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APPLIED ISSUES

Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California

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SUMMARY

1. The global spread of non-native species is a major concern for ecologists, particularly in regards to aquatic systems. Predicting the characteristics of successful invaders has been a goal of invasion biology for decades. Quantitative analysis of species characteristics may allow invasive species profiling and assist the development of risk assessment strategies.
2. In the current analysis we developed a data base on fish invasions in catchments throughout California that distinguishes among the establishment, spread and integration stages of the invasion process, and separates social and biological factors related to invasion success.
3. Using Akaike's information criteria (AIC), logistic and multiple regression models, we show suites of biological variables, which are important in predicting establishment (parental care and physiological tolerance), spread (life span, distance from nearest native source and trophic status) and abundance (maximum size, physiological tolerance and distance from nearest native source). Two variables indicating human interest in a species (propagule pressure and prior invasion success) are predictors of successful establishment and prior invasion success is a predictor of spread and integration.
4. Despite the idiosyncratic nature of the invasion process, our results suggest some assistance in the search for characteristics of fish species that successfully transition between invasion stages.

Keywords: establishment, human interest, integration, non-native species, spread

Introduction

The human-aided spread of non-native species into novel areas is rapidly becoming a major focus of ecologists, conservation biologists and resource managers around the world (Williamson, 1996; Carlton, 2001). The scope of the problem is staggering, with worldwide estimates of 10^2–10^4 documented non-indigenous species per country (Lodge, 1993). Although natural changes in the distributions of species are common, the current flurry of human activity has greatly increased the rate and scale of these movements. In North America alone, hundreds of plants and animals have become established in aquatic systems (Ricciardi & Rasmussen, 1998). Freshwater and estuarine systems are among the most severely invaded ecosystems around the globe (Moyle, 1999; Ricciardi & MacIsaac, 2000). As an example, the food webs of the Laurentian Great Lakes are dominated by the interaction and activities of non-indigenous aquatic species (Ricciardi & MacIsaac, 2000). Indeed, most catchments in North America contain one or more non-native species, native either to other continents or other North American drainages (Gido & Brown, 1999). Within North America there has been an asymmetrical exchange and a strong

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western bias, with the fish faunas of all the western states containing at least 25% non-native species (Rahel, 2000).

The introduction of non-native species is widespread and of growing concern, but the quantitative analysis of these unintended experiments can be useful for addressing questions of prediction and control (Gido & Brown, 1999). Identification of diagnostic characteristics for invasive species has long been a goal of ecologists (Elton, 1958; Williamson, 1996; Kolar & Lodge, 2002). Past efforts at the prediction of future invaders has focused on 'species profiling' through largely qualitative assessment of species traits (Moyle & Light, 1996a,b; Ricciardi & Rasmussen, 1998; Kolar & Lodge, 2002). Currently many invasion ecologists are advocating more quantitative analysis of species traits (Kolar & Lodge, 2001), and the development of predictive risk assessment protocols (Ricciardi & Rasmussen, 1998; Kolar & Lodge, 2002) with particular reference to freshwater fishes (Kolar & Lodge, 2001). This risk assessment process has been successfully applied to the Great Lakes and a list of potential diagnostic traits for fish invaders has been developed for that system (Kolar & Lodge, 2002).

Invasion studies in the past have often relied on 'natural experiments' (Blackburn & Duncan, 2001a,b), which may hide underlying mechanisms. These mechanisms may be as simple as the number of propagules introduced (Kolar & Lodge, 2001), a history of intentional stocking (Dill & Cordone, 1997) or prior invasion success (Kolar & Lodge, 2001). Mechanisms such as these, which represent aspects of human interest in a species, may mask underlying biological characteristics. In order to disentangle these forces it might be useful to analyse biological variables separately from variables representing human interest.

One of the past difficulties of prediction efforts was the failure to recognise that invasion is a process with distinct stages: transport, establishment, spread (Williamson, 1996; Kolar & Lodge, 2001) and integration (*sensu* Vermeij, 1996). Indeed, recent work has suggested that particular species-level traits may facilitate or hinder transit through these stages (Moyle & Light, 1996a,b; Kolar & Lodge, 2002) and that alternate suites of traits may be important at different stages of the process (Kolar & Lodge, 2001; Cassey *et al.*, 2004).

In the current analysis, we quantitatively examine multiple steps in the invasion process for freshwater fish across California and address four major questions. First, are there characteristic differences among successful and failed invasive fish species? Secondly, what characteristics predict whether a successfully established fish species spreads in California? Thirdly, if a species spreads what characteristics predict whether it has become abundant and integrated into the novel environment? Finally, how important are social factors (human interest in a species) in the overall invasion process for freshwater fishes?

Methods

Types of invaders and explanatory variables

We gathered presence and abundance data on every freshwater fish species inhabiting catchments in California (Fig. 1) using information in Moyle (2002). We divided successful invaders into two groups: non-native species that became established in California ($n = 49$ species) and native species established in catchments outside their native range ($n = 22$ species). Data on unsuccessful invaders ($n = 38$ species) were from Dill & Cordone (1997) and were species designated 'fish that achieved no lasting success'.

We examined 10 life history predictor variables: trophic status of the 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. We assigned life history attributes for all fish species in California based on a survey of current literature (Sterba, 1967; Wheeler, 1975; Merrick & Schmida, 1984; Hoestlandt, 1991; Etnier & Starnes, 1993; Moyle, 2002) and personal experience (Appendix). The first eight variables have ecological or biological relevance and the last two are measures of human interest in the species. Categorical and ordinal measures were chosen over continuous measures for all variables (except prior invasion success), because of the lack of reliable continuous quantitative data for the majority of species.

1. Adult trophic status. Six categories were designated: carnivore (C), omnivore (O), herbivore (H), invertivore (I), detritivore (D) and planktivore (P). Trophic categories were determined by the main items (>50%) of diets in adult fish following Goldstein & Simon (1999) but modified by information in Moyle (2002).

