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[Article]

Distribution and Abundance of Nonnative Fishes in Streams of the Western United States

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Abstract.—This report presents data from one of the largest standardized stream surveys conducted in the western United States, which shows that one of every four individual fish in streams of 12 western states are nonnative. The states surveyed included Arizona, California, Colorado, Idaho, Montana, Nevada, North Dakota, Oregon, South Dakota, Utah, Washington, and Wyoming. The most widely distributed and abundant nonnative fishes in the western USA were brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, rainbow trout *Oncorhynchus mykiss*, common carp *Cyprinus carpio*, smallmouth bass *Micropterus dolomieu*, largemouth bass *M. salmoides*, green sunfish *Lepomis cyanellus*, fathead minnow *Pimephales promelas*, yellow perch *Perca flavescens*, yellow bullhead *Ameiurus natalis*, cutthroat trout *O. clarkii*, western mosquitofish *Gambusia affinis*, golden shiner *Notemigonus crysoleucas*, channel catfish *Ictalurus punctatus*, and red shiner *Cyprinella lutrensis*. The greatest abundance and distribution of nonnative fishes was in interior states, and the most common nonnatives were introduced for angling. Nonnative fishes were widespread in pristine to highly disturbed streams influenced by all types of land use practices. We present ranges in water temperature, flow, stream order, riparian cover, human disturbance, and other environmental conditions where the 10 most common introduced species were found. Of the total western U.S. stream length bearing fish, 50.1% contained nonnative fishes while 17.9% contained physical environment that was ranked highly or moderately disturbed by humans. Introduced fishes can adversely affect stream communities, and they are much more widespread in western U.S. streams than habitat destruction. The widespread distribution and high relative abundance of nonnative fishes and their documented negative effects suggest their management and control should elicit at least as much attention as habitat preservation in the protection of native western U.S. stream biota.

Through predation, competition, and hybridization, nonnative fishes have contributed to the decline of biological diversity of U.S. stream fauna. A 1999 compilation of over 17,000 records of nonnative fishes occurrence reported 536 nonnative species in the inland waters of the USA (Fuller et al. 1999; Nico and Fuller 1999). A study of extinctions of North American fish during a 100-year period (1889–1989) indicates that 40 taxa (including 27 species, 13 subspecies, and three genera) were lost (Miller et al. 1989). Nonnative fish species were implicated in 49% of endangered species listings, second only to habitat loss (Magnusson et al. 1998; Wilcove et al. 1998).

Since the mid-19th century, western U.S. streams have been the focus of fish introduction efforts. Believing western waters to be species depauperate, the U.S. Fish Commission used the transcontinental railway system to bring eastern species west. The rate of introductions and the number of species introduced increased since the 1950s with advances in propagation, transportation of species, and the introduction of species from other continents (Fuller et al. 1999). Because eradication of nonnative species often is ineffective or impractical, most nonnative species will remain a part of ecosystems, necessitating further study of these organisms to best predict and manage their impact (Mooney and Drake 1989; Carey 1996).

Few studies have examined the concepts of species introductions in a landscape larger than a watershed or pooled data from many sources to patch together a larger region for analysis (Moyle and Light 1996; Gido and Brown 1999). The Environmental Monitoring and Assessment Program (EMAP; Peck et al. 2001), a standardized survey by the U.S. Environmental Protection Agency (USEPA) of the streams of 12 western states, provided a rare opportunity to investigate the distribution and abundance of nonnative fishes and environmental factors related to their distribution across the western USA. Access to standardized

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data from across the western USA allowed us to document the distribution and abundance of nonnative fish species at a regional scale to seek patterns that may not be evident at smaller scales.

Specific objectives of our study were to (1) quantify the distribution of nonnative fishes across the western USA and at a statewide level; (2) identify the most common nonnative fishes of 12 western states; (3) report the range of conditions that nonnative species inhabit throughout the western USA; (4) evaluate the relationships between nonnative fish abundance and native fish abundance; and (5) examine the relationship between nonnative fish presence and relative abundance and several measures of human disturbance and land use practice.

This information will help managers understand the scope of the distribution of nonnative fishes in the western USA. Such information may also allow scientists to develop workable hypotheses in studying the processes or mechanisms involved with invasions of nonnative fishes on a large scale.

