Ecological Applications, 14(2), 2004, pp. 587–596
© 2004 by the Ecological Society of America

ALIEN FISHES IN CALIFORNIA WATERSHEDS: CHARACTERISTICS OF SUCCESSFUL AND FAILED INVADERS

MICHAEL P. MARCHETTI,[1,4] PETER B. MOYLE,[2] AND RICHARD LEVINE[3]

[1]*Department of Biology, California State University, Chico, California 95929 USA*
[2]*Department of Wildlife, Fish and Conservation Biology, University of California, Davis, California 95616 USA*
[3]*Department of Mathematics and Statistics, San Diego State University, San Diego, California 92182 USA*

Abstract. The literature on alien animal invaders focuses largely on successful invasions over broad geographic scales and rarely examines failed invasions. As a result, it is difficult to make predictions about which species are likely to become successful invaders or which environments are likely to be most susceptible to invasion. To address these issues, we developed a data set on fish invasions in watersheds throughout California (USA) that includes failed introductions. Our data set includes information from three stages of the invasion process (establishment, spread, and integration). We define seven categorical predictor variables (trophic status, size of native range, parental care, maximum adult size, physiological tolerance, distance from nearest native source, and propagule pressure) and one continuous predictor variable (prior invasion success) for all introduced species. Using an information-theoretic approach we evaluate 45 separate hypotheses derived from the invasion literature over these three stages of the invasion process. Our results indicate that successful establishment is best predicted with our global model that includes all seven variables, suggesting an inherent multivariate nature to the establishment stage of the invasion process. Spread of introduced fishes is best predicted using measures of physiological tolerance and propagule pressure. Species integration and impact is best predicted using a measure of prior invasion success. The results from analyses like this will help guide and inform management decisions regarding current and future species introductions.

Key words: Akaike's Information Criterion (AIC_c); alien species; characteristics of invaders; establishment; fish invasion; information-theoretic approach; integration; invasion biology; native species; physiological tolerance; prior invasion success; propagule pressure; spread of invasive species.

INTRODUCTION

Predicting successful invaders is a major goal of invasion biology (Carlton 1996), and there exists a large body of literature describing general characteristics of invasive species (Ehrlich 1989, Williamson and Fitter 1996, Ricciardi and Rasmussen 1998, McKinney and Lockwood 1999). Yet these general descriptions are largely unsatisfactory (Rejmanek and Richardson 1996). Suggestions that successful invaders reproduce rapidly (Lodge 1993*a*, *b*), are habitat or diet generalists (Moyle and Light 1996*a*, *b*), or have a broad native range (Ricciardi and Rasmussen 1998), are not particularly illuminating in the absence of quantitative analysis. Statements that under the right circumstances any species can invade and any habitat can be invaded (Moyle and Light 1996 *a*, *b*) are also not very helpful, especially when developing management strategies to prevent or limit successful invasions.

Vermeij (1996), Williamson (1996), Kolar and Lodge (2001), D'Antonio et al. (2001), and others suggest that species invasion is a complex process with multiple steps: transport, release, establishment, spread, and integration. The first two stages of this process are particularly difficult to study, because they are transitory and often poorly documented. Yet it is clear that we must address each stage of this process independently, because different factors may be acting on different stages. To make invasion ecology more predictive, Kolar and Lodge (2001) suggest studies should quantitatively examine species characteristics at multiple stages of the invasion process.

Much of the literature on invasion biology suffers from the following basic problems: (1) few studies are available that compare successful invasions with failed attempts (Lodge 1993*a*), (2) the distinction between the social context of invasion, such as human interest in the species (Daehler and Strong 1993, Lockwood 1999) and biological variables (e.g., reproductive rates) is not made explicit, (3) introductions from within a region (native species translocated outside their native range) are rarely examined so most databases are incomplete, (4) the appropriate spatial scale for investigation is often not considered (Williamson and Fitter 1996, Ricciardi and Rasmussen 1998) and (5) there is a failure to consider separately the different stages of the invasion process, because different biological characteristics may be important at each stage (Kolar and

Manuscript received 16 September 2002; revised 16 June 2003; accepted 15 July 2003. Corresponding Editor: K. D. Fausch.

[4] E-mail: mmarchetti@csuchico.edu

Lodge 2002). In this study we address all of these common problems. First, we use data on both successful and failed introductions. Second, we include models that directly assess the importance of human interest in invasive species. Third, we include data on intrastate transfers of native species. Fourth, we use watershed-level data from the entire state of California to provide a geographic and latitudinally appropriate spatial scale for investigation (Moyle and Light 1996*a*, *b*). Finally, we conduct our analyses over three different stages of the invasion process. By following this approach, we avoid many of the problems associated with incomplete datasets or widely divergent conditions that characterize analyses of invasions at broader geographic scales (e.g., Gido and Brown 1999, Rahel 2000, McKinney 2001).