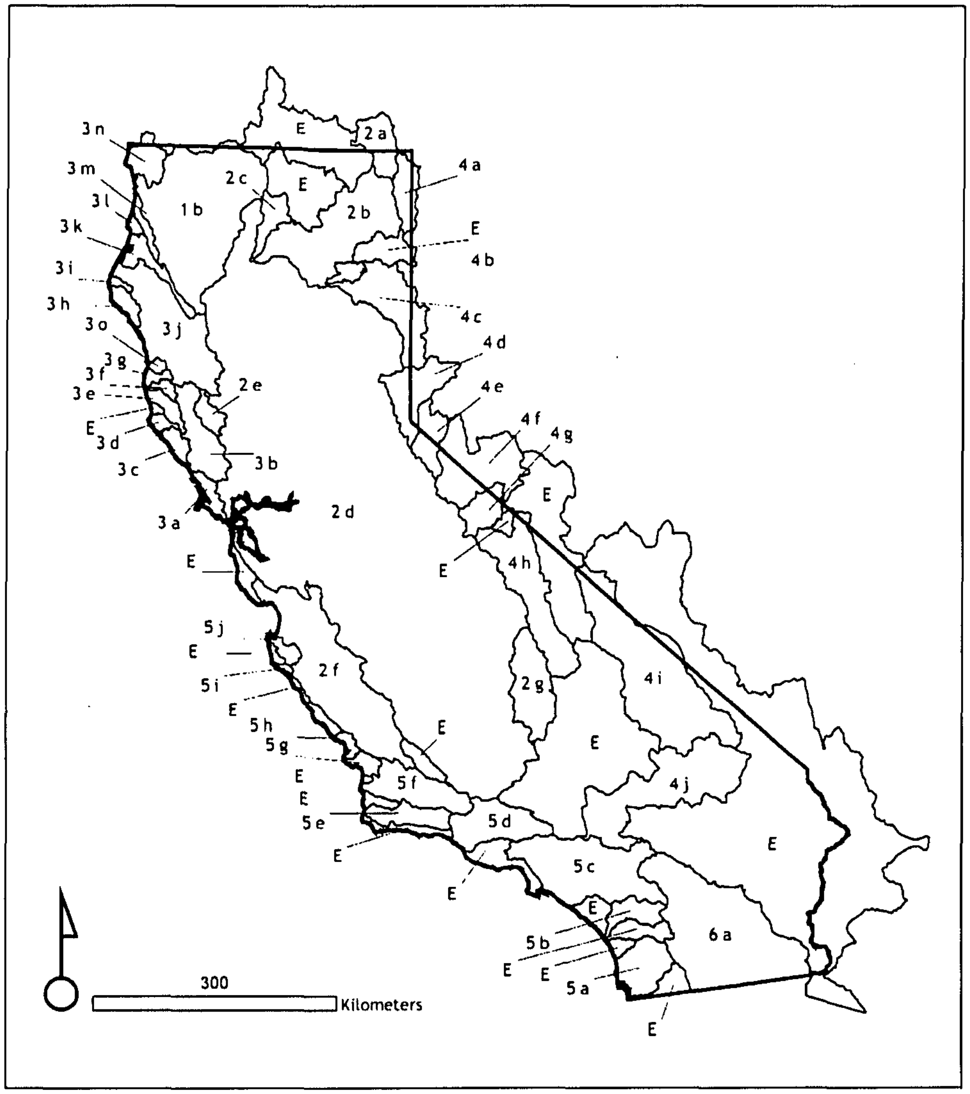

Fig. 1 Map of California catchments. Invasive fish data from catchments designated with a number/letter combination were used in this analysis. Those designated with an E were excluded from the analysis, either because there are no fish in the catchment, or because the catchment extended significantly outside state boundaries. See Moyle (2002) for catchment names.

2. Size of native range. Because quantitative information on native range is limited for many species, the size of a species' native range was scored on a one to four scale based on likely occurrence in waterways in large zoogeographic sub-regions of North America (Moyle & Cech, 2000). For species outside of North America, our classification represents an estimate based on examination of relevant literature for each species. The scoring was as follows: NR1, range occupies <5% of one zoogeographic sub-region, local endemics, e.g. redeye bass (*Micropterus coosae* Hubbs & Bailey); NR2, range occupies 5–50% of one zoogeographic sub-region, e.g. blue catfish (*Ictalurus furcatus* Lesueur), American shad (*Alosa sapidissima* Wilson); NR3, range occupies >50% of one zoogeographic sub-region, e.g. bluegill sunfish (*Lepomis macrochirus* Rafinesque); NR4, range occupies more than one zoogeographic sub-region, e.g. northern pike (*Esox lucius* Linnaeus). These data were treated as ordinal variables for statistical analysis.

3. Parental care. Our parental care categories are based on current literature (Balon, 1975, 1984; Moyle & Cech, 2000) and included the following: PC1, open substrate spawners – fish scatter their eggs in the

environment with no parental care; PC2, brood hiders – fish that hide their eggs but show no additional parental care; PC3, guarders – fish guard their embryos and/or larvae; and PC4, bearers – fish that carry their embryos with them.

4. Maximum fecundity. The maximum number of eggs per female under normal field conditions. Logarithmic categories are used because fecundity estimates are variable among studies or populations but are typically consistent within an order of magnitude. F1 < 100 eggs per female, F2 100–1000 eggs per female, F3 1000–10 000 eggs per female, F4 10 000–100 000 eggs per female and F5) >100 000 eggs per female.

5. Maximum adult size. The maximum length individuals achieve under conditions of good growth and survival in the wild. This excludes individuals growing under conditions that inhibit reproduction (e.g. threadfin shad, *Dorosoma petenense* Günter, in salt water). Categories increase logarithmically by a factor of two. Categories are preferred over direct numerical estimates because measurement methods are variable (e.g. state angling records for species caught by sport anglers versus field data for non-game species) and typical adult lengths are estimated for some species based on limited data. All categories represent measurements of standard length (from tip of snout to end of vertebral column, excluding the tail; MS1, <10 cm; MS2, 11–20 cm; MS3, 21–40 cm; MS4, 41–80 cm; MS5 81–160 cm and MS6, >160 cm).

6. Maximum lifespan: the maximum age large individuals in a wild population living under favourable conditions can be expected to achieve. It excludes ages derived from captive individuals and from individuals growing under conditions that inhibit reproduction (e.g. brook trout in ultraoligotrophic lakes). Categories increase logarithmically by a factor of two and are used because age estimation is often not precise enough to justify use of individual ages (LS1, ≤2 years; LS2; 3–4 years; LS3, 5–8 years; LS4, 9–16 years; LS5, >16 years).

7. Physiological tolerance. This variable represents tolerance to changes in water quality (usually temperature, dissolved oxygen, turbidity and salinity) or to extreme conditions in water quality, following the classification of Halliwell *et al.* (1999), with the addition of an extremely tolerant category: PT1, intolerant. Fishes with low physiological tolerance to changes or extremes in water quality (e.g. coho salmon, *Oncorhynchus kisutch* Walbaum); PT2, moderately tolerant fishes capable of living in water with moderately high variability in water quality (e.g. largemouth bass, *Micropterus salmoides* Lacépède); PT3, tolerant fishes capable of living in waters in which water quality often reaches their limits of physiological tolerance for short periods (e.g. golden shiner, *Notemigonus crysoleucas* Mitchill); and PT4, extremely tolerant fishes capable of living in waters with water quality that excludes most other fishes (e.g. western mosquitofish, *Gambusia affinis* Baird & Girard).