Methods

Data on the presence and abundance of over 180 fish species and hybrids, and various characteristics of riparian systems in which they were found, were collected by electrofishing 689 randomly chosen sites during a 3-year (2000–2002) survey across Arizona, California, Colorado, Idaho, Montana, Nevada, North Dakota, Oregon, South Dakota, Utah, Washington, and Wyoming (Peck et al. 2001). New Mexico was not included in the survey. Sample sites were chosen by a stratified random selection from all reaches of perennial stream identified on 1:100,000-scale U.S. Geological Survey (USGS) maps, excluding the main stems of the Colorado, Columbia, Snake, and Missouri rivers as these rivers were too large to be sampled using the protocol. The sample population was weighted such that sites within each stratum represented the size of the stratum, resulting in estimates that represent conditions for all western U.S. streams (>650,000 km).

The reach of stream surveyed at each site was equal to 40 times the channel width, with a minimum length of 150 m. The reach length was determined to ensure the capture of greater than or equal to 90% of the fish species present (Peck et al. 2001). Crews used a backpack electrofishing unit to perform a single upstream pass (total shocking time = 45–180 min depending upon the size of the stream) through a reach to sample fish, with an effort to sample all habitats present in proportion to their size. Species and numbers of individuals were recorded for each site. The Smithsonian Institution was provided voucher samples of species collected in the field to verify field identification (Peck et al. 2001).

Native fish were defined as those species that naturally occurred at a site, while nonnative fish were defined as species at sites outside of their native range. Native and nonnative origin was determined to the smallest scale possible (stream, drainage basin, or region). Fish origin (native or nonnative) was determined for each species by reviewing 15 sources that included information on species range and history in western states (Churchill and Over 1938; Simon 1951; Bailey and Allum 1962; Minckley 1973; McClane 1974; Wydoski and Whitney 1979; Simpson and Wallace 1982; Page and Burr 1991; LaRivers 1994; North Dakota Game and Fish Department 1994; Holton and Johnson 1996; Sigler and Sigler 1996; Nico and Fuller 1999; Moyle 2002; Nico and Fuller 2003). Species not identified in the field and awaiting identification by the Smithsonian Institution were recorded from 102 sites. If the family was known and was a family with other congenerics known to be native to the drainage or region, the fish was classified as native. If the family was not likely to be native to a drainage or region, the species was classified as nonnative. All fish of unknown species and family (found at six sites) were classified as native to give a conservative estimate of the presence of nonnative fishes in an assemblage.

Presence was used to represent the positive success of a species introduction and relative abundance as a measure of the level of success or predominance of nonnative fish in a fish assemblage at each site. Relative abundance was the product of the total catch of a specific fish species divided by the total number of fish captured. Because relative abundance is a percentage of the total catch, it corrects for variation in total fish productivity among sites that affect other measures of fish abundance, such as fish density by area.

The density of native and nonnative fishes was calculated by dividing the number of native and nonnative fish collected by the surface area of the stream sampled. Surface area was the product of the length of stream in which fish were collected, and the average of channel width taken at five transects across each river.

The physical parameters recorded at each site included latitude, longitude, stream order (Strahler classification: Strahler 1964), channel width and

TABLE 1.—Distribution and relative abundance of nonnative fishes in fish-bearing streams and 95% confidence intervals by state.

State	Stream length (% of total) with nonnative fishes present	Stream length (% of total) with only native fishes	Relative abundance (%) of nonnative fish for entire state	Total number of species detected	Percent of total species that are nonnative
Arizona	66.7 ± 17.0	14.0 ± 12.4	50.5 ± 19.0	27	59.3
California	43.0 ± 15.1	40.0 ± 14.9	25.6 ± 9.2	53	39.6
Colorado	72.6 ± 13.7	9.4 ± 9.0	66.0 ± 10.8	36	52.8
Idaho	25.1 ± 14.7	42.0 ± 16.8	20.4 ± 10.4	21	14.3
Montana	68.6 ± 20.5	14.1 ± 15.4	22.9 ± 11.3	57	31.6
Nevada	44.1 ± 17.0	37.2 ± 16.6	40.5 ± 20.3	71	18.3
North Dakota	60.9 ± 15.4	35.6 ± 15.0	10.8 ± 8.5	23	52.2
Oregon	23.8 ± 13.6	60.8 ± 15.6	13.3 ± 14.4	53	24.5
South Dakota	53.1 ± 14.5	44.9 ± 14.4	38.5 ± 16.0	73	23.3
Utah	65.8 ± 16.5	20.0 ± 13.9	12.3 ± 11.0	41	41.5
Washington	17.7 ± 13.5	48.9 ± 16.7	42.3 ± 12.3	38	18.4
Wyoming	47.0 ± 18.0	25.8 ± 14.8	8.2 ± 17.0	35	25.7

depth (to calculate mean volume), velocity, mean stream gradient, percent of reach that was rapid and riffle, percent of reach that was glide and pool, mean substrate size, percent instream fish cover, and percent canopy cover.