It has been suggested that predictive understanding of the invasion process can only emerge from taxonomically focused studies (Lodge 1993*b*). In the only meta-analysis of vertebrate invasions to date, Kolar and Lodge (2001) identified a suite of species-level traits associated with successful establishment and impact of alien birds including: maximum adult size, physiological tolerance, size of native range, trophic status, and propagule pressure. For fish, Moyle and Light (1996*a*, *b*) suggest four species-level traits that should be useful for predicting invasion success and impact: trophic status, physiological tolerance, propagule pressure, and distance from nearest native source. In our analysis, we use an information-theoretic approach (Burnham and Anderson 2002) to directly evaluate invasion hypotheses based on three sources: characteristics in Kolar and Lodge (2001), characteristics in Moyle and Light (1996*a*, *b*), and suites of related species-level characteristics. We then examine how particular traits and groups of traits contribute to fish invasions in California watersheds at three different stages of the invasion process: establishment, spread, and integration.

Methods

We used the following general analytical approach based on Burnham and Anderson (2002) to assess the influence of species characteristics on three stages of the invasion process. We first gathered information on species presence, characteristics, spread, and abundance. We then developed a priori explanatory models based on existing literature and personal experience, and ranked these models using Akaike's Information Criterion (AIC_c) corrected for small sample bias. This information measure quantifies the predictive power of each model through an evaluation of the expected relative distance between the fitted models and the underlying data-generating mechanisms (Franklin et al. 2000). The small sample criterion (AIC_c) is a function of the log-likelihood of the model under consideration adjusted for the number of parameters characterizing the model and the sample size. The AIC_c provides a measure of the distance between competing models through Kullback-Leibler distance. The models are then compared using Akaike weights, which are a function of AIC_c and are interpreted as the weight of evidence in favor of a given model against all other hypothesized models. In particular, the evidence ratio compares the Akaike weight of each model against the best model, which is the model with the smallest AIC_c and highest weight. The evidence ratios suggest the amount of improvement of the best model over each of the competing models for predicting characteristics of the invasion process. We also used the Akaike weights to evaluate the relative importance of each explanatory variable for predicting characteristics of the invasion process. Overall this method provided an objective, scientifically valid routine for model selection that overcomes the flaws inherent in hypothesis-testing-based iterative model selection routines (Burnham and Anderson 2002).

We summarized information (from Moyle 2002) on presence and abundance for every introduced freshwater fish species inhabiting each watershed in California (Fig. 1; also see Plate 1). We divided introduced species into two groups: alien species that became established in California (N = 49 spp.) and native species established in watersheds outside their native range (N = 22 spp.; see Appendix). We used Dill and Cordone (1997) to identify failed introductions from outside the state (N = 38 species; Appendix). Dill and Cordone (1997) searched California Department of Fish and Game files from 1871 to 1996 to produce a detailed account of all species ever introduced in the state's waterways; including failed introductions. We included in our analysis all species Dill and Cordone (1997) designated as ''fish that achieved no lasting success.''

We initially gathered species-specific data for 10 predictor variables: trophic status of adults, size of species' native range, parental care, average fecundity, maximum adult size, maximum lifespan, physiological tolerance, distance from nearest native source, prior invasion success, and propagule pressure. Upon examination of pairwise correlations, the following variables were found to be highly correlated (Kendall's tau for all three pairwise comparisons >0.66): average fecundity, maximum adult size and maximum lifespan. To eliminate difficulties associated with this correlation, we chose to use maximum adult size as a surrogate for all three life history variables.

We assigned values in discrete categories for seven of the eight remaining variables (the variable ''prior invasion success'' is a continuous variable; see item 7 below) to all fish species based on a survey of current literature and personal experience (see Appendix). Categorical and ordinal measures were chosen over continuous measures due to the lack of reliable quantitative data for the majority of species.

The categories (scores) for each variable are:

1) *Trophic status*.—Six categories of adult trophic status were designated: carnivore (C), omnivore (O),

