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FISH INVASIONS IN CALIFORNIA WATERSHEDS: TESTING HYPOTHESES USING LANDSCAPE PATTERNS

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Abstract. An important goal of invasion biology is to identify physical and environmental characteristics that may make a region particularly receptive to invasions. The inland waters of California (USA) are highly invaded, particularly by fishes, although there is wide variation in numbers of nonnative fishes across the state's watersheds. Here we examine patterns of fish invasions in California watersheds and their associations with natural environmental characteristics, native fish diversity, and various measures of human habitat disturbance. Our analysis is based on an extensive data set on the distribution of freshwater fishes across California's watersheds and on GIS land-use coverages for the entire state. We used canonical correspondence analysis to examine associations between environmental characteristics and the distributions of both native and nonnative fish species. We then employed an information–theoretic model-selection approach to rank hypothesized models derived from the fish invasion literature with regard to how well they predicted numbers of nonnative fishes in California watersheds. Our results indicate that pervasive, anthropogenic, landscape-level changes (particularly the extent of urban development, small-scale water diversions, aqueducts, and agriculture) influenced spatial patterns of invasion. In addition, we find that deliberately stocked fishes have different habitat associations, including a strong association with the presence of dams, than other introduced fishes. In our analysis, watersheds with the most native species also contain the most nonnative species. We find no evidence that existing watershed protection helps to prevent fish invasions in California, but we suggest that restoration of natural hydrologic processes may reduce invasion impacts.

Key words: Akaike information criterion (AIC$_c$); aquatic invasions; aqueducts; California fishes; dams; disturbance; fish stocking; information–theoretic approach; introduced fishes; nonindigenous species; watershed protection.

INTRODUCTION

Biologists have long noted that certain regions and habitats appear to be particularly susceptible to invasions (Elton 1958). Identifying just what makes these regions so invasible is necessary to assist in the management of invasive species as well as in the restoration of native species (Lodge 1993, Vermeij 1996). Much of the literature in this area deals with plants, birds, and insects because of their economic importance and well-documented introduction histories (e.g., Case 1996, Lonsdale 1999, Holway et al. 2002). However, fish invasions have major impacts on freshwater environments (Huston 1994), and invasions are typically cited as the first or second most important threat to the conservation of freshwater diversity (Allan and Flecker 1993, Richter et al. 1997, Kolar and Lodge 2000). Understanding the factors leading to successful invasions of fresh water is important for protecting native species diversity as well as for developing management strategies, risk analyses, and prevention and eradication measures.

Case (1991) suggests that invasions are most likely in places having either low environmental resistance or low biological resistance. Site characteristics hypothesized to favor successful invasion include (1) similar environment to native range of invader, (2) low to moderate environmental variability, (3) high degree of disturbance, especially by human activity, and (4) low native species richness (Elton 1958, Orians 1986, Lodge 1993). In freshwater systems, the number of nonnative species has been linked to hydrologic alteration (the presence of dams, reservoirs, water diversions, and aqueducts) and alteration of the landscape by human activity, especially by urbanization and agriculture, but rarely have these links been examined quantitatively (e.g., Moyle and Light 1996*a*, Gido and Brown 1999, Kolar and Lodge 2000). On theoretical and experimental grounds, ecosystems with high species richness are hypothesized to be much less invasible than those with low species richness (Elton 1958, Til-

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man 1997, Chapin et al. 1998). However, the evidence for such biotic resistance in freshwater systems is mixed, with studies finding both negative and positive correlations between native and nonnative fish species diversity (Gido and Brown 1999, Ross et al. 2001). Similar mixed findings in recent studies of plants have sparked a lively debate on the relationship between diversity of native and nonnative species (Lonsdale 1999, Stohlgren et al. 1999, 2003, Naeem et al. 2000, Kennedy et al. 2002, Rejmanek 2003).

The diversity of invasive species and invaded habitats and the complexity of the invasion process indicate that the success or failure of biotic invasions is highly idiosyncratic. The observation that "any species can invade and any environment can be invaded" (Moyle and Light 1996*b*, Marchetti et al. 2004) suggests that a search for generalities useful in making predictions may be challenging. Kolar and Lodge (2001) and D'Antonio et al. (2001) argue that more quantitative approaches (including meta-analysis of diverse sources of information) are likely to result in useful predictions. Part of the prediction difficulty may lie in the scale at which analyses of invasions have been performed. In order to generate numbers large enough to be analyzed using multivariate statistics, invasion patterns are generally studied either at continental/global scales (e.g., Gido and Brown 1999, Lockwood 1999, Rahel 2000) or at small regional areas which are studied intensively (Ross et al. 2001). These two scales of analysis may be inappropriate to effectively answer questions regarding landscape patterns.

Here we examine landscape-level patterns of freshwater fish invasions in California and their associations with measures of watershed disturbance, environmental characteristics, and native fish diversity. The detailed distributional information on California fishes in Moyle (2002) allows us to consider invasion patterns at what we feel is an appropriate scale of resolution, the individual watersheds of California. California is large enough (over 411 000 km^2) and long enough (spanning 10° of latitude) to encompass a diversity of environments, from arid desert to coastal temperate rainforest, which contain a wide variety of aquatic habitats (Moyle and Ellison 1991). The state is geographically complex, containing distinct zoogeographic regions and numerous watersheds that are isolated from one another so that each can be treated as an independent invasion site. California also has a history of rapid development of its water resources (its modern history essentially begins with the Gold Rush of 1849), resulting in highly disturbed aquatic environments statewide, as well as a history of frequent introductions. At the watershed scale, we therefore sample enough variance in both natural and anthropogenic watershed features to detect patterns structuring fish assemblages. This analysis should also help to answer questions about watersheds as the most appropriate unit for aquatic conservation in California as suggested by Moyle and Yoshiyama (1994).

Many of the nonnative fishes now common in California were introduced deliberately by fisheries managers during the late 19th and early to mid-20th centuries. Because many of these introductions were made into altered habitats, particularly reservoirs, the past behavior of fisheries managers may significantly influence the present distribution of nonnative fishes in California in a way that is not independent of the distribution of certain types of disturbed habitat. Fishes which are deliberately stocked are often matched to their receiving environments, introduced in much larger numbers than other introduced fishes and introduced repeatedly over time; all of which may contribute to their initial success and subsequent spread (Marchetti et al. 2004). Kolar and Lodge (2000) suggest that intentional stocking efforts will have a strong association with nonnative fish diversity. We examine this possibly confounding factor in a portion of our analysis by separately considering fishes that were initially introduced due to deliberate, officially sanctioned stocking for sport, food, or related purposes vs. those that arrived via other means, such as incidental transfer with stocked fishes, bait releases, biocontrol releases, conservation transfers, illegal stocking by individuals, ballast water transfers, aquaculture escapes, and aquarium releases.

This paper specifically addresses the following questions: (1) Do native and nonnative species show different patterns of association with watershed properties? (2) How are watershed properties, specifically measures of hydrologic disturbance, land-use disturbance, natural environmental characteristics, and native fish diversity related to the number of nonnative species present in the watershed? (3) Do deliberately stocked fishes differ from other nonnative fishes in their associations with these watershed properties? (4) Is there evidence that habitat protection can reduce the degree of invasion in watersheds? Our predictions are, first, that native and nonnative fishes will show distinct patterns of association with measures of natural habitat quality and anthropogenic disturbance, with nonnative species being more closely associated with measures of disturbance than native species; and second, that nonnative species diversity will be greatest in watersheds that have been heavily altered by hydrologic and land-use disturbance. Based on the predictions of Moyle and Light (1996*a*, *b*), we further expect to see no evidence of biotic resistance, i.e., no relationship between native and nonnative species diversity. We expect different watershed associations, particularly a greater degree of association with dams and reservoirs, for intentionally stocked fishes than for other nonnative fishes. Finally, because land protection has historically paid little attention to aquatic environments and watershed boundaries, we expect no reduction in nonna-

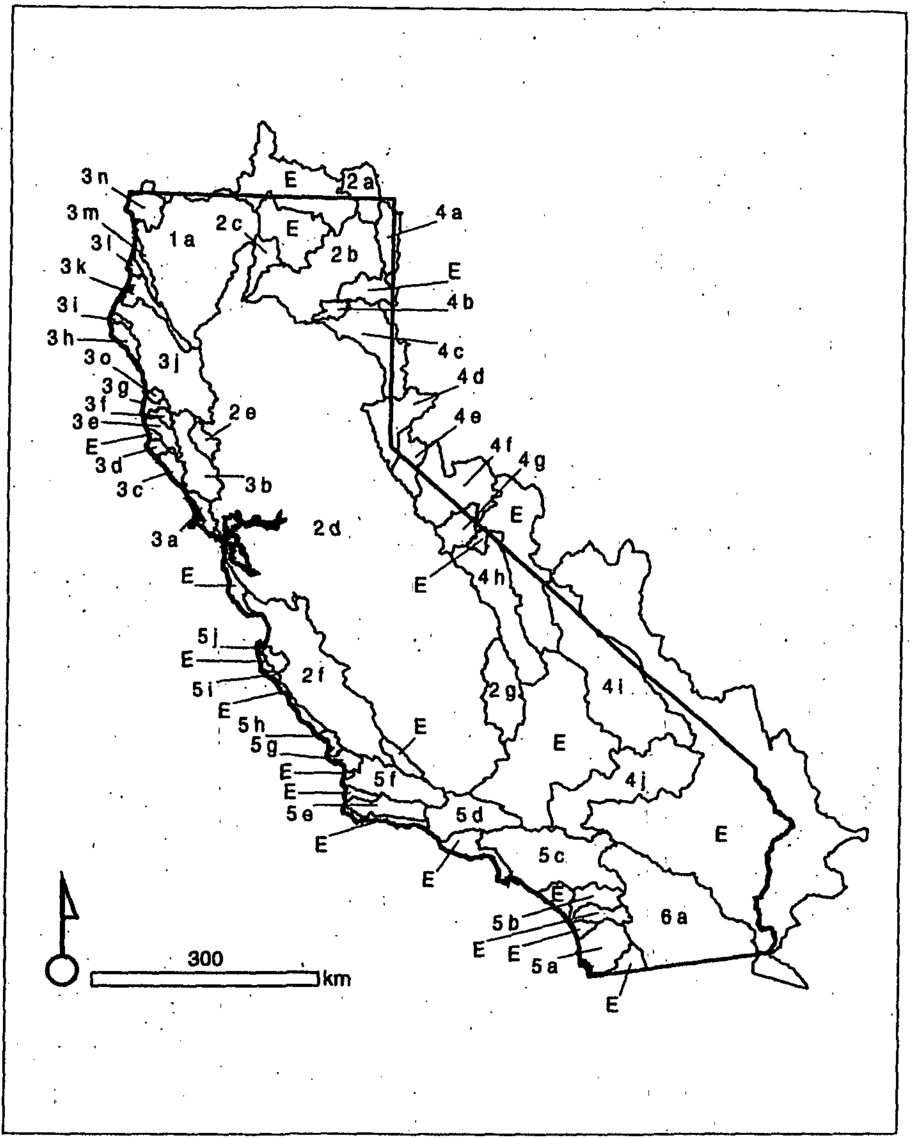

FIG. 1. Watersheds of California. See Table 1 for watershed codes. Watersheds marked "E" were excluded from the analysis (see *Methods* for details).

tive species richness in watersheds with a high proportion of protected land.