The landscape surrounding each sampling site was categorized on the basis of dominant land use and level of human disturbance. Training was conducted in all 12 states to ensure scoring procedures were standard. The land use categories were: forest, range, agriculture, suburban–town, and urban. The level of human disturbance was based upon a scale of 1 (totally developed) to 5 (pristine). This determination was a visual assessment of the degree of impact to stream morphology, riparian structure, and water quality because of human activity.

We used ARCVIEW, a geographical information systems package, to gather data on variables not obtained from the field. Layers of data were imported from various sources and matched to EMAP sites. Average daily temperature change, mean daily January minimum temperature, mean daily July maximum temperature, and mean annual precipitation were based upon 30-year data sets (1961–1990) from 4,775 temperature stations and 6,662 precipitation stations monitored by the National Oceanic and Atmospheric Administration and compiled by the National Climate Data Center (National Climate Data Center 2003). To estimate mean road density and average elevation we used the data associated with surrounding area, based upon a national coverage of a grid of 648 km^2 hexagons developed by the USEPA, from which

TABLE 2.—Abundance and distribution (with 95% confidence intervals) of the most common introduced fishes in the fish-bearing streams of 12 states in the western USA. Numbers are reported for the 10 species occupying the most stream length or having the highest relative abundance. If a species is not in the top ten in a category, an asterisk is substituted for a number.

Species	Stream length (% of total) with species present	Mean relative abundance (%) of species when present	Reason for introduction
Brook trout *Salvelinus fontinalis*	17.2 ± 3.0	64.4 ± 5.4	Sport
Brown trout *Salmo trutta*	15.2 ± 2.8	29.3 ± 5.7	Sport
Channel catfish *Ictalurus punctatus*	*	18.5 ± 26.7	Sport
Common carp *Cyprinus carpio*	9.3 ± 2.3	*	Food
Cutthroat trout *Oncorhynchus clarkii*	*	51.1 ± 31.0	Sport
Fathead minnow *Pimephales promelas*	2.5 ± 1.2	17.3 ± 14.1	Bait
Golden shiner *Notemigonus crysoleucas*	*	33.5 ± 22.1	Bait–forage
Green sunfish *Lepomis cyanellus*	2.6 ± 1.2	*	Sport
Largemouth bass *Micropterus salmoides*	3.0 ± 1.3	*	Sport
Western mosquitofish *Gambusia affinis*	*	47.9 ± 19.8	Biocontrol
Rainbow trout *O. mykiss*	11.4 ± 2.5	19.1 ± 6.5	Sport
Red shiner *Cyprinella lutrensis*	*	15.4 ± 15.7	Bait
Smallmouth bass *M. dolomieu*	6.2 ± 1.9	15.0 ± 8.9	Sport
Yellow bullhead *Ameiurus natalis*	2.1 ± 1.1	*	Sport
Yellow perch *Perca flavescens*	2.2 ± 1.2	*	Sport–forage

TABLE 3.—Distribution, relative abundance, and associated 95% confidence intervals of common nonnative fishes and nonnative fishes overall in fish-bearing western U.S. streams flowing through areas subjected to various land use practices and degrees of human disturbance.

Grouping	Stream length (% of total) containing nonnative fishes	Relative abundance (%) of nonnative fishes	Most common nonnative species	Stream length (% of total) occupied by species
Land use practice				
Agriculture	67.2 ± 12.1	19.0 ± 9.1	Common carp	28.6 ± 10.5
			Brown trout	15.9 ± 9.2
Range	64.3 ± 7.3	23.9 ± 2.4	Brown trout	19.7 ± 7.0
			Rainbow trout	19.0 ± 6.9
Urban	58.2 ± 23.3	25.6 ± 25.0	Golden shiner	26.2 ± 38.5
			Largemouth bass	26.2 ± 38.5
Suburban–town	47.9 ± 20.4	21.3 ± 15.6	Smallmouth bass	13.9 ± 17.5
			Black bullhead	12.3 ± 16.6
Forest	43.8 ± 5.5	26.1 ± 4.1	Brook trout	19.4 ± 8.0
			Brown trout	10.3 ± 5.0
Disturbance level[a]				
1	61.5 ± 21.0	24.8 ± 15.4	Common carp	16.5 ± 15.5
			Mosquitofish	15.4 ± 15.1
2	46.5 ± 10.0	18.3 ± 7.2	Common carp	20.1 ± 10.1
			Largemouth bass	12.3 ± 8.3
3	53.2 ± 7.7	20.0 ± 5.8	Brown trout	16.4 ± 7.6
			Rainbow trout	14.2 ± 7.2
4	56.6 ± 6.7	26.5 ± 4.9	Brook trout	19.3 ± 7.9
			Brown trout	14.7 ± 7.0
5	43.9 ± 9.6	30.2 ± 7.0	Brook trout	21.8 ± 13.7
			Brown trout	7.6 ± 8.3