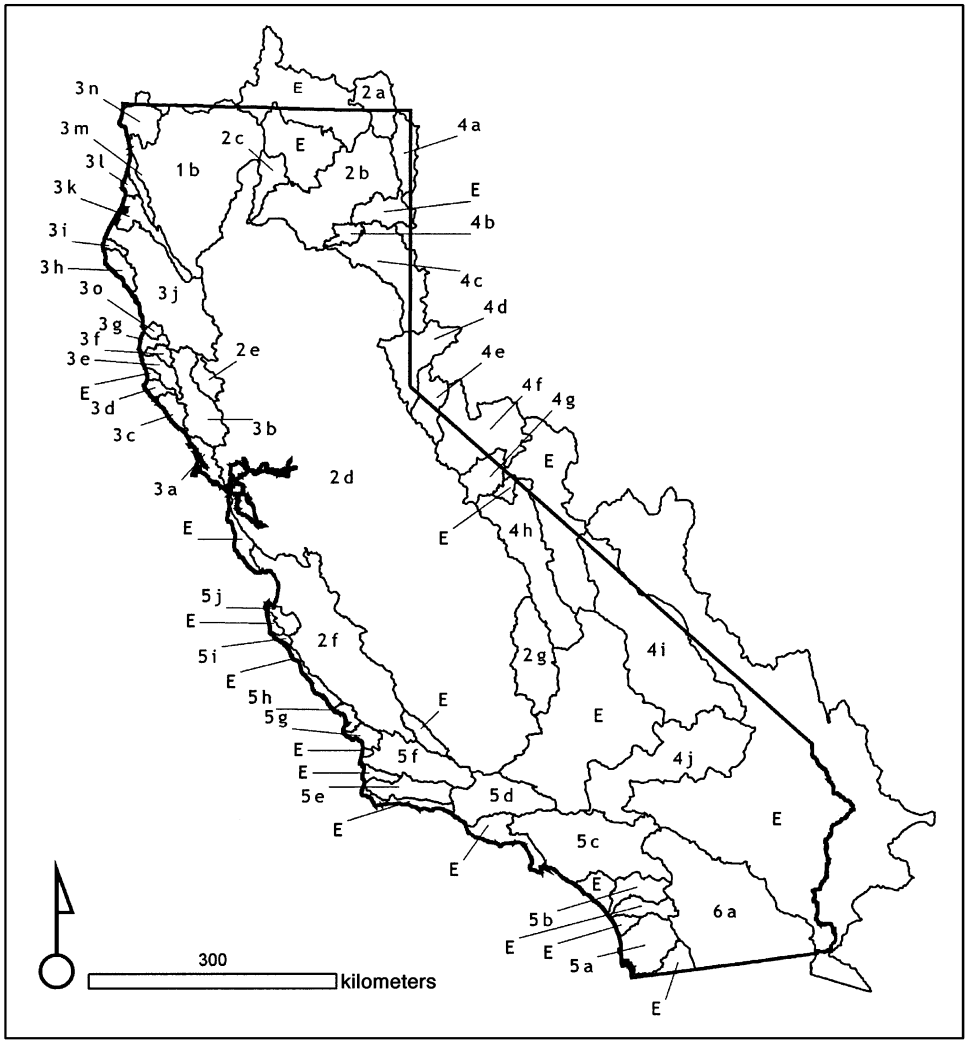

FIG. 1. Map of California watersheds. Invasive fish data from watersheds designated with a number/letter combination were used in this analysis. Those designated with an E were excluded from the analysis, either because there were no fish in the watershed or because the watershed extended significantly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

herbivore (H), invertivore (I), detritivore (D), and planktivore (P). Trophic categories were based on the majority of items (>50%) in the diets of adult fish following Goldstein and Simon (1999), but modified by information in Moyle (2002).

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 1 to 4 scale based on likely occurrence in waterways in large zoogeographic subregions of North America (Moyle and 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 subregion; local endemics, e.g., redeye bass (*Micropterus coosae*); (NR2) range occupies 5–50% of one zoogeographic sub-region, e.g., blue catfish (*Ictalurus furcatus*), American shad (*Alosa sapidissima*); (NR3) range occupies >50% of one zoogeographic subregion, e.g., bluegill sunfish (*Lepomis macrochirus*); (NR4) range occupies more than one zoogeographic subregion, e.g., northern pike (*Esox lucius*).

3) *Parental care*.—Our parental care categories are based on current literature (Balon 1975, 1984, Moyle and 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 adult size*.—This category is the maximum length individuals achieve under conditions of

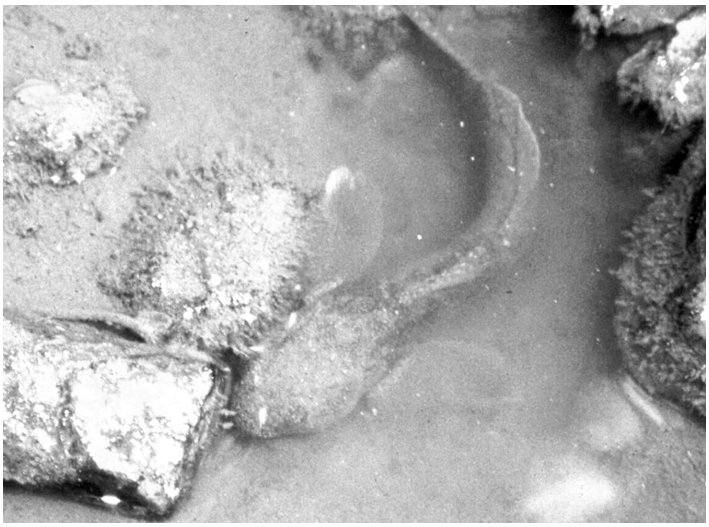

PLATE 1. *Tridentiger bifasciatus* (shimofuri gobi), an exotic fish species introduced from Japan to the San Francisco Bay Delta presumably through ballast water transfer in the early 1980s (Moyle 2002). The species has a fairly broad physiological tolerance, and the males (shown here) typically guard their young. This individual was observed on a mud-flat at low tide in Suisun Marsh in 1998. Photo by Scott Matern, University of California–Davis.

good growth and survival in the wild. The category excludes individuals growing under conditions that inhibit reproduction (e.g., threadfin shad, *Dorosoma petenense*, 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 vs. field data for nongame 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, (MS6) >160 cm.

5) *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 have low physiological tolerance to changes or extremes in water quality (e.g., coho salmon, *Oncorhynchus kisutch*). (PT2) Moderately tolerant fishes are capable of living in water with moderately high variability in water quality (e.g., largemouth bass, *Micropterus salmoides*). (PT3) Tolerant fishes are 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*). (PT4) Extremely tolerant fishes ae capable of living in waters with water quality that excludes most other fishes (e.g., western mosquitofish, *Gambusia affinis*).