METHODS

Fish abundance data

We gathered presence/absence data on every freshwater fish species inhabiting California watersheds (N = 44, Fig. 1) as of January 2000 (Moyle 2002). From these data two measures of fish species abundance were tallied for each watershed: historic (pre-1850) species richness (which includes present native species plus extinct native species), and number of established nonnative species (both from outside California and intrastate introductions; Table 1). A full accounting of the species presence/absence by watershed data can be found in Moyle (2002). Some watersheds within the state were excluded from the analysis either because there are no fish in the watershed, or because the watershed extended significantly outside the state boundaries (Fig. 1).

Measurement of watershed-scale habitat data

A geographic information system and digital map data were used to measure eleven habitat attributes for the 44 watersheds included in the analysis (Table 2). We examined variables related to hydrologic alteration (dams, reservoir area, ditch density, and aqueduct density), land use (proportion developed, proportion ag-

TABLE 1. Diversity of native and nonnative fish species in California watersheds.

Watershed	Watershed code	Original native fish diversity	Nonnative fish diversity	Proportion of nonnative species from stocking
Lower Klamath River	1a	20	14	0.80
Goose Lake	2a	8	11	1.00
Pit River	2b	13	15	0.87
McCloud River	2c	7	4	1.00
Sacramento/San Joaquin River	2d	29	41	0.67
Clear Lake	2e	14	18	0.78
Monterey	2f	19	20	0.80
Kern River	2g	4	7	0.91
Tomales	3a	11	7	0.57
Russian River	3b	21	19	0.71
Gualala River	3c	8	0	
Garcia River	3d	8	0	
Navarro River	3e	9	0	
Big River	3f	8	0	
Noyo River	3g	5	0	
Matolle River	3h	8	0	
Bear River	3i	9	0	
Eel River	3j	14	10	0.50
Mad River	3k	14	8	0.88
Little	3l	9	0	
Redwood	3m	12	6	0.67
Smith River	3n	12	0	
Ten Mile Creek	3o	7	0	
Surprise Valley	4a	3	2	1.00
Eagle Lake	4b	5	2	1.00
Susan River	4c	8	7	1.00
Truckee River	4d	8	15	0.88
Carson River	4e	8	14	0.86
Walker River	4f	8	13	0.92
Mono Lake	4g	0	6	0.50
Owens River	4h	4	14	0.93
Amargosa River	4i	3	2	0.50
Mojave River	4j	1	23	0.61
San Diego	5a	7	26	0.69
Santa Margarita	5c	9	12	0.83
Los Angeles	5d	12	34	0.62
Santa Clara	5e	7	24	0.48
Santa Inez	5f	6	16	0.75
Santa Maria	5g	7	8	0.63
San Luis Obispo	5h	7	8	0.63
Morro	5i	8	10	0.50
Big Sur	5j	6	0	
Carmel River	5k	5	12	0.75
Salton Sea	6a	1	24	0.65

riculture, and proportion with high protection status), and natural environmental characteristics (mean elevation, mean rainfall, and watershed area). Several other variables examined early in the study were excluded due to their high correlations ($r > 0.7$) with retained variables. For example, we excluded road density (highly correlated with proportion developed), mean latitude (highly correlated with mean rainfall), and elevational range (highly correlated with watershed area). In each case, we retained the variable that seemed more inclusive (watershed area, development) or more likely to be directly related to fish diversity in California (rainfall). Variables were scaled to watershed area where appropriate and transformed for (approximate) normality as indicated in Table 2.

Canonical correspondence analysis

To investigate the association between species presence/absence and watershed-scale habitat data, we used direct gradient analysis (canonical correspondence analysis, CCA) employing the CANOCO 4.02 program developed by ter Braak and Smilauer (1999). CCA aids in the recognition and description of patterns in multivariate data. In particular, it describes how a suite of species simultaneously responds to environmental or habitat factors at multiple sites by correlating environmental variables with sample scores (ter Braak and Verdonschot 1995). In CCA biplots, each vector for an environmental variable defines a synthetic axis, and species scores are projected onto that axis (Jongman et al. 1995). In the CCA biplot, each environmental

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TABLE 2. Name,

Variable
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res area
ditch
aqued
develop
agri
protect
elev
rain
streams
ws area
diversity

Notes: Full n
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TABLE 2. Name, description, and transformations of variables used in the models.

Variable	Description	Transformation
dams	Number of dams per 1000 km²; includes dams >7.6 m in height or with storage capacity of ≥61 681 m³	square root (x + .1)
res area	Total surface area of reservoirs per watershed area (100 m²/km²)	arcsine square-root (x)
ditch	Total length of ditches and unlined canals per watershed area (m/km²)	log(x + 1)
aqued	Total length of aqueducts per watershed area (m/km²)	log(x + 1)
develop	Proportion of watershed developed: commercial, industrial, urban, suburban, transportation, mines, and quarries	arcsine square-root (x)
agri	Proportion of watershed in agriculture: cropland, pasture, feeding lots, orchards, groves, vineyards, and nurseries	arcsine square-root (x)
protect	Proportion of watershed with high protection status: U.S. Forest Service Wilderness Areas or Research Natural Areas; National Park Service National Parks, Preserves, Monuments, Seashores, and Wilderness Areas; Bureau of Land Management Wilderness Areas; State Park Wilderness Areas and Reserves; State Fish and Game Ecological Reserves; University of California Natural Reserves; Nature Conservancy preserves; and Audubon Sanctuaries	arcsine square-root (x)
elev	Mean elevation of watershed (m)	log(x)
rain	Mean annual rainfall (mm), averaged spatially and temporally (1961–1990)	log(x)
streams	Total length of natural streams per watershed area (m/km²)	none
ws area	Total area of watershed, including portions of watershed outside California (km²)	log(x)
diversity	Original number of fishes in watershed, including present native fishes plus extinct native fishes	none

Notes: Full normality could not be achieved for the following variables: dams, reservoir area, ditch density, aqueduct density, developed, agriculture, protected, and elevation (Shapiro-Wilk W test, $P < 0.05$ in all cases).

variable therefore has a direction and length; the direction indicates positive values for that variable, while the length of the vector is an indication of its relative importance. The species scores in the biplot indicate each species' relative association with the environmental variables (Jongman et al. 1995). If a species is near a vector, that species is generally associated with the particular environmental variable. Our use of CCA follows recommendations in ter Braak (1986), Palmer (1993), and ter Braak and Verdonschot (1995).

Eleven variables (Table 2, excluding diversity) were initially included in the ordination. We tested these variables for significance by forward selection utilizing the Monte Carlo test ($\alpha = 0.1$, with 99 random permutations) provided by CANOCO. For species data (see Appendix) we used presence/absence information across the 44 watersheds. Following a stepwise procedure, we retained only those environmental variables chosen by forward selection as contributing significant variation to the ordination. We used species ordination biplots to visually assess how native and nonnative species respond to the environmental variables.

Invasions of watersheds: model building

We used the information-theoretic model selection approach of Burnham and Anderson (2002) to evaluate a set of a priori hypotheses regarding the effects of watershed characteristics on the degree of invasion of California watersheds. Our hypotheses were drawn from published sources and our own knowledge of the system; each was expressed as a linear regression model including various combinations of the predictor variables (Table 3). A priori model development is advocated by Burnham and Anderson (2002) among others (e.g., Franklin et al. 2000) to avoid the data dredging approach common with multiple regression analyses. While this approach does not necessarily lead to the "best" model in an absolute sense, it allows explicit comparisons among multiple models and for robust estimation of model parameters using model averaging (Burnham and Anderson 2002).

Models for the degree of invasion of watersheds (number of nonnative fishes in each watershed) were intended to test the relative importance of natural environmental variables and human disturbance variables including hydrologic alteration and land-use disturbance. We explicitly test the importance of native diversity by including or excluding it from models in most categories. Most models include the covariate watershed area as an "a priori obvious" variable: that is, we expected watershed area (which varies from tiny coastal drainages to the enormous Sacramento–San Joaquin drainage) to be strongly associated with the number of nonnative species. We include a global model (required by this statistical approach; model 1) and 12 single-variable models to assess the individual effects of each explanatory variable (models 2–13; Table 3). The remaining models are based on the following hypotheses: (1) Degree of invasion of watersheds is related to natural watershed characteristics (models 14, 15); (2) Degree of invasion is related to general disturbance, and may or may not be affected by protected status (models 16–18); (3) Degree of invasion is related to hydrologic alteration (models 19, 20); (4) Degree of invasion is related to watershed disturbance (land use), again testing the importance of protected status (models

TABLE 3. Variables included in each model describing the number of fish species introduced to California watershed

Model	Model category	Water development: dams	res area	ditch	aqued	Land use: develop	agri	protect	Natural environment: rain	elev	streams	ws area	div
1	G	1	1	1	1	1	1	1	1	1	1	1	1
2	S	1	0	0	0	0	0	0	0	0	0	0	0
3	S	0	1	0	0	0	0	0	0	0	0	0	0
4	S	0	0	1	0	0	0	0	0	0	0	0	0
5	S	0	0	0	1	0	0	0	0	0	0	0	0
6	S	0	0	0	0	1	0	0	0	0	0	0	0
7	S	0	0	0	0	0	1	0	0	0	0	0	0
8	S	0	0	0	0	0	0	1	0	0	0	0	0
9	S	0	0	0	0	0	0	0	1	0	0	0	0
10	S	0	0	0	0	0	0	0	0	1	0	0	0
11	S	0	0	0	0	0	0	0	0	0	1	0	0
12	S	0	0	0	0	0	0	0	0	0	0	1	0
13	S	0	0	0	0	0	0	0	0	0	0	0	1
14	N	0	0	0	0	0	0	0	1	1	1	1	1
15	N	0	0	0	0	0	0	0	1	1	1	1	0
16	D	1	1	1	1	1	1	1	0	0	0	1	0
17	D	1	1	1	1	1	1	0	0	0	0	1	0
18	D	1	1	1	1	1	1	0	0	0	0	1	1
19	W	1	1	1	1	0	0	0	0	0	0	1	0
20	W	1	1	1	1	0	0	0	0	0	0	1	1
21	L	0	0	0	0	1	1	1	0	0	0	1	0
22	L	0	0	0	0	1	1	0	0	0	0	1	0
23	L	0	0	0	0	1	1	0	0	0	0	1	1
24	ML	1	0	0	1	1	1	0	1	0	0	1	0
25	ML	1	0	0	1	1	1	0	1	0	0	1	1
26	GB	1	0	0	0	0	0	0	0	0	0	1	1
27	GB	0	1	0	0	0	0	0	1	0	0	0	1
28	KL	1	0	0	1	1	1	0	0	0	0	0	0
29	KL	1	0	0	1	1	1	0	0	0	0	0	1
30	KL	1	0	0	1	1	1	0	0	0	0	1	0
31	KL	1	0	0	1	1	1	0	0	0	0	1	1
17a	*D*	*0*	*0*	*1*	*0*	*1*	*0*	*0*	*0*	*0*	*0*	*1*	*0*
18a	*D*	*0*	*0*	*1*	*1*	*1*	*0*	*0*	*0*	*0*	*0*	*1*	*1*
18b	*D*	*0*	*0*	*1*	*1*	*1*	*0*	*0*	*1*	*1*	*0*	*0*	*1*
25a	*ML*	*1*	*0*	*0*	*1*	*1*	*0*	*0*	*1*	*0*	*0*	*1*	*1*
31a	*KL*	*1*	*0*	*0*	*1*	*1*	*0*	*0*	*0*	*0*	*0*	*1*	*1*
20a	*W*	*1*	*0*	*1*	*1*	*0*	*0*	*0*	*0*	*0*	*0*	*1*	*1*