[a] Level 1 = highly disturbed, level 5 = no disturbance.

each sample was taken (White et al. 1999). To estimate human density we used the average for the county, based upon the 1995 U.S. Census Bureau survey (U.S. Geological Survey 2003). For all variables, distributions and residuals were checked for outliers and shape, and appropriate transformations were made.

We summarized data by state and region to estimate the representation of native and nonnative fishes in the fish assemblages in streams across the western United States. To evaluate any relationships between the presence of humans or ecosystem alterations and native and nonnative fishes, we used *t*-tests and correlations to compare the presence and abundance of native and nonnative fishes with mean road density, mean human population density, degree of human disturbance, and dominant land use. To evaluate relationships between native and nonnative species, we used *t*-tests and correlations to compare the presence and abun-

TABLE 4.—Relationships (*t*-tests) of nonnative and native fish presence with various biotic, abiotic, and anthropogenic variables in 12 western states in 2000–2002.

Variable	Nonnative fish present		Native fish present	
	t	P	t	P
Number of fish species	7.2	<0.01	6.9	<0.01
Number of native species	1.6	<0.01		
Number of nonnative species			−1.2	0.23
Native fish density (fish/m^2)	−9.4	<0.01		
Nonnative fish density (fish/m^2)			−8.2	<0.01
Latitude (degrees)	−4.3	<0.01	3.4	<0.01
Longitude (degrees)	9.1	<0.01	−3.1	<0.01
Elevation (m)	6.9	<0.01	−6.8	<0.01
Strahler order	6.3	<0.01	6.4	<0.01
Human population (number/km^2)	−1.8	0.07	2.4	0.02
Level of human disturbance (1 [highest]–5 [lowest])	−0.5	0.64	−3.6	<0.01
Road density (km/648 km^2 grid)	1.9	0.06	0.4	0.7

TABLE 5.—Relationships (correlations) of nonnative and native fish relative abundance with selected biotic, abiotic, and anthropogenic variables in 12 western states in 2000–2002. Correlations that were not significant at the 0.05 level are designated NS.

Variable	Native fish relative abundance	Nonnative fish relative abundance	Native fish density	Nonnative fish density	Number of species	Number of native species	Number of nonnative species
Native fish relative abundance (%)	1.00	−0.99	0.41	−0.55	−0.01	0.18	−0.51
Nonnative fish relative abundance (%)	−0.99	1.00	−0.27	0.57	−0.57	−0.60	−0.22
Native fish density (fish/m^2)	0.41	−0.27	1.00	0.71	−0.42	−0.32	−0.45
Nonnative fish density (fish/m^2)	−0.55	0.57	0.71	1.00	−0.60	−0.61	−0.29
Number of fish species	−0.01	−0.57	−0.42	−0.60	1.00	0.95	0.54
Number of native species	0.18	−0.60	−0.32	−0.61	0.95	1.00	0.26
Number of nonnative species	−0.51	−0.22	−0.45	−0.29	0.54	0.26	1.00
Latitude (degrees)	0.23	−0.25	−0.13	−0.38	0.18	0.26	−0.17
Longitude (degrees)	−0.29	NS	−0.06	0.07	0.24	0.18	0.27
Elevation (m)	−0.35	0.34	0.05	0.39	−0.30	−0.39	0.11
Stream order (Strahler system)	−0.02	−0.43	−0.43	−0.53	0.47	0.41	0.34
Population (number/km^2)	0.09	−0.07	−0.11	−0.14	0.11	0.12	0.01
Road density (km/648 km^2 grid)	−0.05	−0.04	−0.04	0.02	0.17	0.16	0.09
Level of human disturbance (1 [highest]–5 [lowest])	−0.07	0.23	0.19	0.26	−0.34	−0.32	−0.18

dance of native and nonnative species with native or nonnative species richness, total species richness, native or nonnative species density, and stream order. We examined characteristics of the 10 most widely distributed nonnative species and the 10 species with the greatest mean relative abundance at sites at which they were present to determine if there were any characteristics shared by these species, The characteristics we considered included reason for introduction, trophic level, species origin, average length, reproductive strategy, water quality tolerance, and thermal tolerance. We also present ranges and averages of physical parameters where the 10 most widely distributed and abundant nonnative fishes were captured. To compare the extent of habitat disturbance on fish communities to the extent of nonnative fish impact on native fish communities, we compared the proportion of fish-bearing stream kilometers that contained nonnative fishes with the proportion of fish-bearing stream kilometers that were associated with high levels of human disturbance.