8. Distance from nearest native source. Categories were used because exact distances are not known, (D1, <150 km) within California or neighbouring states; (D2, 150–1000 km) within western United States and south-western Canada; (D3, 1000–3000 km) within North America outside above areas; and (D4, >3000 km) from other continents.

9. Prior invasion success. The number of countries worldwide in which each species has been introduced and successfully established is based on Lever (1996). The number of countries was transformed using a natural logarithm transformation [$\ln(x+1)$] prior to analysis to rectify violations of homoscedasticity and normality.

10. Propagule pressure. Propagule pressure 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. Categories increase logarithmically by a factor of 10. PP1, <100 individuals released in single introductions; PP2, 100–1000 individuals released in single or multiple releases; PP3, 1000–10 000 individuals released; and PP4, >10 000 individuals released. Categories are used because actual numbers are often rough estimates based on the historical record (Dill & Cordone, 1997) or were determined by the authors based on the most likely scenarios for the introduction. We assumed that illegal unrecorded introductions by anglers (e.g. northern pike) or aquarists (e.g. tiger barb, *Puntius tetrazona* Bleeker) were <100 individuals. The two species of fish believed to have been brought via ballast water (e.g. yellowfin goby, *Acanthogobius flavimanus* Temminck & Schlegel, shimofuri goby, *Tridentiger bifasciatus* Steindacher) are assumed to have been introduced in numbers in the range of 1000–10 000 larvae. Both these estuarine species are found in large concentrated patches as larvae (P. B. Moyle, unpublished data) and it is assumed they were collected into ballast water from similar large concen-

trations as well. Many of the native fish established outside their native range were carried by aqueducts and based on the volume of water moved through aqueducts we estimated propagule size to be 1000–10 000 fish for high-fecundity species with large reproducing populations in reservoirs connected to aqueducts (e.g. San Louis Reservoir, California Aqueduct) and 100–1000 fish for populations established via small aqueducts that connect more directly to native sources (usually streams).

We defined a binary response variable to examine successful establishment by comparing successful fish invaders with unsuccessful fish invaders. We did not include native species established in catchments outside their native range in the analysis of the establishment stage because we do not have data on unsuccessful transfers of native species.

We defined two additional response variables to examine spread and integration stages of invasion: the number of California catchments invaded by a species (a measure of spread) and the species' average abundance in California catchments where it has successfully invaded (a measure of integration). The number of catchments each species has invaded is summarised from data in Moyle (2002).

We scored species abundance in each catchment on a one to five scale using Moyle (2002) and personal knowledge of P. B. Moyle, based on >30 years experience in California catchments: (i) the species is present in low numbers, or present at only one or two localities with very limited distribution [e.g. tench, *Tinca tinca* (Linnaeus), in San Mateo County]; (ii) the species is locally common but with very limited distribution [e.g. Mozambique tilapia, *Oreochromis mossambicus* (Peters), in the Salton Sea]; (iii) the species is fairly common in the catchment (multiple locations) but is not abundant, (e.g. it may be a common fish in reservoirs but not common outside the reservoir habitat, e.g. kokanee salmon, *Oncorhynchus nerka* Walbaum); (iv) the species is widespread in a catchment but not necessarily abundant everywhere where found [e.g. fathead minnow, *Pimephales promelas* (Rafinesque), in the Sacramento-San Joaquin catchment]; and (v) the species is widespread and abundant throughout the catchment [bluegill sunfish, *L. macrochirus* in the Sacramento-San Joaquin catchment]. For each species we computed the numerical average of the abundance categories in all catchments where the species was present and used this value for analysis.

Analysis

We examined three stages of the invasion process with respect to California fishes: establishment, spread and integration. To examine the effect of human interest on the invasion process our entire analysis was repeated with a reduced set of variables. In this reduced analysis we excluded two independent variables, prior invasion success and propagule pressure, both measures of human interest.

When using categorical variables it is possible to make *post hoc* comparisons of within variable factors using a Holm test (a more powerful version of the Bonferroni correction) for multiple comparisons (Aickin & Gensler, 1996; Neter *et al.*, 1996). These comparisons allow us to examine both the presence of significant trends among the within-variable factors as well as the direction of trends using the sign of the parameter estimates. Our *post hoc* comparisons were chosen based on observed natural breaks in the numerical distribution of the data for each variable.

Successful establishment

To aid in interpretation of the data set for establishment, we graphed the percentage success and failure of each subcategory for all categorical variables (Fig. 2). This graph aids in the interpretation of any logistic relationships present in the data.

We used a logistic regression model to examine the relationship between successful establishment and the 10 independent variables of interest. We performed a stepwise model selection procedure using Akaike's Information Criteria (AIC) and Wald test P-values as inclusion criteria. The AIC value provides an unbiased estimate of the regression model fit and is an improvement over using R^2-values for the same purpose (Venables & Ripley, 1999). Our method involved first an implementation of the automated model selection routine stepAIC in the statistical software package S-plus (http://www.insightful.com/support/documentation.asp). The function stepAIC sequentially searches through all possible models, for the one that minimises AIC (Venables & Ripley, 1999). The best models selected by the stepAIC routine often produced unstable model fits for the data set. The automated routine also ignores the scientific relevance of the variables. We then manually implemented a stepwise (both forward selection and backward