Notes: The number 1 indicates that the variable is included in the model; 0 indicates that it is not included. Data in italic type at end of table are post hoc and should be considered tentative. Model categories: G, global model; S, single variable models; N, natural watershed characteristics models; D, general disturbance models; W, hydrologic disturbance models; L, watershed disturbance models; ML, Moyle and Light (1996*a*, *b*) models; GB, Gido and Brown (1999) models; KL, Kolar and Lodge (2000) models. Descriptions of variables are given in Table 2.

21–23); (5) Degree of invasion is positively associated with both hydrologic alteration and watershed disturbance (specifically dams, aqueducts, development, and agriculture) and low environmental severity (high rainfall in California; Moyle and Light 1996*a*, *b*; models 24, 25); (6) Degree of invasion is positively associated with dams and watershed area and negatively with native diversity (Gido and Brown 1999; model 26); (7) Degree of invasion is positively associated with reservoir area and native diversity, and negatively with rainfall (Gido and Brown 1999; model 27); and (8) Degree of invasion is positively associated with dams, waterworks (aqueducts), urbanization (development) and agriculture (Kolar and Lodge 2000; models 28–31). Because of the large number of potential interactions in the data set and the lack of explicit predictions in the literature regarding interactions among the factors we examined, we did not consider interactions among predictor variables in any models.

Model fitting and evaluation

The information–theoretic approach to model selection involves ranking the models using Akaike's Information Criterion (AIC) in order to gauge the relative support (given the data) for each model (Burnham and Anderson 2002). We first evaluated diagnostics from a multiple linear regression fit of the global model (model 1). These indicated a reasonable fit to the data with no deviations from the underlying regression assumptions and showed no evidence of over dispersion as measured by the variance inflation factor (Burnham and Anderson 2002). We then ranked the models using a small-sample variant of Akaike's Information Criterion (AIC_c), which accounts for the bias introduced into the analysis by our relatively small sample size ($N = 44$) and large number of independent variables (12). From AIC_c, we calculated the difference between each AIC_c value and the "best" model AIC_c value (ΔAIC_c) and the Akaike weight (w_i) for each model. The Akaike weight is the relative likelihood of each model, given the data (calculated as the ratio of each model's likelihood to the sum of all the model likelihoods). (See Burnham and Anderson [2002] and Franklin et al. [2000] for derivations and formulas.)

We inspected the model ranking to determine whether more than one model had reasonable support. We considered models as having substantial support where ΔAIC_c was ≤ 2 and some support where ΔAIC_c was between 2 and 7 (Burnham and Anderson 2002). We determined the regression coefficients and their 95% confidence limits (based on standardized data) and model-averaged regression coefficients for this reduced set of models to evaluate the relative support for each parameter in the models (Burnham and Anderson 2002). We computed variances and confidence intervals for the model-averaged regression coefficients using the methods suggested by Burnham and Anderson (2002). Using the full set of a priori models, we calculated cumulative Akaike weights, a measure of variable importance (Burnham and Anderson 2002), for each variable by summing the Akaike weights for each model containing that variable. We then ranked the variables as strongly supported, somewhat supported, and not supported by our models based on the model-averaged regression parameters, significance of variables in the top models (AIC $\leq$ 2), and cumulative Akaike weights. Specifically, we termed a variable strongly supported if its model-averaged confidence intervals did not include zero and its cumulative Akaike weight was >0.75, as somewhat supported if its confidence interval in at least one of the top models (AIC $\leq$ 2) did not include zero, regardless of cumulative Akaike weight, and not supported if none of these criteria was met.

We also explicitly compared the relative support for different subsets of models based on their positions in the rankings. In particular, we were interested in the relative influence of hydrologic alteration, land-use disturbance, and natural watershed characteristics on the number of nonnative fishes in each watershed. We made comparisons on the basis of rankings of both multivariate and single-variable models. In addition, we compare the relative rankings of the subsets of variables associated with hydrologic disturbance and land-use disturbance using cumulative Akaike weights.

On a post hoc basis, we examined each of the top models to determine whether fit could be improved or additional insights gained by minor modifications. For each model we explored (1) dropping variables which did not add to the fit of the model, based on AIC_c values; (2) replacing the variable dams with the moderately correlated ($r = 0.62$) variable reservoir area; and (3) deleting the "a priori obvious" variable watershed area to see if this allowed other effects to enter the models. We retained all post hoc models that were within seven ΔAIC_c units of the (new) top model, and recalculated the model-averaged regression parameters, variances, and confidence intervals. Using the full set of models (including a priori models), we then recalculated the cumulative Akaike weights for each variable. Conclusions from these post hoc analyses should be considered tentative.

Stocked vs. non-stocked nonnative fishes

We examined the lists of introduced fishes in California watersheds and determined the number and proportion of fishes in each watershed which originally reached the state, or were transferred within the state, due to officially sanctioned stocking efforts. We explicitly exclude from this total fishes released for biological control and conservation transfers because we did not expect their distribution patterns to be similar to those of fishes released for sport, food, or forage. Because accurate records on the locations of individual stocking events are either lacking or difficult to obtain, we did not attempt to determine whether a given fish had been deliberately stocked into individual watersheds. Our figures may therefore overestimate the numbers of stocked fish per watershed by including some natural or angler-aided dispersal events. In order to examine the possibility of different associations of stocked and otherwise-introduced fishes with watershed properties, we then repeated the above information–theoretic analyses separately with the two subsets of fishes (intentionally stocked and otherwise-introduced species), using the same models as before (Table 3). We present here only summary data on the relative rankings of top models for each subset, as well as the relative rankings of individual variables based on their cumulative Akaike weights.

RESULTS

Canonical correspondence analysis

Nine environmental variables contributed to the ordination: mean elevation, watershed area, reservoir area, ditch density, aqueduct density, proportion developed, proportion agriculture, stream density, and mean annual rainfall. The first two canonical axes explain 48.1% of the variation in species distribution (26.8 and 21.3%, respectively). The first canonical axis represents gradients in natural environmental habitat attributes (rainfall, watershed area, and stream density) while the second canonical axis represents gradients in anthropogenic habitat attributes (aqueduct density, proportion developed, proportion in agriculture; Fig. 2).

The ordination results for the individual species scores suggest that the fishes of the state respond to the environmental variation among watersheds; the majority of native species show affinity to the natural environmental variation along CCA axis 1 (higher rainfall, changes in elevation, smaller watershed area, and changes in stream density) while the majority of nonnative species show affinity to the anthropogenic hab-

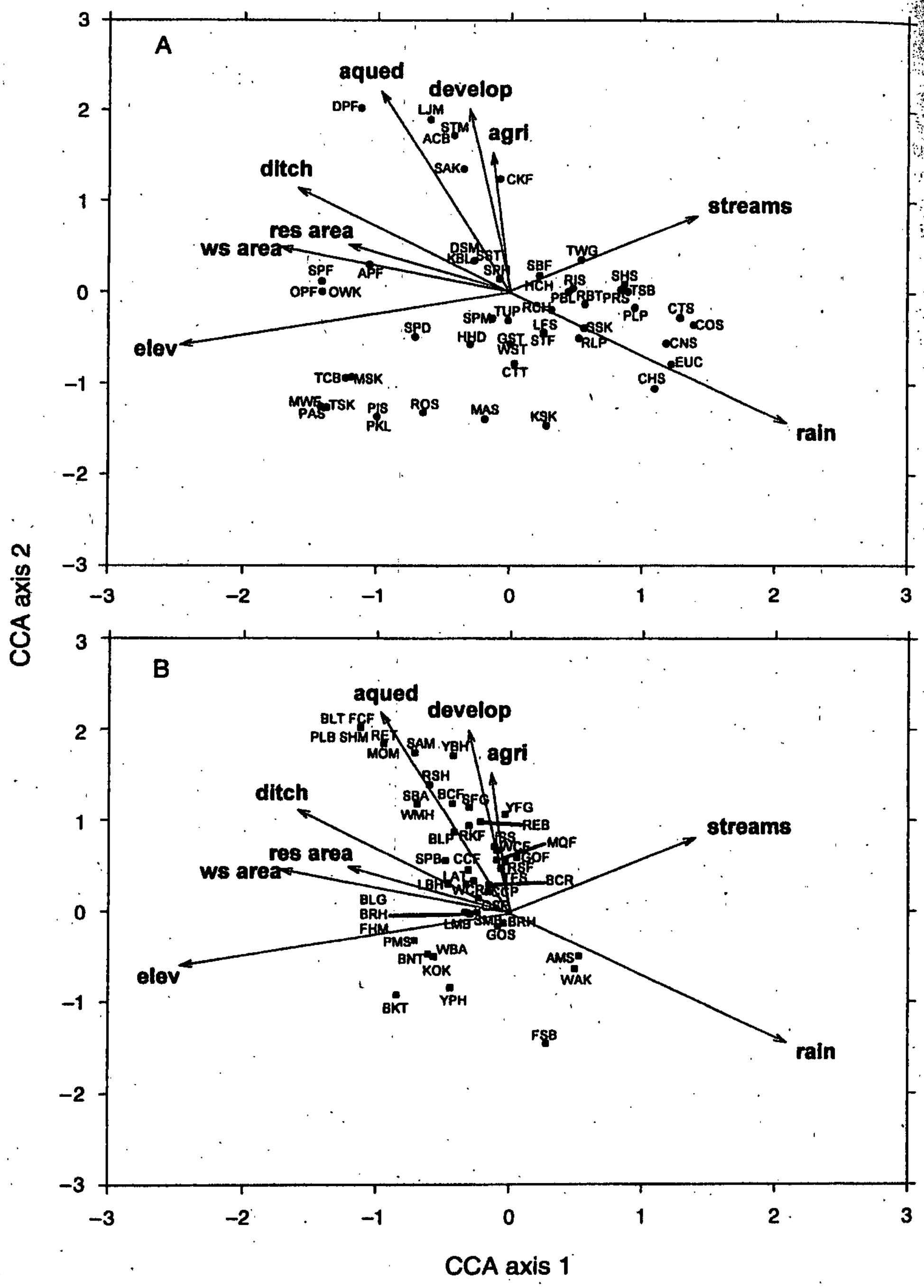

FIG. 2. Bi-plots of the species scores on the first two canonical axes from canonical correspondence analysis (CCA) indicating the influence of environmental variables on individual fish species. The bi-plots have been separated into (A) native species and (B) nonnative species for ease of interpretation. The arrows represent the correlation of the physical variables with the two canonical axes and can be interpreted as such. Points represent each individual species' relative association with the environmental variables. Common and scientific names for the three-letter species codes can be found in the Appendix. Eigenvalues (lambda) are 0.447 and 0.356 for the first two canonical axes, respectively. See Table 2 for environmental variable information.