Results

The 689 sites sampled represented over 650,000 km of streams in the 12 western states, not including New Mexico. Of these stream kilometers, 81.2 ± 2.9% (95% confidence interval) contained fish. All the following results report percentages of fish-bearing streams occupied. We detected 180 species across the region; 118 (65.6%) were native throughout the western USA, 34 (18.8%) were considered native or nonnative depending where captured, and 28 (15.6%) were nonnative across the western USA. Nonnative species were found in over 260,000 (50.1 ± 3.9%) km of western streams. Fish assemblages comprised entirely of nonnative fishes were found in 11.2 ± 2.4% of stream kilometers, while assemblages consisting entirely of native species were found in 49.9 ± 4.0%. Approximately one in every four individual fish in the western USA was nonnative (23.1 ± 2.8%).

Nonnative fish were most prevalent in streams of interior states (i.e., Arizona, Colorado, Nevada, Utah, and Montana). They were detected in over 50% of the stream length of Colorado (72.6 ± 13.7%), Montana (68.6 ± 20.5%), Arizona (66.7 ± 17.0%), Utah (65.8 ± 16.5%), North Dakota (60.9 ± 15.4%), and South Dakota (53.1 ± 14.5%; Table 1). More than 25% of the stream length in Colorado and Nevada contained only nonnative fishes (Table 1). Colorado had the highest relative abundance of nonnative fish where two of three fish were nonnative (66.0 ± 10.8%), followed by Arizona where one in two fish (50.5 ± 19.0%) were nonnative. In North Dakota only 1 in 12 fish was nonnative (8.2 ± 17.3%; Table 1). The total number of fish species found in each state ranged from 21 to 73, while the number of nonnative species present ranged from 3 to 21. More than half of fish species detected in Arizona (59.3%), Colorado (52.8%), and North Dakota (52.2%) were nonnative (Table 1).

The most common nonnative fishes in western U.S. streams were introduced for sport, food, fish

TABLE 5.—Extended.

Variable	Latitude	Longitude	Elevation	Stream order	Population	Road density	Level of human disturbance
Native fish relative abundance (%)	0.23	−0.29	−0.35	−0.02	0.09	−0.05	−0.07
Nonnative fish relative abundance (%)	−0.25	NS	0.34	−0.43	−0.07	−0.04	0.23
Native fish density (fish/m^2)	−0.13	−0.06	0.05	−0.43	−0.11	−0.04	0.19
Nonnative fish density (fish/m^2)	−0.38	0.07	0.39	−0.53	−0.14	0.02	0.26
Number of fish species	0.18	0.24	−0.30	0.47	0.11	0.17	−0.34
Number of native species	0.26	0.18	−0.39	0.41	0.12	0.16	−0.32
Number of nonnative species	−0.17	0.27	0.11	0.34	0.01	0.09	−0.18
Latitude (degrees)	1.00	−0.06	−0.37	NS	−0.08	−0.09	−0.01
Longitude (degrees)	−0.06	1.00	0.34	0.34	−0.31	−0.07	0.05
Elevation (m)	−0.37	0.34	1.00	−0.10	−0.30	−0.31	0.40
Stream order (Strahler system)	NS	0.34	−0.10	1.00	−0.04	0.03	−0.20
Population (number/km^2)	−0.08	−0.31	−0.30	−0.04	1.00	0.25	−0.18
Road density (km/648 km^2 grid)	−0.09	−0.07	−0.31	0.03	0.25	1.00	−0.30
Level of human disturbance (1 [highest]–5 [lowest])	−0.01	0.05	0.40	−0.20	−0.18	−0.30	1.00

forage, mosquito control, and bait (Table 2). These included brook trout, brown trout, rainbow trout, common carp, smallmouth bass, largemouth bass, green sunfish, fathead minnow, yellow perch, yellow bullhead, cutthroat trout, western mosquitofish, golden shiner, channel catfish, and red shiner (Table 2).