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

7) *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 in the global model.

8) *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. (PS1) < 100 individuals released in single introductions. (PS2)100–1000 individuals released in single or multiple releases. (PS3) 1000–10 000 individuals released. And (PS4) > 10 000 individuals released. Categories are used because actual numbers are often rough estimates based on the historical record (Dill and 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*) were <100 individuals, whereas fish brought via ballast water (e.g., yellowfin goby, *Acanthogobius flavimanus*) came in as 1000–10 000 larvae. Many of the native fish established outside their native range were carried by aqueducts, so 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 watersheds 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 response variables to examine spread and integration (impact): the number of California watersheds invaded by a species (a measure of spread), and the species' average abundance in California watersheds where it has successfully invaded (a measure of potential impact). The number of watersheds each species has invaded is based on Moyle (2002). We scored species abundance in each watershed on a 1 to 5 scale using Moyle (2002) and personal knowledge of Moyle, based on >30 years of sampling California watersheds: (1) The species is present in low numbers, or present at only one or two localities with very limited distribution (e.g., tench, *Tinca tinca*, in San Mateo County). (2) The species is locally common but with very limited distribution (e.g., Mozambique tilapia, *Oreochromis mossambicus* in the Salton Sea). (3) The species is fairly common in the watershed (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*). (4) The species is widespread in a watershed but not necessarily abundant everywhere where found (e.g., fathead minnow, *Pimephales promelas*, in the Sacramento–San Joaquin watershed). And (5) The species is widespread and abundant throughout the watershed (bluegill sunfish, *Lepomis macrochirus*, in the Sacramento–San Joaquin watershed). For each species we computed the numerical average of the abundance categories in all watersheds where the species was present and used this value for analysis.

Analysis

We use the information theoretic model selection approach put forth in Burnham and Anderson (2002) to evaluate a set of a priori models that measure the relative importance of eight variables in predicting success and failure of fish invaders (establishment), the number of California watersheds invaded by a species (a measure of spread), and the species' average abundance in California watersheds where it has successfully invaded (a measure of integration and impact).

We derived a set of 45 candidate models (Table 1) based on the following sources:

1) *Invasive species characteristics in Kolar and Lodge's (2001) meta-analysis of avian invasions (model's 10–34)*.—We choose to examine piscine characteristics that were analogous to bird traits in Kolar and Lodge (2001): maximum adult size (analogous to bird height or body length), physiological tolerance (analogous to temperature and habitat match in birds), size of native range (analogous to range area in birds), trophic status (analogous to diet breadth or type) and propagule pressure. We did not include the effects of other characteristics Kolar and Lodge (2001) examined for one of two reasons: either the data were not available for California fishes (egg mass, length of juvenile period, number of reproductive events per season), or the trait was not widely applicable to fishes (migration). We constructed all possible models from these five variables.

2) *Invasive species characteristics hypothesized in Moyle and Light (1996a, b) (models 35–41)*.—Moyle and Light (1996*a*, *b*) suggest that trophic status, physiological tolerance, propagule pressure, and distance from nearest native source should be important in fish invasions. We constructed all possible models from these four variables, four of which were included in models derived from Kolar and Lodge (2001) (models 18, 32–34).

3) *Suites of related characteristics (models 32, 42–44)*.—To explore the effect that suites of related characteristics have on fish invasions we constructed four separate models to examine the following: ecological traits (included physiological tolerance and trophic status); life history traits (included maximum size and parental care); geographical traits (included size of native range and distance traveled); and human interest (included propagule pressure and prior invasion success). Our model to examine ecological traits (model 32) was the same as a model derived from predictions in Kolar and Lodge (2002) and Moyle and Light (1996*a*, *b*).

4) *Our best-informed opinion (model 45)*.—This model was constructed from our best opinion based on 30+ years of studying fish invasions in California.

5) *A global model including all eight explanatory variables (model 1)*.—This model should always be included in this statistical approach (Burnham and Anderson 2002).

6) *Individual models for all eight explanatory variables (models 2–9)*.—Individual models are often recommended for this statistical approach (Burnham and Anderson 2002), and allow us to examine the individual influence of each variable.

The same set of 45 models was evaluated for all three stages of the invasion process.

Model fitting and evaluation

Predicted establishment of an invading species is a categorical variable (success/failure), so we used a logistic regression model for analysis. Models of spread and impact using continuous variables (number of watersheds and average abundance) were analyzed with multiple linear regression.

Diagnostics from the fit of each of the three global models (establishment, spread, integration) indicated a reasonable fit to the data with no deviations from the underlying regression assumptions. In particular, the global logistic regression model (establishment) showed no evidence of overdispersion as measured by

TABLE 1. A priori models and the variables included in each model.