TABLE 4. Summar
watershed.

Model	Model categor
17a	D
18a	D
18b	D
25a	ML
31a	KL
30	KL
31	KL
17	D
25	ML
18	D
22	L
20a	W
24	MI
23	L
21	L
16	D
20	W
19	W
1	C
26	G
27	G
29	K
4	:
28	K
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TABLE 4. Summary of model selection statistics for the set of candidate models for number of species introduced per watershed.

Model	Model category	Adjusted R^2	K	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	w_i	Post hoc $\Delta\mathrm{AIC_c}$	Post hoc w_i
17a	*D*	*0.798*	*5*	136.081	···	···	*0.000*	*0.313*
18a	*D*	*0.812*	*7*	136.086	···	···	*0.004*	*0.314*
18b	*D*	*0.813*	*8*	137.761	···	···	*1.680*	*0.135*
25a	*ML*	*0.807*	*8*	139.103	···	···	*3.022*	*0.069*
31a	*KL*	*0.795*	*7*	140.028	···	···	*3.946*	*0.043*
30	KL	0.790	7	140.994	0.000	0.2274	*4.912*	*0.027*
31	KL	0.795	8	141.764	0.770	0.1547	*5.683*	*0.019*
17	D	0.803	9	142.040	1.046	0.1348	*5.959*	*0.016*
25	ML	0.802	9	142.267	1.273	0.1203	*6.186*	*0.014*
18	D	0.810	10	142.537	1.543	0.1051	*6.456*	*0.012*
22	L	0.765	5	142.762	1.768	0.0940	*6.680*	*0.011*
20a	*W*	*0.781*	*7*	142.846	···	···	*6.765*	*0.011*
24	ML	0.785	8	143.900	2.906	0.0532	*7.819*	*0.006*
23	L	0.761	6	145.019	4.026	0.0304	*8.938*	*0.004*
21	L	0.759	6	145.377	4.383	0.0254	*9.296*	*0.003*
16	D	0.797	10	145.397	4.403	0.0252	*9.316*	*0.003*
20	W	0.777	8	145.447	4.454	0.0245	*9.366*	*0.003*
19	W	0.750	7	148.722	7.728	0.0048	*12.641*	*0.001*
1	G	0.801	14	155.166	14.172	0.0002	*19.084*	*<0.0001*
26	GB	0.656	5	159.472	18.478	<0.0001	*23.390*	*<0.0001*
27	GB	0.630	5	162.644	21.650	<0.0001	*26.563*	*<0.0001*
29	KL	0.632	7	165.708	24.714	<0.0001	*29.626*	*<0.0001*
4	S	0.566	3	166.842	25.848	<0.0001	*30.761*	*<0.0001*
28	KL	0.575	6	170.337	29.343	<0.0001	*34.256*	*<0.0001*
14	N	0.589	7	170.554	29.560	<0.0001	*34.473*	*<0.0001*
12	S	0.512	3	172.030	31.036	<0.0001	*35.949*	*<0.0001*
15	N	0.544	6	177.709	36.716	<0.0001	*41.628*	*<0.0001*
3	S	0.437	3	178.319	37.325	<0.0001	*42.237*	*<0.0001*
6	S	0.346	3	184.916	43.922	<0.0001	*48.835*	*<0.0001*
5	S	0.332	3	185.858	44.864	<0.0001	*49.776*	*<0.0001*
7	S	0.329	3	186.058	45.064	<0.0001	*49.976*	*<0.0001*
2	S	0.241	3	191.463	50.470	<0.0001	*55.382*	*<0.0001*
13	S	0.170	3	195.374	54.380	<0.0001	*59.293*	*<0.0001*
10	S	0.148	3	196.516	55.522	<0.0001	*60.434*	*<0.0001*
9	S	0.127	3	197.596	56.602	<0.0001	*61.514*	*<0.0001*
11	S	−0.023	3	204.582	63.588	<0.0001	*68.500*	*<0.0001*
8	S	−0.024	3	204.618	63.624	<0.0001	*68.536*	*<0.0001*

Notes: The table gives adjusted R^2 for comparison with the less familiar $\mathrm{AIC_c}$ and its derived values. See Table 3 for complete model and model category descriptions. Post hoc models, and the $\Delta\mathrm{AIC_c}$ and w_i values for all models in the post hoc analyses (because the addition of new models changes these values), are shown in italics. K is the number of parameters in each model (number of variables included plus 2). $\Delta\mathrm{AIC_c}$ is the difference between the $\mathrm{AIC_c}$ value for each model and that of the "best" model. The Akaike weight (w_i) is the relative likelihood that each model is the best of the tested models, given the data. The $\Delta\mathrm{AIC_c}$ post hoc and w_i post hoc columns are the revised model selection statistics based on the addition of the six post hoc models. Note that the addition of new models changes the $\Delta\mathrm{AIC_c}$ post hoc and w_i post hoc values.

that variation along CCA axis 2 (more aqueducts, increased development, increased agriculture and more ditches; Fig. 2).

Degree of invasion of watersheds

The best single model describing the number of nonnative species in a watershed was the model drawn from Kolar and Lodge (2000) (model 30), which included dams, aqueducts, development, and agriculture, modified by the addition of watershed area. However, five other models had strong support ($\Delta\mathrm{AIC_c} < 2$, Table 4): the above model with the addition of native diversity (model 31); the general disturbance model (model 17), which included all measures of hydrologic and watershed disturbance as well as watershed area; the Moyle and Light (1996*a*, *b*) model variant which included native diversity (model 25); the general disturbance model including diversity (model 18); and the land-use disturbance model (model 22). An additional five models had moderate support ($2 < \Delta\mathrm{AIC_c} < 7$; Table 4).

Individual model and model-averaged regression coefficients for dams, ditch density, aqueduct density, development, agriculture, native diversity, and watershed area were consistently positive (Table 5), consistent with the positive associations of each of these variables with nonnative fish numbers in the univariate models. However, strong support exists in the selected multivariate models only for the effects of development and watershed area. Each of these variables had model-averaged regression coefficients whose 95% confidence intervals did not include zero as well as cumulative Akaike weights close to 1, indicating that they significantly added to the fit of virtually all the high-ranked

TABLE 5. Standardized regression coefficients (95% confidence limits) for the top-ranked models for number of nonnative fishes per watershed by variable.

Model, category	dams	res area	ditch	aqueducts	developed	agriculture
30 KL	0.174 (0.000, 0.348)			0.171 (−0.009, 0.350)	0.262† (0.063, 0.461)	0.158 (−0.013, 0.32
31 KL	0.170 (−0.002, 0.343)			0.222† (0.029, 0.414)	0.246† (0.048, 0.445)	0.098 (−0.093, 0.28
17 D	0.156 (−0.051, 0.363)	−0.069 (−0.305, 0.168)	0.224† (0.003, 0.445)	0.144 (−0.047, 0.335)	0.278† (0.084, 0.472)	0.105 (−0.073, 0.28
25 ML	0.147 (−0.025, 0.320)			0.241† (0.050, 0.433)	0.236† (0.041, 0.432)	0.108 (−0.207, 0.2
18 D	0.153 (−0.051, 0.357)	−0.073 (−0.306, 0.160)	0.231† (0.013, 0.448)	0.198 (−0.002, 0.399)	0.261† (0.069, 0.453)	0.039 (−0.155, 0.2
22 L					0.422† (0.257, 0.587)	0.187† (0.011, 0.36
24 ML	0.176 (−0.001, 0.353)			0.177 (−0.010, 0.365)	0.261† (0.059, 0.463)	0.157 (−0.016, 0.3
23 L					0.425† (0.259, 0.592)	0.159 (−0.041, 0.
21 L					0.420† (0.252, 0.587)	0.183† (0.002, 0.36
16 D	0.154 (−0.061, 0.368)	−0.068 (−0.309, 0.173)	0.225† (0.000, 0.449)	0.145 (−0.049, 0.339)	0.277† (0.080, 0.474)	0.104 (−0.078, 0.
20 W	0.268† (0.066, 0.470)	−0.072 (−0.322, 0.178)	0.235† (0.012, 0.458)	0.340† (0.152, 0.529)		
Mean	0.141 (−0.070, 0.353)	−0.021 (−0.191, 0.150)	0.066 (−0.325, 0.458)	0.165 (−0.069, 0.398)	0.276† (0.044, 0.509)	0.121 (−0.084, 0
Cum. w_i	0.850	0.295	0.295	0.850	0.971	0.971

Notes: The model-averaged regression coefficients and confidence intervals were calculated as suggested in Burnham and Anderson (2002). Cumulative Akaike weights ("Cum. w_i"), a measure of variable importance (Burnham and Anderson 2002), were calculated by summing the Akaike weights for all models containing that variable. Elevation and stream density did not appear in any of the top-ranked models. Explanations of variables are given in Table 2. Model numbers and categories are defined in Table 3.

† The 95% confidence limits for these data do not include zero.

models. The effects of ditch density, aqueduct density, agriculture, and native diversity have moderate support based on these models, and other predictors have little or no support (Table 5).

The post hoc analyses identified six models with stronger support than the related models from the initial analysis (Tables 3 and 4). Three were variants of the general disturbance models (17a, 18a, 18b), one was a variant of the Moyle and Light (with native diversity; model 25a), one was a variant of the Kolar and Lodge (with diversity; model 31a), and the last was a variant of the hydrologic disturbance (with diversity; model 20a). Watershed size and development again had strong support based on their model-averaged regression parameters and high cumulative Akaike weights, and the variables ditch density, aqueduct density, native diversity, and rainfall had moderate support (Table 6).