The effect of isolation from human activity on nonnative fish presence and abundance was mixed. We did not find nonnative fishes, as a group, more likely to be present in highly disturbed streams, but the most commonly occurring species did differ according to human disturbance level (Table 3). Counterintuitively, we found that relative abundance of nonnative fish was higher in less disturbed streams, although nonnative fish were also highly abundant in the most disturbed streams (correlation: $r = 0.23$, $P < 0.01$; Table 3). Nonnative fishes were also found in areas that had lower human population densities (t-test: $t = -1.8$, $P = 0.07$; Table 4). However, nonnative fishes were more likely to be present in areas that had higher road density (t-test: $t = 1.9$, $P = 0.06$).

The distribution and abundance of nonnative fishes varied by land use type. Streams in forested areas were least likely (43.8 ± 5.5% of stream length) to contain nonnative fishes. This was significantly lower than range and agricultural areas where nonnative fishes occupied 64.3 ± 7.3% and 67.2 ± 12.1% of the stream length, respectively (analysis of variance: $F = 6.5$, $P < 0.0001$; Tukey–Kramer honestly significant difference). Nonnative species were present in 58.2 ± 23.3% of stream length flowing through urban areas and 47.9 ± 20.4% of stream length passing through suburbs and towns (Table 3).

There were no characteristics of physical habitat that were common to sites hosting nonnative fishes as a group (Tables 4, 5). The range of physical parameters that each type of nonnative fish could occupy differed greatly and was specific to each species (Table 6).

Generally, the abundance of nonnative fish and native fish was inversely related. Nonnative fishes were more likely to occur in streams that had a greater number of native fish species (t-test: $t = 1.6$, $P < 0.01$), but less likely to occur in streams that had higher densities of native fishes (t-test: $t = -9.4$, $P < 0.01$; Table 4). The abundance of nonnative fish was lower in streams that had greater native fish species richness (correlation: $r = -0.60$, $P < 0.01$) and in streams with higher densities of native fish (correlation: $r = -0.27$, $P < 0.01$; Table 5). Nonnative fishes were more likely to be present in higher order streams that hosted species rich communities (t-test: $t = 6.3$, $P < 0.01$). However, nonnative fishes were found at higher levels of relative abundance in lower order streams (correlation: $r = -0.43$, $P < 0.01$; Table 5).

Discussion

Based on abundance and distributions alone, introduced fishes are probably affecting native ecosystems in interior western states more than others in the western USA. These states have a relatively

TABLE 6.—Mean, 95% confidence interval, and range (in parentheses) of habitat characteristics for nonnative populations of 10 fish species in 12 western states in 2000–2002; NA = not available.

Characteristic	Black bullhead	Brown trout	Channel catfish	Common carp	Fathead minnow
Stream order (Strahler system)	2.4 ± 1.4	3.4 ± 0.5	4.4 ± 3.0	5.0 ± 0.4	5.1 ± 1.1
	(0.0–7.0)	(1.0–7.0)	(0.0–7.0)	(0.0–8.0)	(0.0–7.0)
Mean cross-sectional area (m^2)	1.4 ± 3.1	3.5 ± 1.3	NA	5.4 ± 2.1	2.8 ± 2.4
	(0.5–4.0)	(0.4–20.0)	NA	(0.4–19.4)	(0.5–4.6)
Velocity (m/s)	1.0 ± 1.0	1.1 ± 1.0	NA	1.1 ± 1.1	1.1 ± 1.2
	(1.0–1.1)	(1.0–5.3)	NA	(1.0–2.6)	(1.0–1.4)
Mean stream gradient (%)	0.9 ± 2.0	2.5 ± 0.6	NA	0.7 ± 0.2	0.7 ± 0.7
	(0.3–1.9)	(0.5–9.3)	NA	(0.1–1.7)	(0.1–1.6)
Percent of reach that is rapid and riffle (%)	20.7 ± 70.3	50.0 ± 9.1	NA	5.5 ± 2.5	23.3 ± 23.0
	(0.5–50.0)	(3.0–99.9)	NA	(0.5–26.0)	(5.4–50.0)
Percent of reach that is glide and pool (%)	79.5 ± 70.9	50.0 ± 9.1	NA	94.4 ± 2.6	76.7 ± 23.0
	(50.0–99.9)	(0.5–96.0)	NA	(74.0–99.9)	(50.0–94.6)
Mean annual precipitation (cm)	22.4 ± 10.2	22.7 ± 3.1	9.0 ± 3.1	15.5 ± 1.4	11.2 ± 1.7
	(10.0–32.5)	(7.5–65.0)	(7.5–17.5)	(5.0–45.0)	(7.5–27.5)
Mean January minimum air temperature (°C)	−3.5 ± 1.4	−2.5 ± 0.8	−1.9 ± 1.2	−2.6 ± 0.7	−1.4 ± 0.8
	(−8.1–−0.6)	(−8.1–0.6)	(−5.0–0.0)	(−6.1–0.6)	(−3.9–0.6)
Mean July maximum air temperature (°C)	30.2 ± 2.4	27.3 ± 0.9	34.4 ± 2.8	31.2 ± 0.8	32.4 ± 1.7
	(29.4–38.3)	(18.3–35.0)	(29.4–38.3)	(23.9–38.3)	(23.9–38.3)
Mean daily air temperature change (°C)	13.4 ± 4.4	6.4 ± 0.9	9.0 ± 4.9	5.5 ± 1.0	5.9 ± 1.9
	(4.2–20.0)	(0–20.0)	(4.2–20.0)	(1.0–25.0)	(4.2–20.0)
Mean substrate size (mm)	0.13 ± >500	31.60 ± 2.00	NA	0.32 ± 2.00	6.30 ± 7.90
	(0.01–39.80)	(0.03–316.20)	NA	(0.01–6.40)	(0.79–125.90)
Percent instream fish cover (%)	94.9 ± 13.6	98.5 ± 1.4	NA	87.0 ± 9.4	99.1 ± 1.2
	(90.1–99.9)	(72.2–99.9)	NA	(1.0–99.9)	(90.1–99.9)
Percent canopy cover (%)	3.1 ± 10.5	21.2 ± 6.2	NA	5.4 ± 3.6	2.0 ± 3.6
	(<0.01–7.5)	(<0.01–76.6)	NA	(<0.1–48.0)	(<0.1–6.8)
Level of human disturbance (1 [highest]–5 [lowest])	3.4 ± 0.7	3.6 ± 0.2	2.9 ± 0.7	2.6 ± 0.2	2.8 ± 0.4
	(2–4)	(1–5)	(2–4)	(1–5)	(1–4)