Model no.	Model categories	Maximum size	Size of native range	Physio-logical tolerance	Trophic status	Propagule pressure	Distance to native source	Parental care	Prior invasion success
1	A	1	1	1	1	1	1	1	1
2	I	1	0	0	0	0	0	0	0
3	I	0	1	0	0	0	0	0	0
4	I	0	0	1	0	0	0	0	0
5	I	0	0	0	1	0	0	0	0
6	I	0	0	0	0	1	0	0	0
7	I	0	0	0	0	0	1	0	0
8	I	0	0	0	0	0	0	1	0
9	I	0	0	0	0	0	0	0	1
10	K	1	1	1	1	1	0	0	0
11	K	0	1	1	1	1	0	0	0
12	K	1	1	1	1	0	0	0	0
13	K	1	0	1	1	1	0	0	0
14	K	1	1	0	1	1	0	0	0
15	K	0	1	1	1	0	0	0	0
16	K	0	1	1	0	1	0	0	0
17	K	1	1	1	0	0	0	0	0
18	K,M	0	0	1	1	1	0	0	0
19	K	1	0	1	1	0	0	0	0
20	K	1	0	1	0	1	0	0	0
21	K	0	1	0	1	1	0	0	0
22	K	1	1	0	1	0	0	0	0
23	K	1	1	0	0	1	0	0	0
24	K	1	0	0	1	1	0	0	0
25	K	1	1	0	0	0	0	0	0
26	K	1	0	1	0	0	0	0	0
27	K	1	0	0	1	0	0	0	0
28	K	1	0	0	0	1	0	0	0
29	K	0	1	1	0	0	0	0	0
30	K	0	1	0	1	0	0	0	0
31	K	0	1	0	0	1	0	0	0
32	K,M,E	0	0	1	1	0	0	0	0
33	K,M	0	0	1	0	1	0	0	0
34	K,M	0	0	0	1	1	0	0	0
35	M	0	0	1	1	1	1	0	0
36	M	0	0	1	1	0	1	0	0
37	M	0	0	0	1	1	1	0	0
38	M	0	0	1	0	1	1	0	0
39	M	0	0	0	1	0	1	0	0
40	M	0	0	1	0	0	1	0	0
41	M	0	0	0	0	1	1	0	0
42	L	1	0	0	0	0	0	1	0
43	G	0	1	0	0	0	1	0	0
44	H	0	0	0	0	1	0	0	1
45	B	1	1	1	0	1	0	1	1

Notes: See *Methods* for variable details. A ''1'' indicates that the variable is included in the model; a ''0'' indicates that the variable is not included in the model. Model categories: A = global model; I = individual variable models; K = models based on Kolar and Lodge (2001); M = models based on Moyle and Light (1996*a*, *b*); B = best opinion model; E = ecological parameter model; L = life history parameter model; G = geographic parameter model; H = human interest parameter model.

the variance inflation factor (Burnham and Anderson 2002).

Given the adequate fit of the global models to the data, comparisons between the 45 selected submodels were performed using AIC_c. The likelihood function was that of a logistic regression model (Binomial-Logit) for the analysis of establishment and that of a multiple regression model (Gaussian) for analyses of the measures of spread and impact. For each analysis we present the maximum log-likelihood estimate, the Akaike weights (relative likelihood of a given model against all hypothesized models; sum to one over all models) and evidence ratios (a ratio of the Akaike weights for the given model vs. the AIC_c-best model) to rank and compare each predictive model and, most importantly, to gauge the relative importance of each variable for predicting establishment, spread, and integration of a species.

All analyses were performed using PC Splus 6.0 (Splus 2002) utilizing built-in routines (LM and GLM) and code written for the Burnham and Anderson (2002) formulae by R. Levine. It is important to note that although we use quantitative methods on categorical predictor variables, this set of analyses is essentially a qualitative assessment of the variables that are important in fish invasion.

TABLE 2. Summary of model selection statistics for evaluating introduced species spread (i.e., number of watersheds) in California.

Model no.	No. variables in model†	Maximum likelihood estimate	AIC_c value	Akaike weights	Evidence ratio
20	3	34.53	−36.68	0.36	1.00
33	2	26.89	−35.45	0.19	1.85
38	3	30.61	−34.74	0.14	2.63
16	3	29.87	−33.27	0.07	5.50
9	1	19.58	−32.80	0.05	6.95
44	2	23.03	−32.74	0.05	7.15
40	2	25.39	−32.47	0.04	8.21

Notes: Only models that carry 10% or more of the Akaike weight of the model with the highest weight are presented. The models are sorted from best to worst according to AIC_c values. Model numbers are described in Table 1.

† The number of variables in the model does not include the intercept, which is itself a variable.

RESULTS

Successful establishment is best predicted by the global model (model 1), which includes all eight variables. This is by far the best model because it contained 99.9% of the Akaike weight. No other models are reasonable competitors with the global model.

Invasive species spread (number of watersheds invaded) is best predicted by a model that includes maximum size, physiological tolerance, and propagule pressure (model 20, based on Kolar and Lodge 2001). The evidence ratios suggest models 33, 38, 16, 9, 44, and 40 are also reasonable competitors with the best model (Table 2). The majority of these models include physiological tolerance, propagule pressure, or both variables.

Invasive species integration (average abundance) is best predicted by model 9, an individual model examining prior invasion success (Table 3). The evidence ratios suggest that model 44 is a reasonable competitor with the best model. Model 44 is the human interest model, examining the combined effect of prior invasion success and propagule pressure.