Models examining land-use disturbance (models 16, 17) were ranked higher than models examining hydrologic alteration (models 19, 20), however, the general disturbance models (models 21–23) were ranked higher still, suggesting that both land use and water development contribute to the number of nonnative fishes in watersheds (Table 5). The five highest ranked models included effects from both categories. The global model and natural environment models, in contrast, were ranked close to the bottom of the list of multivariate models suggesting little association of the number of nonnative species with the natural environmental variables we measured (other than watershed area, which appeared in all of the strongest models). The cumulative Akaike weight for the two-variable combination development and agriculture (land-use disturbance) was 0.97, while dams and aqueduct density (which appeared together in all models testing the effects of hydrologic disturbance) had a somewhat smaller cumulative Akaike weight of 0.85 (Table 5). In the post hoc models (Table 6), however, the less significant of these variable pairs dropped out of the top models, giving an overall ranking of watershed disturbance variables of: development (cumulative w_i = 0.99), ditch density (0.80), aqueduct density (0.67), dams (0.22), agriculture (0.11), and reservoir area (0.03).

All four univariate models examining measures of hydrologic alteration (dams, reservoirs, ditches, and aqueducts) had positive associations ($P < 0.001$ in each case) with the degree of invasions (individual univariate correlations are as follows: dams = 0.508, reservoir area = 0.671, ditches = 0.759, and aqueducts = 0.589). The two univariate models of watershed disturbance (development and agriculture) also had positive associations ($P < 0.0001$ in each case) with the degree of invasions (individual univariate correlations are as follows: development = 0.601 and agriculture

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Variable				
agriculture	protected	rain	ws area	diversity
0.158 (−0.013, 0.328)			0.519† (0.355, 0.683)	
0.098 (−0.093, 0.288)			0.478† (0.305, 0.651)	0.128 (−0.059, 0.314)
0.105 (−0.073, 0.282)			0.440† (0.239, 0.641)	
0.108 (−0.207, 0.232)		−0.207 (−0.487, 0.073)	0.342† (0.092, 0.592)	0.323† (0.002, 0.644)
0.039 (−0.155, 0.234)			0.394† (0.188, 0.601)	0.136 (−0.044, 0.317)
0.187† (0.011, 0.363)			0.578† (0.416, 0.740)	
0.157 (−0.016, 0.330)		0.023 (−0.143, 0.190)	0.527† (0.351, 0.703)	
0.159 (−0.041, 0.358)			0.567† (0.399, 0.734)	0.057 (−0.128, 0.242)
0.183† (0.002, 0.364)	−0.020 (−0.180, 0.139)		0.584† (0.413, 0.754)	
0.104 (−0.078, 0.285)	−0.008 (−0.159, 0.143)		0.442† (0.235, 0.648)	
			0.351† (0.132, 0.571)	0.201† (0.030, 0.371)
0.121 (−0.084, 0.325)	−0.00 (−0.036, 0.035)	−0.024 (−0.310, 0.263)	0.470† (0.234, 0.706)	0.080 (−0.250, 0.410)
0.971	0.051	0.174	1.000	0.435

= 0.587). Of the natural watershed characteristics, rainfall was negatively associated with the degree of invasions ($P = 0.01$: univariate correlation = −0.384), and positive associations included elevation ($P < 0.01$: univariate correlation = 0.410), watershed area ($P < 0.0001$: univariate correlation = 0.723), and native diversity ($P < 0.005$: univariate correlation = 0.435).

Stocked vs. nonstocked nonnative fishes

Only 30% of the nonnative fishes established in California (including native fishes that have been transferred among basins) originally derived from deliberate stocking for sport, food fisheries, or forage. However, these include many of the most widespread fishes in the state, so at the level of individual watersheds stocked fishes account for 48–100% (mean 75%) of the nonnative fishes present (Table 1; figures exclude watersheds with no nonnative fishes).

Both stocked and nonstocked fishes were associated with measures of watershed disturbance, however, the top models differed strikingly for each group. The best a priori model for stocked fishes was the hydrologic disturbance model (model 20) that included native diversity. This model, with an Akaike weight of 0.614, had no close competitors, with the next closest models having Akaike weights of 0.122 and below and ΔAIC_c values >3 (Table 7). The top a priori models ($\Delta AIC_c \leq 2$) for nonstocked fishes included two land-use disturbance models and the Kolar and Lodge (2000) model including dams, aqueduct density, development, agriculture, and watershed size. At least some of the post hoc models for both groups of fishes included variables associated with both hydrologic disturbance and land-use disturbance, but the specific variables that emerged as important differed between groups, with dams and ditch density strongly supported in the models for stocked fishes, while aqueducts and development were strongly supported in models for nonstocked fishes.

In the analysis of a priori models for stocked fishes, all four variables measuring hydrologic disturbance (dams, reservoir area, ditches, and aqueducts) had high cumulative Akaike weights (0.93–0.99, Table 8), reflecting the high rankings of the hydrologic disturbance models for this group. In contrast, measures of land-use disturbance (development and agriculture) in this analysis, had cumulative Akaike weights of only 0.26 (Table 8). In the analysis of a priori models for nonstocked fishes, land-use disturbance variables had cumulative Akaike weights of 1.00, while hydrologic disturbance variables ranked lower with cumulative Akaike weights of 0.03–0.45 (Table 8).

When we examine the post hoc model variants, the general ranking of variables having at least some support in the models for stocked fishes was: watershed size (cumulative $w_i = 1.00$), dams (1.00), ditch density (0.98), native diversity (0.67), development (0.65), and aqueduct density (0.37) (Table 8). The comparable variable ranking for models of nonstocked fishes was: watershed size (cumulative $w_i = 1.00$), proportion developed (1.00), aqueduct density (0.74), and native diversity (0.44) (Table 8).

TABLE 6. Standardized regression coefficients (95% confidence limits) for the top-ranked models for number of nonnative fishes per watershed by variable, including post hoc model variants.

Model, category	dams	ditch	aqueducts	developed
17a D		0.332† (0.138, 0.527)		0.412† (0.264, 0.560)
18a D		0.285† (0.092, 0.478)	0.158 (−0.027, 0.344)	0.330† (0.163, 0.496)
18b D		0.200 (−0.017, 0.417)	0.196† (0.012, 0.380)	0.307† (0.130, 0.484)
25a ML	0.148 (−0.022, 0.318)		0.244† (0.060, 0.428)	0.237† (0.045, 0.429)
31a KL	0.186† (0.016, 0.356)		0.237† (0.048, 0.427)	0.261† (0.065, 0.457)
30 KL	0.174 (0.000, 0.348)		0.171 (−0.009, 0.350)	0.262† (0.063, 0.461)
22 L				0.422† (0.257, 0.587)
20a W	0.235† (0.070, 0.399)	0.229† (0.009, 0.449)	0.320 (0.147, 0.493)	
Mean	0.028 (−0.290, 0.345)	0.241 (−0.037, 0.520)	0.121 (−0.141, 0.382)	0.339† (0.133, 0.546)
Cum. w_i	0.223	0.804	0.670	0.986

Notes: The model-averaged regression coefficients, confidence intervals, and variable importance were calculated as suggested in Burnham and Anderson (2002). Reservoir area, protection, and stream density did not appear in any of these models. Explanations of variables are given in Table 2. Models and categories are given in Table 3.

† The 95% confidence limits for these data do not include zero.

DISCUSSION

Patterns of native and nonnative species occurrence (CCA)

The ordination results generally support our predictions that nonnative fishes will be most strongly aligned with measures of habitat alteration, while most native fishes are associated with measures of natural environmental variation. Some of the variation in species associations we see in the ordinations is related to background biogeographic patterning such as north–south gradients of rainfall and species diversity (M. P. Marchetti, *unpublished data*). Yet some of this natural variation in native species associations is swamped by the pervasive habitat and water-development changes across California. Water diversions and altered hydrologic patterns have changed the forces that structure aquatic assemblages and created habitat that is positively associated with a suite of nonnative fishes. This suite includes slow-water fishes (tilapia, mollies, catfishes, etc.) and lake-associated sport fishes (basses and sunfishes). This is not surprising given the fact that a majority of habitat alterations (dams, aqueducts, canals, and ditches) across the state have created lentic habitat from lotic habitat, and the new nonnative species assemblages reflect this change.

Despite this overall pattern, there are some anomalous species associations. There are six native species strongly associated with human disturbance (positive values on CCA axis 2; Fig. 2A): the longjawed mudsucker (*Gillichthys mirabilis*, LJM), striped mullet (*Mugil cephalus*, STM), California killifish (*Fundulus parvipinnis*, CKF), arroyo chub (*Gila orcutti*, ACB), Santa Ana sucker (*Catostomus santaanae*, SAK), and desert pupfish (*Cyprinodon macularius*, DPF). The reasons for their positive loadings on the second CCA axis (anthropogenic disturbance) are likely a result of all six species having spatially limited native distribution patterns in aquatic environments which are highly modified. Estuaries in California are heavily impacted by human disturbance (primarily through exports of fresh water), and the first three species above are estuarine species that occasionally venture into fresh water. The arroyo chub, Santa Ana sucker, and desert pupfish are all from small Southern California watersheds, and are all at risk of extinction in their native range (the Santa Ana sucker is listed as threatened and the pupfish is listed as endangered). In general, forces of anthropogenic disturbance (urban development, water diversion) are strongly associated with these species' restricted natural habitats in Southern California.

In addition, there are nine nonnative species strongly associated with low levels of human disturbance (negative values on CCA axis 2; Fig. 2B): brook trout (*Salvelinus fontialis*, BKT), brown trout (*Salmo trutta*, BNT), kokanee salmon (*Oncorhynchus nerka*, KOK), brook stickleback (*Culaea inconstans*, FSB), yellow perch (*Perca flavescens*, YPH), wakasagi (*Hypomesus nipponensis*, WAK), pumpkinseed (*Lepomis gibbosus*, PMS), American shad (*Alosa sapidissima*, AMS), and white bass (*Morone chrysops*, WBA). The reasons for these negative associations are varied, but in general, these nonnative species are found in relatively undisturbed habitat around the state. The first three (salmonids) have been widely introduced into mid- to high-

TABLE 6. Extended.