low diversity of native species yet a great proportion of endemic species. Southwestern states have lost the greatest number of native fish species to extinction, led by Nevada, which has lost seven (Miller et al. 1989).

Because the majority of the most prominent nonnative fishes continue to be introduced for angling, managers wishing to preserve native fishes need to consider the implications of stocking these species, and what steps will be necessary to eliminate and mitigate their impact (Pascual et al. 2002).

Many authors have suggested that environments undisturbed by human activity are more resistant to invasion by introduced species (Arthington et al. 1983; Moyle and Light 1996; Suarez et al. 1998; Wilcove et al. 1998; Ross et al. 2001). However, we did not find nonnative fishes, as a group, more likely to be present in more disturbed streams (Table 3). Additionally, we found an inverse relationship between nonnative fish relative abundance and human disturbance level, although nonnative fishes also were also highly abundant in the most disturbed streams. That presence and abundance of nonnative fish was higher in less disturbed streams seemed counterintuitive. However, there was a notable difference in the type of species found to be most prevalent according to human disturbance level (Table 3). Nonnative salmonid species, the most widely distributed and abundant introduced fishes in western U.S. streams, were associated with low levels of human disturbance. Species that are more tolerant of degraded or enriched waters—such as common carp, mosquitofish, centrarchids, and ictalurids—were most common in the less pristine reaches of agricultural and urban regions. Disturbance did not necessarily favor nonnative fishes as a group, but it might have allowed nonnative species that were very tolerant of degraded conditions to prosper.

Though forestlands had the lowest proportion of stream length with nonnative fish species present, we found that when nonnatives were present, they were at the highest levels of relative abundance compared with all other landscapes (Table 3). Agricultural regions had the greatest proportion of stream length hosting nonnative species, but the lowest average relative abundance of nonnative fishes. There was also a difference in the type of species found to be most prevalent within each type of land use (Table 3). This also supports the belief that nonnative species as a group are not more likely to be present in a particular environment type or are associated with a specific level

TABLE 6.—Extended.