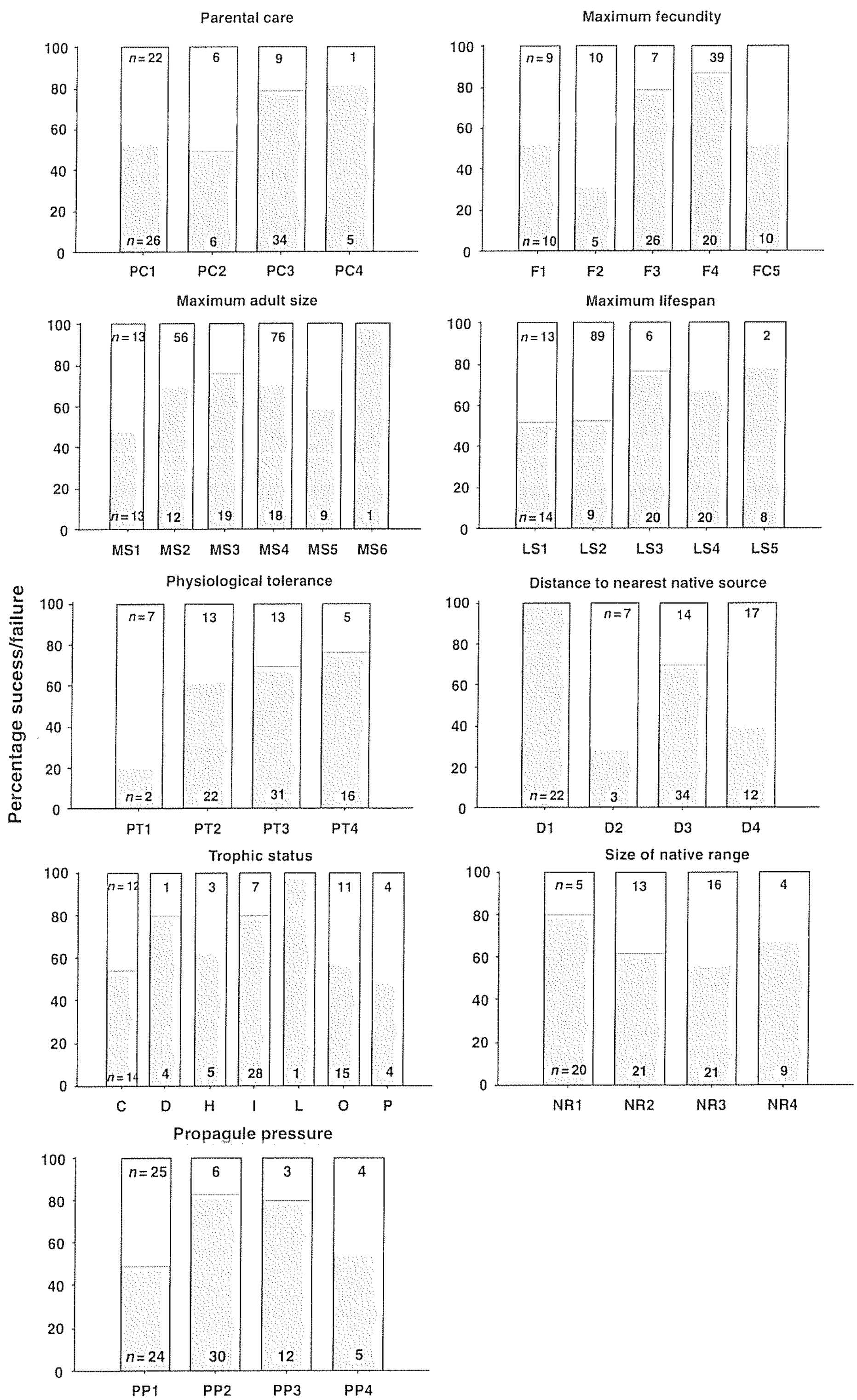

Fig. 2 Percentage of successful versus failed fish invasions for each variable subcategory; used to indicate logistic relationships. Filled portions indicate the percentage of successfully introduced species, open portions indicate failed introductions. Numbers in bars indicate the number of successful versus failed invaders in each subcategory. See text for complete descriptions of subcategories.

elimination) routine (Neter *et al.*, 1996) to select among the class of best models chosen by stepAIC (Venables & Ripley, 1999). Our model selection routines considered all main effects and two-way interactions. The stepwise routine was performed in S-plus (http://www.insightful.com/support/documentation.asp). We also preformed *post hoc* statistical comparisons of within variable subgroups.

Spread

We used a multiple regression model to study the relationship between a measure of spread (the number of catchments successfully invaded by a species) and the 10 independent variables of interest. We performed a stepwise model selection procedure using AIC and Wald test *P*-values, with an inclusion criteria for the Wald test requiring $P \leq 0.15$ (Hosmer & Lemeshow, 2000). The S-plus routine stepAIC and the stepwise technique were applied analogously across the linear and logistic regression models, differing only in the link function (logit for the logistic regression model, identity for the regression model, Agresti, 1996). Again, the model selection routines considered all main effects and two-way interactions. The stepwise routine was performed using S-plus (http://www.insightful.com/support/documentation.asp). We log-transformed the number of catchments variable [$\ln(x+1)$] as suggested by residual diagnostics and Box-Cox transformations performed during the model selection process. We also performed *post hoc* statistical comparisons of within variable subgroups.

Integration

We used a multiple regression model to study the relationship between a measure of integration (the average abundance of an invaded species) and the 10 independent variables of interest. We used a similar model selection procedure as above (using AIC and Wald test *P*-values as inclusion criteria). We performed *post hoc* statistical comparisons of within variable subgroups.

Results

Full models

The final logistic regression model suggests the following variables are important for predicting successful establishment: propagule pressure, parental care, maximum life span, physiological tolerance, size of native range and prior invasion success (Table 1). The significant ($\alpha = 0.05$) *post hoc* comparisons indicate that a longer lifespan, higher physiological tolerance and smaller native ranges contribute to successful establishment (Table 1).

Table 1 Final logistic regression model examining successful establishment for the full set of independent variables. The top table presents Wald tests for each of the six significant variables. See text for description of variable subcategories. Final whole model AIC = 119.39, $R^2 = 0.41$. The bottom table presents *post hoc* comparisons between variable sub categories

Variable	d.f.	Wald chi-square	*P* >chi-square
Propagule pressure	3	10.97	0.012
Parental care	3	9.67	0.022
Maximum lifespan	4	7.67	0.10
Physiological tolerance	3	8.81	0.032
Size of native range	3	8.58	0.035
Prior invasion success	1	2.03	0.15

Variable	Subcategory comparisons	Parameter estimate	SE	*t*-Value	*P*-value
Propagule pressure	PP1,2 versus PP3,4	−0.82	0.44	−1.86	0.071
Parental care	PC1 versus others	−0.43	0.20	−2.14	0.040
Maximum lifespan	ML1,2 versus ML3, 4, 5	−0.33	0.14	−2.42	0.021*
Physiological tolerance	PT1 versus others	−1.10	0.37	−2.97	0.0048*
Size native range	NR1 versus others	0.55	0.21	2.58	0.014*

*Significant comparisons using the Holm test at $\alpha = 0.05$.

Table 2 Final multiple regression model examining spread (the number of catchments) with the full set of independent variables. The top table presents likelihood ratio tests for each of the four significant variables. See text for description of variable subcategories. The final model AIC = −28.53, R^2 = 0.51. The bottom table presents *post hoc* comparisons between variable sub categories

Variable	d.f.	*F*-ratio	*P*-value
Maximum lifespan	4	3.96	0.0067
Distance from nearest native source	3	5.57	0.0020
Adult trophic status	6	2.67	0.023
Prior invasion success	1	14.87	0.00030

Variable	Subcategory comparisons	Parameter estimate	SE	*t*-Value	*P*-value
Maximum lifespan	ML4 versus others	0.13	0.05	2.74	0.0083*
Distance from nearest native source	D1,2 versus D3,4	−0.39	0.17	−2.36	0.022*
Trophic status	H versus others	−0.19	0.07	−2.59	0.012*

*Significant comparisons using the Holm test at $\alpha = 0.05$.