Variable				
agriculture	rain	elevation	ws area	diversity
			0.43† (0.246, 0.617)	
			0.356† (0.165, 0.548)	0.158 (−0.001, 0.317)
	−0.293† (−0.491,−0.095)	0.174 (−0.006, 0.354)		0.466* (0.272, 0.660)
	−0.216 (−0.451, 0.019)		0.358† (0.123, 0.593)	0.335† (0.096, 0.574)
			0.487† (0.315, 0.659)	0.172† (0.007, 0.338)
0.158 (−0.013, 0.328)			0.519† (0.355, 0.683)	
0.187† (0.011, 0.363)			0.578† (0.416, 0.740)	
			0.331† (0.125, 0.536)	0.197† (0.028, 0.365)
0.007 (−0.324, 0.338)	−0.059 (−0.530, 0.412)	0.026 (−0.303, 0.354)	0.343† (0.038, 0.648)	0.157 (−0.229, 0.544)
0.114	0.224	0.135	0.865	0.621

elevation lakes, reservoirs, and streams of the Sierra Nevada mountains that are surrounded by relatively undeveloped terrestrial habitats. Most of the lakes and streams were fishless prior to the introductions. American shad are found in the less-altered Klamath and Russian River regions in the northeastern part of the state as well as the highly modified Sacramento–San Joaquin watershed. The other five species have restricted distributions (mainly in reservoirs) in northern California, and their negative associations are likely a result of their distributions being limited to these few, relatively unaltered watersheds.

Disturbance and invasions

Fish invasions in California are clearly related both to altered hydrology and to watershed disturbance, with top-ranked models including variables from both categories. In particular, our analysis points to the importance of development, aqueducts, ditches, agriculture, and possibly dams in predicting numbers of nonnative fishes in California watersheds. Many authors have listed these factors among others as related to invasibility of freshwater systems (e.g., Moyle and Light 1996*b*, Moyle 1999, Gido and Brown 1999, Kolar and Lodge 2000, Rahel 2002). Notably, the entirely verbal models of Kolar and Lodge (2000) and Moyle and Light (1996*b*) had more support given the data used in our analysis than the more rigorously derived models of Gido and Brown (1999). This may suggest that the factors associated with fish invasions in California watersheds differ from those affecting North American watersheds as a whole. However, we do not believe this to be the case. The fit of Gido and Brown's models to our data was better than the fit of their models to their own (North American) data (adjusted $R^2 = 0.66$ and 0.63 for the California data vs. 0.40 and 0.26 for the North American data). Given the importance of various measures of land-use development in our models, it seems more likely that the lack of variables related to these forms of development in Gido and Brown's (1999) analysis contributed to the differences in our results.

The strong association between development and number of nonnative species may be partly a human population effect, rather than solely an effect of land-use disturbance per se. Although we were unable to obtain population data for our watersheds because of the lack of correspondence between watershed boundaries and political boundaries, the proportion of developed land is likely a good estimator of human population density. Several studies of plants have identified human population size as the most important predictor of nonnative plant species richness (Chown et al. 1998, McKinney 2001, Rejmanek 2003). In addition, McKinney (2001) found that human population size was associated with nonnative fish diversity in U.S. states.

Hydrologic disturbance encompasses several types of anthropogenic change believed to favor nonnative fishes in California: the stabilization of flow regimes of naturally variable rivers and streams (Baltz and Moyle 1993, Marchetti and Moyle 2001, May and Brown 2002, Brown and Ford 2002); the creation of new types of habitat (reservoirs and ditches) which favor nonnative fishes adapted to lentic conditions (Moyle 2002, May and Brown 2002); and increased connectivity among watersheds due to the construction of large-scale water diversions and aqueducts (Moyle 1999, Kolar and Lodge 2000). Previous studies of Putah Creek suggest that in some instances the success of nonnative species may be reversible if a natural flow regime is restored (Marchetti and Moyle 2000, 2001). Similarly, Trexler et al. (2000) found that most non-

TABLE 7. Model rankings for the top models of number of stocked vs. other nonnative fish species per watershed.

Model, category	Variables	Adjusted R^2	K	AIC_c	ΔAIC_c	w_i	Post hoc ΔAIC_c	Post hoc w_i
Stocked								
18a D	d,dt,dv,w,nd	*0.810*	*7*	*−64.373*	···	···	*0.000*	*0.350*
17a D	d,dt,dv,w	*0.800*	*6*	*−63.906*	···	···	*0.467*	*0.277*
20a W	d,dt,a,w,nd	*0.806*	*7*	*−63.431*	···	···	*0.941*	*0.219*
20 W	d,r,dt,a,w,nd	0.803	8	−60.967	0.000	0.614	*3.406*	*0.064*
19a W	d,dt,a,w	*0.781*	*6*	*−59.752*	···	···	*4.621*	*0.035*
25a ML	d,a,rf,w,nd	*0.782*	*7*	*−58.321*	···	···	*6.052*	*0.017*
18 D	d,r,dt,a,dv,ag,w,nd	0.807	10	−57.741	3.226	0.122	*6.632*	*0.013*
19 W	d,r,dt,a,w	0.779	7	−57.687	3.279	0.119	*6.686*	*0.012*
17 D	d,r,dt,a,dv,ag,w	0.791	9	−56.421	4.546	0.063	*7.952*	*0.007*
31 KL	d,a,dv,ag,w,nd	0.746	8	−54.956	6.872	0.020	*9.417*	*0.003*
Other nonnatives								
31a KL	a,dv,w,nd	*0.651*	*6*	*−39.322*	···	···	*0.000*	*0.378*
30a KL	a,dv,w	*0.631*	*5*	*−38.501*	···	···	*0.821*	*0.251*
22a L	dv,w	*0.605*	*4*	*−36.972*	···	···	*2.350*	*0.117*
22 L	dv,ag,w	0.613	5	−36.360	0.000	0.330	*2.962*	*0.086*
30 KL	d,a,dv,ag,w	0.633	7	−35.477	0.883	0.212	*3.845*	*0.055*
21 L	dv,ag,p,w	0.610	6	−34.465	1.895	0.128	*4.857*	*0.033*
31 KL	d,a,dv,ag,w,nd	0.638	8	−34.156	2.204	0.110	*5.165*	*0.029*
23 L	dv,ag,w,nd	0.604	6	−33.755	2.605	0.090	*5.566*	*0.023*
24 ML	d,a,dv,ag,r,w	0.626	8	−32.835	3.525	0.057	*6.486*	*0.015*
25 ML	d,a,dv,ag,r,w	0.633	9	−31.635	4.725	0.031	*7.687*	*0.008*
17 D	d,r,dt,a,dv,ag,w	0.623	9	−30.500	5.860	0.018	*8.822*	*0.005*

Notes: Post hoc models, and the ΔAIC_c and w_i values for all models in the post hoc analyses, are in italics. Variables included in each model are listed: d, dams; r, reservoirs; dt, ditch density; a, aqueduct density; dv, development; ag, agriculture; p, proportion protected; rf, rainfall; w, watershed area; and nd, native diversity.

native fishes were not well adapted for persisting in the least disturbed but highly fluctuating freshwater marshes within the Florida Everglades. The ever increasing alteration of waterways worldwide, related to increasing human populations, led Kolar and Lodge (2002) to urge strong measures to prevent more introductions into fresh waters because of increased probabilities of success and detrimental impacts.

A close look at some of the most widely introduced fishes in California lends support to the importance of disturbance, particularly hydrologic alteration, in promoting successful introductions. Many species of salmonids and centrarchids are favored game fish and have been widely stocked across most of California during the last century. Almost all habitat with the potential to contain these species has received them (Moyle 2002), but despite their ubiquity of introduction, not all habitats have maintained their populations. Centrarchids in particular tend to be most common and abundant in highly disturbed areas where natural flow regimes have been altered (Moyle 2002). This and much other research across the state suggests a positive relationship between hydrologic disturbance and invasion success in fishes (Moyle and Nichols 1974, Baltz and Moyle 1993, Marchetti and Moyle 2001).

Invasions and native diversity

Our study found no evidence of biotic resistance to fish invasions in California, and in fact detected a moderate positive univariate correlation (0.435) between native and nonnative fish diversity at the watershed scale. This correlation may be due to other watershed variables which covary with native diversity (e.g., watershed area and habitat diversity), as has been suggested for plants (Shea and Chesson 2002, Rejmánek 2003, Stohlgren et al. 2003). Shea and Chesson (2002) suggest that at large spatial scales, these covarying factors will overwhelm the underlying negative relationship between native and nonnative species diversity predicted by niche theory. In the current study, the addition of native diversity improved the fit of several (though not all) models containing watershed area as well as other natural environmental variables (Table 4), possibly suggesting that not all relevant covariates were included in our study. However, in all models the sign of the regression coefficient for native diversity remained positive, giving no hint of any underlying negative relationship between native and nonnative species diversity.

For fish, as for plants (Levine 2000), the richness–invasibility relationship may be related to the scale of the study. Ross et al. (2001) and Gido and Brown (1999) both suggest that large regions (states and watersheds, respectively) in North America with high species richness were less invaded than those with low richness. However, Gido and Brown's (1999) analysis strongly suggests this is an artifact of the larger species pool of North American fishes available to be easily introduced to the more species-depauperate watersheds. When they removed North American species from their analysis they actually found a positive relationship between native and nonnative fish diversity

TABLE 8. Ranking of variable importance, based on cumulative Akaike weights, for the models of all nonnative fish species and models of number of stocked vs. other nonnative fishes per watershed.

	All nonnative fishes		Stocked		Not stocked	
	A priori	Post hoc	A priori	Post hoc	A priori	Post hoc
Dams	0.85	0.22	0.99	1.00	0.45	0.11
Reservoir area	0.29	0.03	0.93	0.10	0.03	0.00
Ditch density	0.29	0.80	0.93	0.98	0.03	0.00
Aqueduct density	0.85	0.67	0.99	0.37	0.45	0.74
Proportion developed	0.97	0.99	0.26	0.65	1.00	1.00
Proportion agriculture	0.97	0.11	0.26	0.02	1.00	0.25
Proportion protected	0.05	0.01	0.02	0.00	0.13	0.03
Mean rainfall	0.17	0.22	0.02	0.02	0.09	0.02
Mean elevation	0.00	0.13	0.00	0.00	0.00	0.00
Stream density	0.00	0.00	0.00	0.00	0.00	0.00
Watershed area	1.00	0.87	1.00	1.00	0.99	1.00
Original diversity	0.44	0.62	0.78	0.67	0.25	0.44

Note: Weights are based on both the a priori and post hoc models given in Table 7.

(Gido and Brown 1999). On local or regional scales, species richness may have little relevance to invasion success. Caley and Schluter (1997), for example, provide evidence that most local faunas are not saturated with species, including freshwater fish faunas. Moyle and Light (1996*b*) suggest that at the local scale, all freshwater systems are highly invasible, regardless of local species richness, depending on availability of resources at the time of invasion.