The relative importance of each of the eight variables in predicting establishment, spread, and integration can be estimated using a weighted sum of the Akaike weights across the 45 models (Table 4). The larger the weight, the more important the variable is toward predicting the response variable of interest across all models (Burnham and Anderson 2002). All variables are equal in their weight for predicting establishment due to the overwhelming support for the inclusive global model (model 1). The most important variables for predicting spread (number of watersheds) are propagule pressure, physiological tolerance, maximum size, and distance traveled. Size of the native range and prior invasion success are relatively less important but may play a role in a predictive model. No support is shown for either trophic status or parental care. The most important variables for predicting integration and impact (average abundance) are prior invasion success and propagule pressure. Relatively less important variables are maximum size, physiological tolerance, size of native range, and distance traveled. No support is shown for either trophic status or parental care.

DISCUSSION

California has the highest number of fish introductions of any state in the United States (Fuller et al. 1999), and presents an unequaled opportunity to examine some of the ecological factors at work over different stages of the invasion process. The results of this study suggest that establishment of alien species is an

TABLE 3. Summary of model selection statistics for evaluating introduced species integration (i.e., average abundance) in California.

Model no.	No. variables in model†	Maximum likelihood estimate	AIC_c value	Akaike weights	Evidence ratio
9	1	20.22	−34.08	0.59	1.00
44	2	22.46	−31.60	0.17	3.50
6	1	20.06	−29.21	0.05	11.50
33	2	23.68	−29.04	0.05	12.50

Notes: Only models that carry 10% or more of the Akaike weight of the model with the heighest weight are presented. The models are sorted from best to worst according to AIC_c values. Model numbers are described in Table 1.

† The number of variables in the model does not include the intercept, which is itself a variable.

TABLE 4. Weight of evidence of support across all models for each variable.

Response variables	Establishment (successful invasion)	Spread (number of watersheds)	Integration (average abundance)
Maximum size	1.00	0.38	0.09
Size of native range	1.00	0.10	0.07
Physiological tolerance	1.00	0.82	0.08
Trophic status	1.00	0.00	0.00
Propagule presssure	1.00	0.83	0.34
Distance traveled	1.00	0.23	0.02
Parental care	1.00	0.00	0.00
Prior invasion success	1.00	0.10	0.76

Notes: The weights are calculated by summing Akaike weights across all the models in which that variable occurs (Burnham and Anderson 2002). The larger the weight, the more important the variable is toward predicting the response of interest.

idiosyncratic process, but that suites of factors may be important for understanding the ability of alien species to spread and integrate into an invaded ecosystem.

Establishment

The best predictor for establishment of fish species in California is our global model that includes all eight variables. This model essentially supports all the hypotheses, because all of the variables are deemed important for establishment of alien fishes. The global model is overwhelmingly supported as the best model, and there are no other models that exhibit similar Akaike weights and evidence ratios. In addition, the weight-of-evidence support across all models (Table 4) suggests that none of the eight variables are better or worse for constructing predictive models for establishment. This is not surprising given that establishment depends on a host of factors, including biotic, abiotic, and anthropogenic forces (D'Antonio et al. 2001).

The difficulty in accurately predicting which species will establish has led to general rules-of-thumb such as the ten's rule (Williamson 1996) and simple empirical generalizations (Ricciardi and Rasmussen 1998). The inherent multivariate nature of our results suggests that development of more specific predictive models based on species characteristics will be very difficult. Recent risk assessment models developed by Kolar and Lodge (2002) for fish invasions in the Great Lakes seem to be applicable mainly to relatively homogeneous habitats and latitudes. Predictive risk assessment models may not be appropriate for more heterogeneous habitats or across the latitudinal gradients represented in California.

The primacy of the global model (equal support for all predictor variables) may lend some tentative weight to the prediction in Moyle and Light (1996*a*, *b*) that given intermediate levels of human disturbance, any species with appropriate physiological characteristics can invade. The plurality of species-level factors implies that establishment success is the result of a suite of factors, possibly including nonbiological factors such as human disturbance. Very few watersheds in California are entirely without moderate levels of human disturbance (Moyle 2002), and it is interesting to note that no watershed in the state is entirely without alien species.

Spread

The spread of invasive species is often mapped and modeled (Williamson 1996), but the characteristics of invaders at this stage are not well studied. A few studies indicate that species with easily dispersed propagules, such as planktonic larvae (Horvath and Lamberti 1997, Leppakoski and Olenin 2000) or mobile spores (Jules et al. 2002), are more likely to spread to other areas. In addition, the number of propagules (propagule pressure) is a factor for invasive plant spread (Lonsdale 1999, D'Antonio et al. 2001), and physiological criteria have been implicated in the spread of the invasive Argentine ant (*Linepithema humile*) (Holway et al. 2002) as well as for fishes in the Florida everglades (Trexler et al. 2000).

In the current analysis, our best model predicting spread (number 20) and the two others with the most support (numbers 33 and 38) are based on variables from Kolar and Lodge (2001) and Moyle and Light (1996*a*, *b*), although neither source explicitly examined questions of spread. All three models contain the variables physiological tolerance and propagule pressure. In addition the weight of evidence across all models (Table 4) suggests that propagule pressure and physiological tolerance are the best variables for predicting spread. Our results may suggest positive association between these two variables, presumably because physiologically tolerant species are more likely to survive the establishment phase in larger numbers.