Table 3 Final multiple regression model examining integration (average fish abundance) with the full set of independent variables. The top table presents likelihood ratio tests for each of the five significant variables. See text for description of variable subcategories. Final whole model AIC = −37.58, R^2 = 0.46. The bottom table presents *post hoc* comparisons between variable sub categories

Variable	d.f.	*F*-ratio	*P*-value
Maximum adult size	4	2.78	0.037
Physiological tolerance	3	1.90	0.14
Distance from nearest native source	3	2.93	0.042
Adult trophic status	6	1.66	0.15
Prior invasion success	1	13.79	0.00049

Variable	Subcategory comparisons	Parameter estimate	SE	*t*-Value	*P*-value
Maximum adult size	MS2 versus others	0.18	0.22	3.19	0.0024*
Physiological tolerance	PT1,2 versus PT3,4	−0.16	0.16	−1.01	0.32
Distance from nearest native source	D4 versus others	−0.10	0.08	−1.16	0.25
Adult trophic status	I versus others	−0.09	0.03	−2.69	0.0095*

*Significant comparisons using the Holm test at $\alpha = 0.05$.

The multiple regression to predict spread (the number of California catchments that a species has successfully invaded) was significant, explaining 51% of the variance (Table 2). The following independent variables were included in this final model: maximum lifespan, distance from nearest native source, adult trophic status and prior invasion success (Table 2). The significant ($\alpha = 0.05$) *post hoc* comparisons suggest the following: (i) fish with a 9–16 year lifespan (LS4) are found in more catchments, (ii) fish that travelled shorter distances are found in fewer catchments and (iii) herbivorous fish are found in fewer catchments than other trophic categories (Table 2).

The multiple regression to predict integration (the average abundance of a species) was significant, explaining 46% of the variance (Table 3). The following independent variables were included in this final model: maximum adult size, physiological tolerance, distance from nearest native source, adult trophic status and prior invasion success (Table 3). The significant ($\alpha = 0.05$) *post hoc* comparisons of the within variable factors suggest the following: (i) fish with a maximum size of 11–20 cm (MS2) are more abundant and (ii) fish that are invertivores are less abundant (Table 3).

Reduced models

The repeat analyses excluding human-interest variables (propagule pressure and prior invasion success), generally indicate reduced effects (lower R^2-values;

Table 4 Final logistic regression model examining successful establishment using the reduced set of independent variables (not including propagule pressure and prior invasion success). The top table presents Wald tests for each of the three significant variables. See text for description of variable subcategories. The final whole model AIC = 126.83, $R^2 = 0.27$. The bottom table presents *post hoc* comparisons between variable subcategories

Variable	d.f.	Wald chi-square	P > chi-square
Parental care	3	8.62	0.035
Maximum fecundity	4	16.68	0.0022
Physiological tolerance	3	6.16	0.10

Variable	Subcategory comparisons	Estimate	SE	t-Value	P-value
Parental care	PC1 versus others	−0.49	0.18	2.02	0.052
Maximum fecundity	F2 versus others	0.24	0.14	1.68	0.097
Physiological tolerance	PT1 versus others	−0.65	0.28	−2.36	0.025

All comparisons are significant using the Holm test at $\alpha = 0.10$, but none of the comparisons are significant under the Holm test at $\alpha = 0.05$.

Table 5 Final multiple regression model examining spread (number of catchments a species has invaded) with the reduced set of independent variables (not including propagule pressure and prior invasion success). The top table presents likelihood ratio tests for each of the five significant variables. See text for description of variable subcategories. The final model AIC = −14.65, $R^2 = 0.59$. The bottom table presents *post hoc* comparisons between variable subcategories

Variable	d.f.	F-ratio	P-value
Parental care	3	1.91	0.14
Maximum lifespan	4	4.75	0.0025
Physiological tolerance	3	1.88	0.14
Distance from nearest native source	3	6.58	0.00076
Adult trophic status	6	1.66	0.15

Variable	Subcategory comparisons	Parameter estimate	SE	t-Value	P-value
Parental care	PC1 versus others	−0.18	0.08	−2.18	0.034
Maximum lifespan	LS4 versus others	0.14	0.05	2.98	0.0044*
Physiological tolerance	PT1,2 versus PT3,4	−0.50	0.25	−2.00	0.050
Distance from nearest native source	D1,2 versus D3,4	−0.50	0.18	−2.84	0.0065*
Adult trophic status	H versus others	−0.20	0.08	−2.51	0.015*

*Significant comparisons using the Holm test at $\alpha = 0.05$.

Tables 4, 5, 6), except for the multiple regression to predict spread where the reduced model produced a higher R^2 value. The *post hoc* comparisons of the within variable factors indicated the same direction of effect when the variable was included in the full model.

An overall summary of all 10 independent variables and their inclusion or exclusion in all the various models is provided (Table 7).

Discussion

Our analysis supports the idea that successful invasive species generally have distinguishable characteristics from species that failed to establish. Two species-level characteristics appear to affect all stages of the invasion process (Table 7). First, species with a narrow range of physiological tolerance do not successfully establish as often as ones that are more tolerant, demonstrating that physiological constraints may place limits on the establishment of non-native species (Lodge, 1993). This is consistent with findings for the establishment success of fishes in the Great Lakes (Kolar & Lodge, 2002) where fish with wider ranges of temperature and salinity tolerances were more successful, although this may not be a universal property of non-native species (McMahon, 2002).

Table 6 Final multiple regression model examining integration (average abundance of species) using the reduced set of independent variables (not including propagule pressure and prior invasion success). The top table presents likelihood ratio tests for each of the four significant variables. See text for description of variable subcategories. The final whole model AIC = −28.01, $R^2 = 0.31$. The bottom table presents *post hoc* comparisons between variable subcategories

Variable	d.f.	*F*-ratio	*P*-value
Parental care	3	2.05	0.12
Maximum adult size	4	2.92	0.029
Physiological tolerance	3	2.81	0.048
Distance from nearest native source	3	4.32	0.0082

Variable	Subcategory comparisons	Parameter estimate	SE	*t*-Value	*P*-value
Parental care	PC3 versus others	−0.10	0.07	−1.54	0.13
Maximum adult size	MS2 versus others	0.18	0.05	3.39	0.0013*
Physiological tolerance	PT1,2 versus PT3,4	−0.55	0.22	−2.46	0.017*
Distance from nearest native source	D1,2 versus D3,4	−0.38	0.15	−2.50	0.015*

*Significant comparisons using the Holm test at $\alpha = 0.05$.

Table 7 Analyses summary: X indicates inclusion in the model. Full models considered all 10 variables, while reduced models did not include the two anthropogenic variables, propagule pressure and prior invasion success

Statistical test	Logistic regression		Multiple regression predicting number of catchments		Multiple regression predicting average abundance	
Invasion stage examined	Establishment		Spread		Integration	
Model	Full	Reduced	Full	Reduced	Full	Reduced
Size of native range	X					
Parental care	X	X		X		X
Maximum fecundity		X				
Maximum adult size					X	X
Maximum lifespan	X		X	X		
Physiological tolerance	X	X		X	X	X
Distance from nearest native source			X	X	X	X
Adult trophic status			X	X	X	
Propagule pressure	X	–		–		–
Prior invasion success	X	–	X	–	X	–

Secondly, fishes with prior invasion success are likely to be successfully introduced in California catchments, suggesting that successful non-natives are likely to be species that are ecological generalists, as well as being favoured by humans (Kolar & Lodge, 2001).