Characteristic	Green sunfish	Largemouth bass	Mosquitofish	Rainbow trout	Red shiner
Stream order (Strahler system)	4.2 ± 0.8 (1.0–7.0)	3.0 ± 1.2 (0.0–7.0)	2.9 ± 1.0 (1.0–7.0)	4.2 ± 0.6 (1.0–7.0)	4.7 ± 1.0 (0.0–7.0)
Mean cross-sectional area (m^2)	7.8 ± 3.9 (0.5–19.4)	2.9 ± 3.7 (0.3–11.1)	3.9 ± 1.8 (0.1–7.1)	4.5 ± 2.7 (0.1–24.8)	8.7 ± 7.6 (0.5–19.4)
Velocity (m/s)	1.0 ± 1.2 (1.0–2.6)	1.2 ± 1.3 (1.0–2.6)	1.2 ± 1.1 (1.0–1.4)	1.2 ± 1.1 (1.0–2.0)	1.2 ± 1.1 (1.0–5.2)
Mean stream gradient (%)	0.8 ± 0.3 (0.1–1.9)	2.9 ± 2.1 (0.4–4.9)	0.8 ± 1.3 (0.1–1.7)	3.1 ± 1.6 (0.5–12.1)	0.9 ± 0.5 (0.3–1.6)
Percent of reach that is rapid and riffle (%)	13.3 ± 10.7 (0.5–50.0)	25.1 ± 15.7 (0.5–38.7)	12.7 ± 11.4 (0.5–50.0)	51.5 ± 10.9 (0.5–90.0)	25.0 ± 14.6 (8.0–50.0)
Percent of reach that is glide and pool (%)	86.8 ± 10.8 (50.0–99.9)	74.6 ± 16.7 (60.7–99.9)	87.3 ± 11.4 (50.0–99.9)	48.3 ± 10.6 (10.0–99.9)	75.0 ± 14.6 (50.0–92.0)
Mean annual precipitation (cm)	13.7 ± 1.2 (7.5–22.5)	26.6 ± 7.9 (7.5–45.0)	11.0 ± 2.6 (5.0–17.5)	19.6 ± 2.1 (7.5–40.0)	12.3 ± 2.2 (5.0–22.5)
Mean January minimum air temperature (°C)	−1.8 ± 0.8 (−8.1–0.6)	−3.5 ± 1.0 (−6.1–0.6)	−1.0 ± 0.9 (−6.1–0.6)	−2.8 ± 0.7 (−8.1–0.6)	−1.8 ± 0.9 (−5.0–0.6)
Mean July maximum air temperature (°C)	31.9 ± 0.9 (29.4–38.3)	31.1 ± 1.4 (23.9–38.3)	35.8 ± 1.4 (23.9–38.3)	27.7 ± 1.0 (18.3–38.3)	33.3 ± 1.7 (29.4–38.3)
Mean daily air temperature change (°C)	7.8 ± 2.8 (0.1–25.0)	13.1 ± 3.3 (0.1–25.0)	16.6 ± 2.9 (4.2–25.0)	5.9 ± 1.0 (0.1–15.8)	8.1 ± 3.1 (0.1–20.0)
Mean substrate size (mm)	1.60 ± 5.00 (0.01–125.90)	5.00 ± 31.60 (0.01–100.00)	0.50 ± 7.90 (0.01–125.90)	5.10 ± 2.00 (3.20–398.00)	5.00 ± 4.00 (1.60–31.60)
Percent instream fish cover (%)	91.6 ± 11.0 (54.5–99.9)	99.9 ± 0.0 (99.9–99.9)	99.9 ± 0.0 (99.9–99.9)	98.6 ± 1.4 (90.9–99.9)	92.3 ± 13.0 (63.6–99.9)
Percent canopy cover (%)	8.7 ± 8.0 (<0.1–32.0)	22.3 ± 12.3 (<0.1–48.0)	16.4 ± 7.1 (<0.1–32.0)	26.6 ± 9.2 (<0.1–76.6)	6.9 ± 12.7 (<0.1–32.0)
Level of human disturbance (1 [highest]–5 [lowest])	3.1 ± 0.4 (1–4)	2.7 ± 0.4 (1–5)	1.9 ± 0.5 (1–4)	3.4 ± 0.3 (1–5)	3.2 ± 0.4 (2–4)

of human disturbance, but specific introduced species are more suited for particular environments.

Similar to Levine (2000), we found that nonnative species were more likely to be present at sites with greater native species richness. Because of the unique characteristics of each nonnative species and each assemblage of native species, there is most likely a nonnative species that would be able to invade a native fish community despite the number of species.

Habitat destruction and the introduction of nonnative fishes can lead to population fragmentation and local or regional extinction of native fish populations. Both have impacted native fishes of the western USA. Traditionally, habitat destruction has often received more attention in trying to understand the declines of native fishes. However, we found that human disturbance was not associated with the presence of native fishes as a group (Table 3), yet native fishes as a group had a consistent negative association with the presence, abundance, and density of nonnative fishes. Additionally, nonnative fishes were present in a much greater proportion of western streams (50.1 ± 3.9%) than those affected by moderate to high levels of human impact (17.9 ± 2.2%). Without deemphasizing the importance of landscape disturbance by humans, we conclude that nonnative fishes pose an equivalent, if not greater, threat to native fishes than habitat degradation in western U.S. streams.

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