Most research on the characteristics of invaders uses spatial scales on the order of states or countries, which vary widely in size and often have little connection with natural zoogeographic boundaries. By employing California watersheds as the basic geographic unit of invasion, we utilize natural landscape units that are relatively isolated from one another from a fish's perspective, and that have strong environmental gradients from upstream to downstream (Moyle 2002). The watersheds used in this study are discreet hydrologic units

(Fig. 1) and show little connectivity among them, except through human agency. Movement of fishes between watersheds is mainly the result of factors such as water transfers (i.e., aqueducts, canals, and diversions) and human capriciousness (e.g., differential introductions of four species of centrarchid basses into California reservoirs, release of native minnows after use as bait). As a result, our analysis indicates that species that became widely established are spread by humans (as opposed to natural dispersal from a center of origin) and are well suited to local and regional environmental conditions (physiological tolerance). Thus rainbow trout (*Oncorhynchus mykiss*), naturally widespread in California, have become established in the headwaters of virtually every watershed in California to which they were not native. This fits their worldwide pattern of establishment; despite being subject to thousands of introductions, rainbow trout have only become established where the hydrologic regime fits their life cycle (Fausch et al. 2001).

Integration

Prior invasion success (number of countries in which a species has been successfully introduced) is our best predictor of species integration and impact. The only model with similar predictive power is the human interest model (number 44) that combines prior invasion success with propagule pressure. There have been few systematic studies examining the effect of species traits on the integration and impact of invasive species (D'Antonio et al. 2001), and our study suggests that successful history of invasion is a good predictor.

There are some conceptual problems with using average abundance and distribution as a measure of species integration or impact. Species impact is essentially a subjective phenomenon, usually defined by ecological or evolutionary criteria, such as alteration of food web dynamics or extinctions of resident species (Parker et al. 1999). In the present case, we assume that relative abundance is a reasonable, if crude, measure of impact simply because an abundant invader is more likely to have changed the ecosystem it has invaded than a rare one. One surrogate measure of impact might be the cumulative number of extinctions in watersheds. However, even on a watershed basis, there have been relatively few extinctions of native fishes in California (Moyle 2002), although the declining abundances of many native species suggests that the full impact of alien fishes has not yet occurred.

Management implications

Our results suggest that preventing the transport and release of freshwater fishes into and within California is the best policy to avoid further ecological damage. This includes the spread of species already established in a few watersheds and the spread of native species into watersheds to which they are not native. Unfortunately, most fish introductions today are made illegally or as byproducts of other human activity (Moyle 2002). These methods of introduction highlight the complicated and potentially idiosyncratic nature of many invasions. A suite of forces that act together may produce an outcome that is difficult to predict a priori.

While our study is unique in that we were able to compare successful with unsuccessful invasion attempts in natural (rather than political) geographic units, our results are not definitive in predicting establishment. Most fish that successfully establish in new freshwater environments have a general set of characteristics that facilitate the process, as well as traits that make them desirable to humans. On the other hand, none of our eight traits alone absolutely predicts whether a particular invader is likely to become established. However, our results do suggest a suite of factors important to invasive fishes at the spread and integration stages that can be used in making management decisions across the state and in other locations.

Acknowledgments

We would like to thank J. Hardin for early statistical design and assistance. T. Light provided invaluable assistance during the initial and final stages of this work. We would like to thank S. A. Matern, C. Davidson, and M. Hoopes for providing theoretical input and comments regarding this study and J. Lockwood for a very helpful manuscript review. We also thank K. Fausch and two anonymous reviewers for thoughtful reviews of early versions of this manuscript. M. P. Marchetti would also like to thank K. Grossman and P. Camusi for motivational support throughout this study. The University of California, Water Resources Center, as part of Water Resources Center Project UCAL-WRC-W-880, supported M. P. Marchetti as a postdoctoral researcher during the formative portions of this work.

Literature Cited

Balon, E. K. 1975. Reproductive guilds in fishes: a proposal and definition. Journal of the Fisheries Research Board of Canada **32**(6):821–864.

Balon, E. K. 1984. Patterns in the evolution of reproductive styles in fishes. Pages 35–53 *in* G. W. Potts and R. J. Wootton, editors. Fish reproduction: strategies and tactics. Academic Press, London, UK.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Carlton, J. T. 1996. Pattern, process and prediction in marine invasion ecology. Biological Conservation **78**:97–106.

Daehler, C. T., and D. R. Strong, Jr. 1993. Prediction and biological invasion. Trends in Ecology and Evolution **10**: 380.

D'Antonio, C. M., L. A. Meyerson, and J. Denslow. 2001. Exotic species and conservation. Pages 59–80 *in* M. E. Soule and G. H. Orians, editors. Conservation biology: research priorities for the next decade. Island Press, Washington, D.C., USA.

Dill, W. A., and A. J. Cordone. 1997. History and status of introduced fishes in California, 1871–1996. Fish Bulletin **178**. California Department of Fish and Game, Sacramento, California, USA.

Ehrlich, P. R. 1989. Attributes of invaders and the invading processes: vertebrates. Pages 315–328 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson. Biological invasions: a

global perspective. John Wiley and Sons, New York, New York, USA.