Characters favoured at different stages of invasion

Our analysis suggests the suite of characteristics that favour successful establishment are different from those that facilitate a species' spread (number of catchments invaded) or integration (average abundance of a species), beyond the common factors described above. This is consistent with other studies (Kolar & Lodge, 2001, 2002) and suggests the need for further stage-specific studies of invasions.

During the establishment phase fish species with parental care appear to have an advantage, presumably because such care increases survival of individual young and reduces dispersal into unfavourable environments. Additionally, for establishment, size of native range seems to be particularly important in the full model, presumably as a measure of the natural capacity of the species to invade new areas. The presence of both physiological tolerance and parental care in the full and reduced models predicting establishment suggests that these traits may be robust biological contributors to establishment success and together are a strong predictor of invasion success.

It is interesting to note that increased propagule pressure appears to confer an advantage only during the initial establishment phase for fishes in California. The reduced success of low propagule pressure (<1000 individuals) is a reflection of the importance of stochastic events during early stages of invasion. This result is similar to the findings of Kolar & Lodge (2001) for avian invasions, where increases in both numbers of individuals released and number of introduction attempts (both aspects of propagule pressure) were positively indicated for the establishment phase and only weakly indicated for the integration phase.

During the spread stage it appears that being long-lived, being of regional origin, and not being an herbivore confer an advantage, while during the integration phase, being small, being of regional origin and not being an invertivore seems to provide advantage. These results are in stark contrast to findings for invasive fishes in the Great Lakes (Kolar & Lodge, 2002) where slow growth was positively associated with spread and small eggs were positively associated with impact. These dissimilar findings support suggestions in Moyle & Light (1996a,b) that prediction of universal invasive species traits is likely to prove difficult.

While it is useful to identify characteristics associated with invasion success it is equally important to identify characteristics that are seemingly unrelated to success. In the current study this would include maximum fecundity, propagule pressure and size of native range, although all three of these traits were positively associated with success in at least one model. Kolar & Lodge (2001) found similar results across taxa, with no traits being universally unrelated to success at some stage.

Human interest

Our repeat analysis with the reduced set of variables generated slightly different models, both in terms of number of included variables and the explanatory power (reduced R^2-value). This effectively demonstrates the role social factors play in successful establishment, spread and eventual impact of an invasion. Prior invasion success was included in all three full model analyses and therefore may serve as a surrogate or integrator for other human-interest variables. The general importance of measures of human interest for the invasion process in freshwater fish is similar to the findings of Lockwood (1999) and Blackburn & Duncan (2001a,b for avian introductions that indicated social factors tend to obscure biological generalisations related to invasion success.

It is not surprising that prior invasion success and human preferences are important predictors of a successful fish invader. This may reflect a pervasive process of biotic homogenisation that is occurring worldwide (McKinney & Lockwood, 1999; Rahel, 2000; Marchetti *et al.*, 2001; Scott & Helfman, 2001; Rahel, 2002). Globally, aquatic habitats are being modified in similar ways, creating a more cosmopolitan sub-set of environments from the original scope of planetary diversity. It is likely that species that are successful at establishing populations in one cosmopolitan region will be more likely to successfully colonies a new but similarly modified region. The current analysis lends support to this phenomenon.

Appropriate scale

Most studies on the characteristics of invaders of necessity utilise spatial scales on the order of states or countries, which vary widely in size and often have little connection with natural zoogeographic areas. By using catchments as the basic geographic unit of invasion, we are using natural landscape units, for which spread from one to another has to be accomplished by humans. Our results indicate that species from nearby areas are more likely to spread and integrate than those from more distant areas, suggesting the importance of adaptation to regional environmental conditions. Thus rainbow trout (*Oncorhynchus mykiss*, Walbaum) have become established in the headwaters of virtually every catchment in California to which they were not native. This reflects the findings of Fausch *et al.* (2001) on their worldwide establishment; despite being subject to thousands of introductions, they have only become established and spread where the hydrologic regime fits their life cycle (Fausch *et al.*, 2001).

Management implications

The present study allows us to compare unsuccessful and successful non-indigenous fish across natural geographic units within California. Unfortunately our results are far from definitive in terms of species profiling. It appears the majority of non-native fish species successful in California possess a common set of characteristics, including desirability to humans that aid in the invasion process. However, it is clear from our study that these same traits do not predict with certainty whether a non-native species will transit through the stages of the invasion process. Yet our analysis does help to further characterise these traits, which may assist in management and control decisions of this growing global phenomena.

The assertion that halting the growing transport and release of fishes into non-natal waters may be the best policy to avoid further ecological damage, is generally supported by our analysis. Unfortunately, today most fish introductions are being made illegally or as by-products of other human activity (Moyle, 2002). If a new species does establish a founder population in a catchment, then eradication efforts are more easily justified if its ecological traits match the profile of successful spread and integration discussed here. For example, the northern pike (*E. lucius*) was recently established in a single reservoir in California. For this introduction the species has overcome traits that our analysis suggests should limit its establishment success [open substrate spawner (PC1) and low propagule pressure]. Yet it has a suite of other traits that may facilitate its spread and integration (high desirability, long lifespan, broad physiological tolerance, proximity to native source) and give it the ability to alter ecosystems it invades (piscivorous diet and large adult body size) (Moyle, 2002). Eradication of this species from the reservoir is therefore clearly justified on biological and conservation grounds because it has successfully passed through the establishment phase and possesses traits that may foster its spread and integration. This example serves to highlight the complicated and potentially idiosyncratic nature of many invasions. A suite of forces that act together can produce an outcome that is difficult to predict a priori, yet information from this and other studies may eventually help to characterise some of the biological traits possessed by non-native species of concern.