Protected status

We found no evidence that land protection, as it is currently practiced, reduces the number of nonnative fish species in watersheds. This variable had the weakest univariate relationship with the number of nonnative species (model 8, Table 4) and also failed to add to the fit of any multivariate models. Major reasons for this may be that protected areas are typically at higher elevations, are generally focused on terrestrial ecosystems, and therefore pay little attention to watershed boundaries (Moyle and Yoshiyama 1994). Most of the waters in protected areas were historically fishless and introductions of sport fishes have consequently been widespread (Moyle 2002). This suggests that strategies to protect native fishes and other aquatic organisms have to be focused on some combination of restoring ecosystem processes, prevention of further introductions, eradication of local populations of alien species, and special management of lakes and streams that are still dominated by native fishes (Moyle and Yoshiyama 1994).

Human interest

One common difficulty with the study of invasions is that the underlying mechanisms facilitating the invasion are often hidden by our reliance on "natural experiments" (Blackburn and Duncan 2001*a*). In order to draw rigorous conclusions regarding characteristics of successfully invaded regions, taxa would need to be introduced across a landscape at random and in varying numbers (Blackburn and Duncan 2001*a, b*). This is clearly not the case in California. Fish species have been introduced for a variety of reasons in the state, both deliberately and as a by-product of other human activity (Moyle 2002). Each introduction method carries a bias in terms of numbers of individuals introduced (propagule pressure) and localities of introduction. For example, forage and game species are likely to be released in high numbers across large areas (particularly into reservoirs) while bait and aquarium fish releases are likely to involve small numbers in localized areas. Therefore it is not reasonable to assume that all species had the same opportunities for establishment across the state, although aqueducts and rapid transport by humans do promote biotic homogenization.

We demonstrate elsewhere (Marchetti et al. 2004) that propagule pressure is an important contributing factor to the spread and integration of nonnative fishes in California. Human interest clearly plays a large role in determining the fate of introductions; more interest generally equals more propagules, which means greater success over larger areas (Marchetti et al. 2004). In cases where habitat alteration precedes an introduction it becomes difficult to assess whether the alteration or human desire (e.g., stocking pressure) is the true driving force behind a species success, or whether it is really a synergistic interaction between the two forces. Unfortunately the data on total stocking pressure for California watersheds is either not available, or not comparable across taxa and/or watersheds. However, our separate analyses of stocked and nonstocked introduced fishes gives some idea of the influence of human interest on the relationship of nonnative fishes with measures of habitat alteration.

Although only a third of the nonnative and translocated native fishes in California were initially introduced for fisheries-related stocking purposes, these widespread fishes often represent the majority of nonnative fishes in individual watersheds. When considering these fishes separately from those introduced by other means, important details emerge which are obscured in the larger overall analysis. Stocked fishes were strongly associated with measures of hydrologic disturbance, particularly the presence of dams and ditches, while other nonnative fishes were strongly associated with measures of land-use disturbance, particularly development, and secondarily with the presence of aqueducts.

The relationship of dams to the presence of stocked fishes is intuitive given the wide variety of sport and forage fishes that are routinely stocked in reservoirs. The importance of ditch density in both the analysis of stocked fishes and the overall analysis, however, is a bit obscure. The density of ditches (which include all unlined canals and other water diversions) may simply reflect an overall level of hydrologic alteration. Such diversions are likely to be particularly common in stream reaches downstream of dams which are used to deliver irrigation water. These systems typically have highly altered hydrology, with winter flood flows reduced or lacking, and summer (irrigation season) flows much higher than prealtered levels. These streams tend to support large numbers of nonnative sportfishes such as sunfishes, basses, and catfishes, which may be unable to persist in the more fluctuating flows common in unaltered California streams (Brown 2000, Marchetti and Moyle 2001).

In contrast, the diversity of other nonnative fishes (e.g., goldfish *Carassius auratus*, sailfin molly *Poecilia latipinna*, and shimofuri goby *Tridentiger bifasciatus*), has very little association with the variable dams, which is probably why this variable did not receive strong support in the overall analysis. Instead, land-use disturbance, particularly development, was the most important predictor (along with watershed size) of number of non-stocked introduced fishes in watersheds. As pointed out above, the amount of developed land area in a watershed may serve as a surrogate for human population density, which is likely a contributing factor in several important vectors of fish introductions, including aquarium releases, bait-bucket releases, biocontrol releases, and even ballast-water transfers.

Conclusions

The invasion process is inherently complex. A successful invader must survive a series of events: transport to the invasion site, initial establishment, spread to a broad area, and then integration into the existing biotic community (Moyle and Light 1996*b*, Kolar and Lodge 2001). Not surprisingly, most invasions fail (Moyle and Light 1996*b*, Williamson 1996). Success of invaders in the face of such low odds is often related to frequent invasion attempts (i.e., introductions by humans), release from natural enemies (predators, competitors, disease, parasites) and the presence of novel, unusually favorable environments (generally created by humans; Elton 1958, Sax and Brown 2000). The current analysis supports the idea that altered environments play a key role in this process. Our results suggest that human disturbance (particularly urbanization and water development) promotes the successful establishment and spread of nonnative species in California watersheds. Biotic resistance from native fish species, on the other hand, seems to have little influence on the invasion process. Instead, we find a generally positive relationship between native and nonnative fish diversity. Human interest in particular species is clearly a factor for invasion success, as evidenced by the wide distribution of most intentionally stocked species. Stocked fishes are also more likely to be associated with the presence of certain types of altered habitats, particularly reservoirs, than are other nonnative fishes, suggesting that the habitat associations of nonnative fishes are not independent of the behavior of fisheries managers.

What can be done to stem the tide of fish invasions into freshwater systems? This study unfortunately found little evidence that land protection, as currently practiced in California, reduces the diversity of nonnative species in watersheds. Managing protected lands at the watershed or bioregional scale, and for native fish assemblages and natural hydrologies, would likely be more successful in this regard (Moyle and Yoshiyama 1994). Given the close association of nonnative fishes with hydrologically altered habitats, the restoration of natural processes in aquatic systems can be expected to minimize the establishment of alien fishes, while helping to maintain native fish populations (Marchetti and Moyle 2000, 2001, Trexler et al. 2000). Addressing the human activities most likely to result in further introductions, whether through regulation or education, will also be important. Although deliberate fish stocking has declined in California in the last few decades (Dill and Cordone 1997), worldwide it is on the rise due to increasing human populations and economic pressures (Kolar and Lodge 2000). Other activities associated with fish introductions, including the aquarium trade, baitfishing, and international shipping, continue to increase in California, as elsewhere (Moyle 2002). Understanding the roles of these vectors in fish invasion patterns, as well as their interactions with the pervasive habitat alterations explored in this paper, will be an important avenue of future research.

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LITERATURE CITED

Allan, J. D., and A. S. Flecker. 1993. Biodiversity conservation in running waters: identifying the major factors that threaten destruction of riverine species and ecosystems. Bioscience 43:32–43.

Baltz, D. M., and P. B. Moyle. 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. Ecological Applications 3:246–255.

Blackburn, T. M., and R. P. Duncan. 2001*a*. Establishment patterns of exotic birds are constrained by non-random patterns in introduction. Journal of Biogeography 28:927–939.

Blackburn, T. M., and R. P. Duncan. 2001*b*. Determinants of establishment success in introduced birds. Nature 414:195–197.

Brown, L. R. 2000. Fish communities and their associations with environmental variables, lower San Joaquin River drainage, California. Environmental Biology of Fishes 57:251–269.

Brown, L. R., and T. Ford. 2002. Effects of flow on the fish communities of a regulated California river: implications for managing native fishes. River Research and Applications 18:331–342.

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

Caley, M. J., and D. Schluter. 1997. The relationship between local and regional diversity. Ecology 78:70–80.

Case, T. J. 1991. Invasion resistance, species build-up, and community collapse in metapopulation models with interspecies competition. Biological Journal of Linnaean Society 42:239–266.

Case, T. J. 1996. Global patterns in the establishment and distribution of exotic birds. Biological Conservation 78:69–96.

Chapin, F. S., III, et al. 1998. Ecosystem consequences of changing biodiversity. Bioscience 48:45–52.

Chown, S. L., N. J. M. Gremmen, and K. J. Gaston. 1998. Ecological biogeography of Southern Ocean islands: species–area relationships, human impacts, and conservation. American Naturalist 152:562–575.

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. State of California Department of Fish and Game, Sacramento, California, USA.

Elton, C. S. 1958. The ecology of invasions of plants and animals. Methuen, London, UK.

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.

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

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

Huston, M. 1994. Biological diversity. Cambridge University Press, New York, New York, USA.

Jongman, R. H. G., C. J. F. ter Braak, and O. F. R. Van Tongeren. 1995. Data analysis in community and landscape ecology. Cambridge University Press, New York, New York, USA.

Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. Nature 417:636–638.

Kolar, C. S., and D. M. Lodge. 2000. Freshwater nonindigenous species: interactions with other global changes. Pages 3–30 *in* H. A. Mooney and R. J. Hobbs, editors. Invasive species in a changing world. Island Press, Washington, D.C., USA.

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.

Levine, J. M. 2000. Species diversity and biological invasions: relating local processes to community pattern. Science 288:761–763.

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. Biological invasions: lessons for ecology. Trends in Ecology and Evolution 8:133–136.

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

Marchetti, M. P., and P. B. Moyle. 2000. Spatial and temporal ecology of native and introduced fish larvae in lower Putah Creek, California. Environmental Biology of Fishes 58:75–87.

Marchetti, M. P., and P. B. Moyle. 2001. Effects of flow regime and habitat structure on fish assemblages in a regulated California stream. Ecological Applications 11:530–539.

Marchetti, M. P., P. B. Moyle, and R. Levine. 2004. Alien fishes in California watersheds: characteristics of successful and failed invaders. Ecological Applications 14:587–596.

May, J. T., and L. R. Brown. 2002. Fish communities of the Sacramento River Basin: implications for conservation of native fishes in the Central Valley, California. Environmental Biology of Fishes 63:373–388.

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

Moyle, P. B. 1999. Effects of invading species on freshwater and estuarine ecosystems. Pages 177–191 *in* O. T. Sandlund, P. J. Schei, and A. Viken, editors. Invasive species and biodiversity management. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Moyle, P. B. 2002. Inland fishes of California. Second edition. University of California Press, Berkeley, California, USA.

Moyle, P. B., and J. Ellison. 1991. A conservation-oriented classification system for California's inland waters. California Fish and Game 77:161–180.

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 fresh water: empirical rules and assembly theory. Biological Conservation 78:149–162.

Moyle, P. B., and R. D. Nichols. 1974. Decline of the native fish fauna of the Sierra-Nevada foothills, central California. American Midland Naturalist 92:74–83.

Moyle, P. B., and R. M. Yoshiyama. 1994. Protection of aquatic biodiversity in California: a five tiered approach. Fisheries 19:6–18.

Naeem, S., J. M. H. Knops, D. Tilman, K. A. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91:97–108.

