-scale differences produce differences in species composition and life-history traits between fish from Catalonia (or other small, coastal basins) and fish from large Iberian rivers. As a result, it is as important to prevent the introduction of exotic fish species to the Iberian peninsula so as to prevent the translocation of Iberian species in basins where they are not native. Moreover, the identification of invasive fish features seems to profoundly depend on river basin size, as many other ecological patterns and processes.

Finally, we conclude that the possibility of prediction of success for future invasive species is limited due to small differences in life-history and ecological traits between native and exotic species. In our study, only fecundity, age at maturity, water quality flexibility, tolerance to pollution and habitat showed some significant differences. A multivariate analysis was more powerful in detecting such differences. Further studies in different regions and scales are needed to understand the role of life-history traits in invasive fish success.

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