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Appendix

Successfully introduced fish species. See methods for variable descriptions and interpretation of values

	Common name	Latin name	Authority	Parental care	Maximum fecundity	Maximum adult size	Maximum lifespan	Physiological tolerance	Distance from nearest native source	Adult trophic status	Size of native range	Propagule pressure	Prior invasion success
1	American shad	*Alosa sapidissima*	Wilson	1	5	4	3	2	3	P	2	4	0
2	Bigscale logperch	*Percina macrolepida*	Stevenson	3	2	2	2	3	2	I	1	1	0
3	Black bullhead	*Ameiurus melas*	Rafinesque	3	3	3	3	4	3	O	3	2	21
4	Black crappie	*Pomoxis nigromaculatus*	Lesueur	3	5	3	4	3	3	I	3	2	3
5	Blue catfish	*Ictalurus furcatus*	Lesueur	3	4	5	5	2	3	C	2	2	0
6	Blue tilapia	*Oreochromis aurea*	Steindacher	3	3	2	2	3	4	H	4	2	20
7	Bluegill	*Lepomis macrochirus*	Rafinesque	3	4	3	4	3	3	I	3	2	13
8	Brook stickleback	*Eucalia inconstans*	Kirtland	3	1	1	1	2	3	I	3	1	0
9	Brook trout	*Salvelinus fontinalis*	Mitchell	2	2	4	3	1	3	I	2	3	
10	Brown bullhead	*Ameiurus nebulosus*	Lesueur	3	3	4	4	3	3	O	3	2	21
11	Brown trout	*Salmo trutta*	Linnaeus	2	4	5	4	2	4	C	4	4	26
12	Channel catfish	*Ictalurus punctatus*	Rafinesque	3	3	5	4	3	3	C	3	2	8
13	Common carp	*Cyprinus carpio*	Linnaeus	1	5	5	4	4	4	O	4	2	46
14	Fathead minnow	*Pimephales promelas*	Rafinesque	3	3	1	1	4	3	D	3	4	3
15	Flathead catfish	*Pylodictis oliveris*	Rafinesque	3	4	5	5	3	3	C	2	2	0
16	Golden shiner	*Notemigonus crysoleucas*	Mitchill	1	3	3	3	3	3	I	3	2	0
17	Goldfish	*Carassius auratus*	Linnaeus	1	4	3	4	4	4	D	4	2	33
18	Grass carp	*Ctenopharyngoden idella*	Steindacher	1	5	5	4	2	4	H	3	2	9
19	Green sunfish	*Lepomis cyanellus*	Rafinesque	3	3	3	3	4	3	I	3	1	9
20	Inland silverside	*Menidia beryllina*	Cope	1	3	2	1	3	3	P	2	3	0
21	Kokanee	*Oncorhynchus nerka*	Walbaum	2	3	4	3	2	2	P	4	2	1
22	Lake trout	*Salvelinus namaycush*	Walbaum	2	3	5	5	1	3	C	3	3	4
23	Largemouth bass	*Micropterus salmoides*	Lacepede	3	4	4	4	3	3	C	3	2	53
24	Mozambique tilapia	*Oreochromis mossambicus*	Peters	3	3	3	3	4	4	H	3	2	58
25	Northern pike	*Esox lucius*	Linnaeus	1	4	5	5	2	3	C	4	1	7
26	Porthole livebearer	*Poeciliopsis gracilis*	Heckel	4	1	1	1	3	2	O	1	1	2
27	Pumpkinseed	*Lepomis gibbosus*	Linnaeus	3	4	3	4	2	3	I	2	1	16
28	Rainwater killifish	*Lucania parva*	Baird & Girard	3	1	1	1	4	3	I	2	2	0
29	Red shiner	*Cyprinella lutrensis*	Baird & Girard	1	2	1	1	3	3	O	3	2	0
30	Redbelly tilapia	*Tilapia zilli*	Gervais	3	3	3	3	3	4	H	4	1	15
31	Redear sunfish	*Lepomis microlophus*	Gunther	3	4	3	3	2	3	I	2	3	6
32	Redeye bass	*Micropeterus coosae*	Hubbs & Bailey	3	3	3	3	2	3	I	1	2	1
33	Sailfin molly	*Poecilia latipinna*	Lesueur	4	1	1	1	4	3	D	2	1	8
34	Shimofuri goby	*Tridentiger bifasciatus*	Steindacher	3	3	1	1	3	4	I	2	3	1
35	Shortfin molly	*Poecilia mexicana*	Steindacher	4	1	1	1	3	4	H	2	1	6
36	Smallmouth bass	*Micropterus dolomieu*	Lacepede	3	4	4	4	2	3	C	2	2	12
37	Spotted bass	*Micropterus punctulatus*	Rafinesque	3	4	4	3	3	3	C	2	2	2
38	Striped bass	*Morone saxitalis*	Walbaum	1	5	5	5	2	3	C	2	2	2
39	Tench	*Tinca tinca*	Linnaeus	1	5	4	4	4	4	I	4	1	15
40	Threadfin shad	*Dorosoma petenense*	Gunther	1	4	2	2	2	3	P	2	2	1
41	Wakasagi	*Hypomesus nipponensis*	McAllister	1	3	2	2	2	4	P	1	4	1
42	Warmouth	*Lepomis gulosus*	Cuvier	3	4	3	3	3	3	I	2	2	2
43	Western mosquitofish	*Gambusia affinis*	Baird & Girard	4	1	1	1	4	3	I	2	2	68
44	White bass	*Morone chrysops*	Rafinesque	1	5	4	4	2	3	C	3	2	0
45	White catfish	*Ameirus catus*	Linnaeus	3	3	4	4	4	3	C	2	1	1

Appendix *(Continued)*

	Common name	Latin name	Authority	Parental care	Maximum fecundity	Maximum adult size	Maximum lifespan	Physiological tolerance	Distance from nearest native source	Adult trophic status	Size of native range	Propagule pressure	Prior invasion success
46	White crappie	*Pomoxis annularis*	Rafinesque	3	5	3	4	2	3	I	3	2	1
47	Yellow bullhead	*Ameiurus natilis*	Lesueur	3	3	4	4	3	3	I	3	1	0
48	Yellow perch	*Perca flavescens*	Mitchill	1	4	3	3	2	3	I	3	3	0
49	Yellowfin goby	*Acanthogobius flavimanus*	Temminck & Schlegel	3	3	3	2	3	4	I	2	3	3

Native species introduced outside their native range. See methods for variable descriptions and interpretation of values