Orians, G. H. 1986. Site characteristics favoring invasions. Pages 133–148 *in* H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, New York, USA.

Palmer, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74:2215–2230.

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

Rahel, F. J. 2002. Homogenization of freshwater fish faunas. Annual Review of Ecology and Systematics 33:291–315.

Rejmanek, M. 2003. The rich get richer—responses. Frontiers in Ecology and the Environment 1:122–123.

Richter, B. D., D. P. Braun, M. A. Mendelson, and L. L. Master. 1997. Threats to imperiled freshwater fauna. Conservation Biology 11:1081–1093.

Ross, R. M., W. A. Lellis, R. M. Bennett, and C. S. Johnson. 2001. Landscape determinants of nonindigenous fish invasions. Biological Invasions 3:347–361.

Sax, D. F., and J. H. Brown. 2000. The paradox of invasion. Global Ecology and Biogeography 9:363–371.

Shea, K., and P. Chesson. 2002. Community ecology as a framework for biological invasions. Trends in Ecology and Evolution 17:170–176.

Stohlgren, T. J., D. T. Barnett, and J. T. Kartesz. 2003. The rich get richer: patterns of plant invasions in the United States. Frontiers in Ecology and the Environment 1:11–14.

Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69:25–46.

ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179.

ter Braak, C. J. F., and P. Smilauer. 1999. CANOCO for Windows. Version 4.02. Center for Biometry, Wageningen, The Netherlands.

ter Braak, C. J. F., and P. F. M. Verdonschot. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sciences 57:255–289.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland diversity. Ecology 78:81–92.

Trexler, J. C., W. F. Loftus, F. Jordan, J. J. Lorenz, J. C. Chick, and R. M. Kobza. 2000. Empirical assessment of fish introductions in a subtropical wetland: an evaluation of contrasting views. Biological Invasions 3:265–377.

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

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

APPENDIX

Common and scientific names of fish species utilized in the analyses.

Common name	Scientific name	Abbreviation	Status	Vector
Amargosa pupfish	*Cyprinodon nevadensis*	APF	N	con
American Shad	*Alosa sapidissima*	AMS	E	sto
Arroyo chub	*Gila orcutti*	ACB	N	con
Bigscale logperch	*Percina macrolepida*	BLP	E	inc
Black bullhead	*Ameiurus melas*	LBH	E	sto
Black crappie	*Pomoxis nigromaculatus*	BCR	E	sto
Blue catfish	*Ictalurus furcatus*	BCF	E	sto
Blue tilapia	*Oreochromis aurea*	BLT	E	sto
Bluegill	*Lepomis macrochirus*	BLG	E	sto
Brook stickleback	*Culea inconstans*	FSB	E	bat
Brook trout	*Salvelinus fontinalis*	BKT	E	sto
Brown bullhead	*Ameiurus nebulosus*	BRH	E	sto
Brown trout	*Salmo trutta*	BNT	E	sto
California killifish	*Fundulus parvipinnis*	CKF	N	not
California roach	*Lavinia symmetricus*	RCH	N	bat
Channel catfish	*Ictalurus punctatus*	CCF	E	sto
Chinook salmon	*Oncorhynchus tshawytscha*	CNS	N	not
Chum salmon	*Oncorhynchus keta*	CHS	N	not
Coastrange sculpin	*Cottus aleuticus*	CTS	N	not
Coho salmon	*Oncorhynchus kisutch*	COS	N	sto
Common carp	*Cyprinus carpio*	CCP	E	sto
Cutthroat trout	*Oncorhynchus clarki*	CTT	N	sto
Delta smelt	*Hypomesus transpacificus*	DSM	N	not
Desert pupfish	*Cyprinodon macularius*	DPF	N	con
Eulachon	*Thaleichthys pacificus*	EUC	N	not
Fathead minnow	*Pimephales promelas*	FHM	E	sto
Golden shiner	*Notemigonus crysoleucas*	GOS	E	bat
Goldfish	*Carassius auratus*	GOF	E	aqu
Green sturgeon	*Acipenser medirostris*	GST	N	not
Green sunfish	*Lepomis cyanellus*	GSF	E	sto
Hardhead	*Mylopharodon conocephalus*	HHD	N	not
Hitch	*Lavinia exilicauda*	HCH	N	bat
Inland silverside	*Menidia beryllina*	ISS	E	bio
Kern brook lamprey	*Lampetra hubbsi*	KBL	N	not
Klamath small scale sucker	*Catostomus rimiculus*	KSK	N	not
Kokanee	*Oncorhynchus nerka*	KOK	E	sto
Lahontan redside	*Richardsonius egregius*	LRS	N	bat
Lake trout	*Salvelinus namaycush*	LAT	E	sto
Largemouth bass	*Micropterus salmoides*	LMB	E	sto

APPENDIX. Co

Common n
Longfin smelt
Longjaw mudsuc
Marbled sculpin
Mountain sucke
Mountain whitef
Mozambique mc
Owens pupfish
Owens sucker
Pacific brook la
Pacific lamprey
Paiute sculpin
Pit Klamath brc
Pit sculpin
Porthole livebe
Prickly sculpin
Pumpkinseed
Rainbow trout
Rainwater killi
Red shiner
Redbelly tilap
Redear sunfish
Redeye bass
Riffle sculpin
River lamprey
Rough sculpi
Sacramento b
Sacramento p
Sacramento p
Sacramento s
Sacramento s
Sailfin molly
Salt Creek p
Santa Ana s
Shimofuri g
Shortfin mol
Smallmouth
Speckled da
Spotted bas
Staghorn sc
Starry floun
Striped bas
Striped mul
Tahoe suck
Threadfin s
Threespine
Tidewater
Tui chub
Tule perch
Wakasagi
Warmouth
Western m
White bas
White cat
White cra
White stu
Yellow bu
Yellow pe
Yellowfin

Notes:
(E). See
species re
transfer;
aqu, aqu
release;
transferr

APPENDIX. Continued.

Common name	Scientific name	Abbreviation	Status	Vector
Longfin smelt	*Spirinchus thaleichthys*	LFS	N	not
Longjaw mudsucker	*Gillichthys mirabilis*	LJM	N	sto
Marbled sculpin	Cottus klamathensis	MAS	N	not
Mountain sucker	*Catostomus platyrhynchus*	MSK	N	wat
Mountain whitefish	*Prosopium williamsoni*	MWF	N	not
Mozambique mouthbrooder	*Oreochromis mossambica*	MOM	E	aqu
Owens pupfish	*Cyprinodon radiosus*	OPF	N	not
Owens sucker	*Catostomus fumeiventris*	OWK	N	wat
Pacific brook lamprey	*Lampetra richardsoni*	PBL	N	not
Pacific lamprey	*Lampetra tridentata*	PLP	N	not
Paiute sculpin	*Cottus beldingi*	PAS	N	not
Pit Klamath brook lamprey	*Lampetra lethophaga*	PKL	N	not
Pit sculpin	*Cottus pitensis*	PIS	N	not
Porthole livebearer	*Poeciliopsis gracilis*	PLB	E	aqu
Prickly sculpin	*Cottus asper*	PRS	N	wat
Pumpkinseed	*Lepomis gibbosus*	PMS	E	sto
Rainbow trout	*Oncorhynchus mykiss*	RBT	N	sto
Rainwater killifish	*Lucania parva*	RKF	E	inc
Red shiner	*Cyprinella lutrensis*	RSH	E	sto
Redbelly tilapia	*Tilapia zilli*	RET	E	sto
Redear sunfish	*Lepomis microlophus*	RSF	E	sto
Redeye bass	*Micropterus coosae*	REB	E	sto
Riffle sculpin	*Cottus gulosus*	RIS	N	not
River lamprey	*Lampetra ayersi*	RLP	N	not
Rough sculpin	*Cottus asperrimus*	ROS	N	not
Sacramento blackfish	*Orthodon microlepidotus*	SBF	N	sto-i
Sacramento perch	*Archoplites interruptus*	SPH	N	sto
Sacramento pikeminnow	*Ptychocheilus grandis*	SPM	N	sto-i
Sacramento splittail	*Pogonichthys macrolepidotus*	SST	N	not
Sacramento sucker	*Catostomus occidentalis*	SSK	N	wat
Sailfin molly	*Poecilia latipinna*	SAM	E	aqu
Salt Creek pupfish	*Cyprinodon salinus*	SPF	N	con
Santa Ana sucker	*Catostomus santaanae*	SAK	N	inc
Shimofuri goby	*Tridentiger bifasciatus*	SFG	E	shp
Shortfin molly	*Poecilia mexicana*	SHM	E	aqu
Smallmouth bass	*Micropterus dolomieu*	SMB	E	sto
Speckled dace	*Rhinichthys osculus*	SPD	N	bat
Spotted bass	*Micropterus punctulatus*	SPB	E	sto
Staghorn sculpin	*Leptocottus armatus*	SHS	N	not
Starry flounder	*Platichthys stellatus*	STF	N	not
Striped bass	*Morone saxatilis*	SBA	E	sto
Striped mullet	*Mugil cephalus*	STM	N	sto
Tahoe sucker	*Catostomus tahoensis*	TSK	N	bat
Threadfin shad	*Dorosoma petenense*	TFS	E	sto
Threespine stickleback	*Gasterosteus aculeatus*	TSB	N	inc
Tidewater goby	*Eucyclogobius newberryi*	TWG	N	not
Tui chub	*Siphateles bicolor*	TCB	N	bat
Tule perch	*Hysterocarpus traski*	TUP	N	wat
Wakasagi	*Hypomesus nipponensis*	WAK	E	sto
Warmouth	*Lepomis gulosus*	WMH	E	sto
Western mosquitofish	*Gambusia affinis*	MQF	E	bio
White bass	*Morone chrysops*	WBA	E	sto
White catfish	*Ameiurus catus*	WCF	E	sto
White crappie	*Pomoxis annularis*	WCR	E	sto
White sturgeon	*Acipenser transmontanus*	WST	N	not
Yellow bullhead	*Ameiurus natalis*	YBH	E	sto
Yellow perch	*Perca flavescens*	YPH	E	sto
Yellowfin goby	*Acanthogobius flavimanus*	YFG	E	shp

Notes: Abbreviations refer to the CCA biplots. Status refers to whether the species is native to California (N) or exotic (E). See Moyle (2002) for full details of presence/absence in each California watershed. Predominant vectors by which the species reached California or was transferred among basins within California are indicated in the last column: con, conservation transfer; sto, legally stocked for fisheries or forage; sto–i, illegally stocked; inc, unintentionally stocked with other species; aqu, aquarium release (in some cases from commercial facilities); wat, water transfer (aqueduct or canal); bio, biocontrol release; shp, shipping (mainly ballast water); bat, bait fish or bait bucket transfers; not, fish species was not introduced or transferred among basins.