Fausch, K. D., Y. Taniguchi, S. Nakano, G. D. Grossman, and C. R. Townsend. 2001. Flood disturbance regimes influence rainbow trout invasion success among five Holarctic regions. Ecological Applications **11**:1438–1455.

Franklin, A. B., D. R. Anderson, R. J. Gutierrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. Ecological Monographs **70**:539–590.

Fuller, P. L., L. G. Nico, and J. D. Williams. 1999. Nonindigenous fishes introduced into inland waters of the United States. Special Publication **27** American Fisheries Society, Bethesda, Maryland, USA.

Gido, K. B., and J. H. Brown. 1999. Invasion of North American drainages by alien fish species. Freshwater Biology **42**:387–399.

Goldstein, R. M., and T. P. Simon. 1999. Toward a united definition of guild structure for feeding ecology of North American freshwater fishes. Pages 123–202 *in* T. P. Simon, editor. Assessing the sustainability and biological integrity of water resources using fish communities. CRC Press, New York, New York, USA.

Halliwell, D. B., R. W. Langdon, R. A. Daniels, J. P. Kurtenbach, and R. A. Jacobson. 1999. Classification of freshwater fish species of the Northeastern United States for use in the development of indices of biological integrity with regional applications. Pages 301–338 *in* T. P. Simon, editor. Assessing the sustainability and biological integrity of water resources using fish communities. CRC Press, New York, New York, USA.

Holway, D. A., A. V. Suarez, and T. J. Case. 2002. Role of abiotic factors in governing susceptibility to invasion: a test with Argentine ants. Ecology **83**:1610–1619.

Horvath, T. G., and G. A. Lamberti. 1997. Drifting macrophytes as a mechanism for zebra mussel (*Dreissena polymorpha*) invasion of lake-outlet streams. American Midland Naturalist **138**:29–36.

Jules, E. S., M. J. Kauffman, W. D. Ritts, and A. L. Carroll. 2002. Spread of an invasive pathogen over a variable landscape: a nonnative root rot on Port Orford cedar. Ecology **83**:3167–3181.

Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology and Evolution **16**:199–204.

Kolar, C. S., and D. M. Lodge. 2002. Ecological predictions and risk assessment for alien fishes in North America. Science **298**:1233–1236.

Leppakoski, E., and S. Olenin. 2000. Non-native species and rates of spread: lessons from the brackish Baltic Sea. Biological Invasions **2**:151–163.

Lever, C. 1996. Naturalized fishes of the world. Academic Press, London, UK.

Lockwood, J. L. 1999. Using taxonomy to predict success among introduced avifauna: relative importance of transport and establishment. Conservation Biology **13**:560–567.

Lodge, D. M. 1993*a*. Biological invasions: lessons for ecology. Trends in Ecology and Evolution **8**:133–136.

Lodge, D. M. 1993*b*. Species invasions and deletions: community effects and responses to climate and habitat change. Pages 367–387. *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer, Sunderland, Massachusetts, USA.

Lonsdale, W. M. 1999. Concepts and synthesis: global patterns of plant invasions, and the concept of invasibility. Ecology **80**:1522–1536.

McKinney, M. L. 2001. Effects of human population size, area, and time on non-native plant and fish diversity in the United States. Biological Conservation **100**:243–252.

McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology and Evolution **14**: 450–453.

Moyle, P. B. 2002. Inland fishes of California, revised and expanded. University of California Press, Berkeley, California, USA.

Moyle, P. B., and J. J. Cech, Jr. 2000. Fishes: an introduction to ichthyology. Fourth edition. Prentice Hall, Englewood Cliffs, New Jersey, USA.

Moyle, P. B., and T. Light. 1996*a*. Fish invasions in California: do abiotic factors determine success? Ecology **77**: 1666–1670.

Moyle, P. B., and T. Light. 1996*b*. Biological invasions of freshwater: empirical rules and assembly theory. Biological Conservation **78**:149–161.

Parker, I. M., D. Simberloff, M. W. Lonsdale, K. Goodell, M. J. Wonham, P. M. Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers, and L. Goldwasser. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions **1**:3–19.

Rahel, F. J. 2000. Homogenization of fish faunas across the United States. Science **288**:854–856.

Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology **77**:1655–1661.

Ricciardi, A., and J. B. Rasmussen. 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. Canadian Journal of Fisheries and Aquatic Sciences **55**:1759–1765.

Splus. 2002. Splus 6.0. Insigntful Corporation, Seattle, Washington, USA.

Trexler, J. C., W. F. Loftus, F. Jordan, J. J. Lorenz, J. H. Chick, and R. M. Kobza. 2000. Empirical assessment of fish introductions in a subtropical wetland: an evaluation of contrasting views. Biological Invasions **2**:265–277.

Vermeij, G. J. 1996. An agenda for invasion biology. Biological Conservation **78**:3–9.

Williamson, M. H. 1996. Biological invasions. Chapman and Hall, London, UK.

Williamson, M. H., and A. Fitter. 1996. The varying success of invaders. Ecology **77**:1661–1666.

APPENDIX

Tables showing fish species introduced into California watersheds are available in ESA's Electronic Data Archive: *Ecological Archives* A014-007-A1.