	Common name	Latin name	Authority	Parental care	Maximum fecundity	Maximum adult size	Maximum lifespan	Physiological tolerance	Distance from nearest native source	Adult trophic status	Size of native range	Propagule pressure	Prior invasion success
1	Amargosa pupfish	*Cyprinodon nevadensis*	Eigenmann & Eignmann	3	1	1	1	4	1	O	1	1	0
2	Arroyo chub	*Gila orcutti*	Eigenmann & Eignmann	1	3	2	2	3	1	O	1	1	0
3	California roach	*Lavinia symmetricus*	Baird & Girard	1	3	2	3	3	1	O	1	1	0
4	Cutthroat trout	*Oncorhynchus clarki*	Richardson	2	3	4	3	2	1	C	3	3	0
5	Desert pupfish	*Cyprinodon macularius*	Baird & Girard	3	1	1	1	4	1	O	1	1	0
6	Hitch	*Lavina exilicauda*	Baird & Girard	1	4	2	3	3	1	I	1	3	0
7	Lahontan red side	*Richardsonius egregius*	Girard	1	3	2	2	3	1	I	1	1	0
8	Longjaw mudsucker	*Gillichthys mirabilis*	Cooper	3	4	2	1	4	1	I	1	2	0
9	Mountain sucker	*Catostomus platyrhynchus*	Cope	1	3	3	4	2	1	O	2	2	0
10	Owens sucker	*Catostomus fumeiventis*	Miller	1	3	3	4	3	1	O	1	3	0
11	Prickly sculpin	*Cottus asper*	Richardson	3	3	2	2	3	1	I	3	3	0
12	Rainbow trout	*Oncorhynchus mykiss*	Walbaum	2	2	4	3	2	1	I	3	4	58
13	Sacramento blackfish	*Orthodon microlepidotus*	Ayers	1	5	4	4	4	1	D	1	3	0
14	Sacramento perch	*Archoplites interruptus*	Girard	3	5	4	3	3	1	I	1	2	0
15	Sacramento pike minnow	*Ptychochelius grandis*	Ayers	3	4	4	4	3	1	C	1	1	0
16	Sacramento sucker	*Catostomus occidentalis*	Ayers	1	4	4	5	3	1	O	1	2	0
17	Santa Ana sucker	*Catostomus santaanae*	Snyder	1	3	3	3	2	1	O	1	1	0
18	Speckled dace	*Rhinichthys osculus*	Girard	1	2	1	2	3	1	I	2	1	0
19	Tahoe sucker	*Catostomus tahoensis*	Gill & Jordan	1	4	4	5	3	1	O	1	1	0
20	Threespine stickleback	*Gasterosteus aculeatus*	Linnaeus	3	1	1	1	3	1	I	4	1	0
21	Tui chub	*Gila bicolor*	Girard	1	4	3	5	4	1	O	1	1	0
22	Tule perch	*Hysterocarpus traski*	Gibbons	4	1	2	3	2	1	I	1	1	0

Species with failed introductions. See methods for variable descriptions and interpretation of values

	Common name	Latin name	Authority	Parental care	Maximum fecundity	Maximum adult size	Maximum lifespan	Physiological tolerance	Distance from nearest native source	Adult trophic status	Size of native range	Propagule pressure	Prior invasion success
1	Alligator gar	*Lepisosteus spatula*	Lacepede	1	5	6	4	3	3	C	2	1	0
2	American eel	*Anguilla rostrata*	Lesueur	1	5	5	5	3	3	C	3	1	0
3	Angelfish	*Pterophyllum spp.*	?	3	2	2	3	1	4	I	3	1	0
4	Arawana	*Osteoglossum bicirrhosum*	Vndelli	3	2	5	2	2	4	C	3	1	0
5	Arctic greyling	*Thymallus arcticus*	Pallas	2	3	3	3	1	2	I	4	3	0
6	Argentiene pearlfish	*Cynolebias bellottii*	Steindachner	2	1	1	1	4	4	I	2	1	0
7	Atlantic salmon	*Salmo salar*	Linnaeus	2	3	4	3	1	3	C	4	3	4
8	Ayu	*Plecoglossus altivelis*	Temminck & Schlegel	1	3	3	2	3	4	H	2	4	0
9	Bighead carp	*Hypophthalmichthys nobilis*	Richardson	1	5	4	4	3	4	O	3	1	8
10	Bigmouth buffalo	*Ictiobus cyprinellus*	Valanciennes	1	5	4	4	2	3	O	3	1	3
11	Blackfin pearlfish	*Cynolebias nigripinnis*	Regan	2	1	1	1	4	4	I	2	2	0
12	Bluefin killifish	*Lucania goodei*	Jordan	3	1	1	1	3	3	I	2	1	0
13	Bluntnose minnow	*Pimephales notatus*	Rafinesque	3	2	1	2	3	3	O	3	1	0
14	Bonneville cisco	*Prosopium gemmifer*	Snyder	1	3	2	3	1	2	P	1	4	0
15	Brook silversides	*Labidesthes sicculus*	Cope	3	2	2	1	3	2	P	3	2	0
16	Emerald shiner	*Notropis atherinoides*	Rafinesque	1	3	2	2	2	3	P	3	1	0
17	European eel	*Anguilla anguilla*	Linnaeus	1	5	5	4	3	4	C	3	1	0
18	Giant rivulus	*Rivulus harti*	Boulenger	2	2	1	2	1	3	C	2	1	1
19	Grass pickerel	*Esox americanus*	Lesueur	1	3	4	4	2	3	C	2	2	0
20	Green guapote	*Cichlasoma beani*	Jordan	3	2	3	2	2	2	O	3	1	0
21	Green swordtail	*Xiphophorus helleri*	Heckel	1	1	1	1	3	4	O	1	1	16
22	Guppy	*Poecilla reticulata*	Peters	1	1	1	1	3	4	O	2	2	34
23	Jack dempsey	*Cichlasoma octofasciatum*	Regan	3	2	3	2	1	4	O	1	1	3
24	Japanese medaka	*Oryzias latipes*	Temminck & Schlegel	1	1	1	1	2	4	O	3	1	0
25	Lake whitefish	*Coregonus clupeaformis*	Mitchill	1	4	4	4	2	3	P	2	4	1
26	Mexican tetra	*Astyanax mexicanus*	Filippi	1	2	2	1	2	2	I	2	1	0
27	Milkfish	*Chanos chanos*	Forsskal	1	5	5	2	3	4	D	4	1	0
28	Muskellunge	*Esox masquinongy*	Mitchil	1	5	5	4	2	3	C	2	3	0
29	Pacu	*Colossoma spp.*	?	1	4	4	4	2	4	H	3	1	0
30	Rio pearlfish	*Cynolebias whitei*	Myers	2	1	1	1	3	4	I	2	2	0
31	Rock bass	*Ambloplites rupestris*	Rafinesque	3	4	3	3	2	3	C	3	2	3
32	Shortfin eel	*Anguilla australis*	Richardson	1	5	5	5	3	4	C	4	1	0
33	Southern platyfish	*Xiphophorus maculatus*	Gunther	4	1	1	1	4	2	O	1	1	11
34	Tiger barb	*Puntius tetrazona*	Bleeker	1	2	1	1	2	4	H	2	1	0
35	Variable platyfish	*Xiphophorus variatus*	Meek	1	1	1	1	4	2	O	1	1	3
36	Walking catfish	*Clarias batrachus*	Linnaeus	3	3	3	3	4	3	C	3	1	7
37	Walleye	*Stizostedion vitreum*	Mitchill	1	5	4	4	1	3	C	3	4	0
38	Zebra danio	*Danio rerio*	Hamilton	1	2	1	1	2	4	O	3	1	2

C, carnivore; O, omnivore; H, herbivore; I, invertivore; D, detritivore; P, planktivore.