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Relations between introduced fish and environmental conditions at large geographic scales

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Abstract

Data collected from 20 major river basins between 1993 and 1995 as part of the US Geological Survey's (USGS) National Water-Quality Assessment (NAWQA) Program were analyzed to assess patterns in introduced and native fish species richness and abundance relative to watershed characteristics and stream physicochemistry. Sites ($N = 157$) were divided into three regions-northeast, southeast, and west- to account for major longitudinal differences in precipitation/runoff and latitudinal limits of glaciation that affect zoogeographic patterns in fish communities. Common carp (*Cyprinus carpio*) and largemouth bass (*Micropterus salmoides*) were the most frequently collected introduced fish species across all river basins combined. Based on the percentage of introduced fish species, the fish communities most altered by the presence of introduced fish occurred in the western and northeastern parts of the US. Native fish species richness was not an indicator of introduced fish species richness for any of the three regions. However, in the west, introduced fish species richness was an indicator of total fish species richness and the abundance of introduced fish was negatively related to native fish species richness. Some relations between introduced fish species and environmental conditions were common between regions. Increased introduced fish species richness was related to increased population density in the northeast and southeast; increased total nitrogen in the northeast and west; and increased total phosphorous and water temperature in the southeast and west. These results suggest that introduced fish species tend to be associated with disturbance at large geographic scales, though specific relations may vary regionally.

Keywords: Introduced fish; Biomonitoring; Disturbance; Streams

1. Introduction

Invasion of introduced biota is one of the most important issues in natural resource management today (Williams and Meffe, 1998). Globally, introduced biota comprise the first or second most important impact on freshwater ecosystems in most regions on earth (Kolar and Lodge, 2000). As a result, international organizations have joined forces to develop a global invasive species strategy (Mooney, 1999). In the United States, as one response to the broad concern over the impacts of introduced biota, a Presidential executive order (executive order 13112 of 3 February 1999) was established to facilitate control of the invasion of introduced biota and minimize the economic and ecological impacts that introduced species cause. The cost to US taxpayers of introduced species has been estimated to range from hundreds of millions to billions of dollars each year (U.S. Congress, Office of Technology

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Assessment, 1993). These estimates do not include effects on native ecosystems, such as extinction of native species, which are not viewed as an economic cost.

The impacts of introduced fish species on native biota will likely increase significantly because of the large increase in the number of introduced fish species over the last few decades (Williams and Meffe, 1998). Within the United States, 536 unique fish taxa (including fish species and hybrids) are reported to have been introduced outside of their native ranges since the early 1800s (Fuller et al., 1999). Of these, 458 fish taxa were introduced between 1950 and 1995 (Williams and Meffe, 1998).

Environmental degradation, including the alteration of habitat, is often an important factor in interactions between native and introduced species. Urbanization and the conversion of natural habitats to agriculture are major global changes that affect the distribution and abundance of native and introduced species (Kolar and Lodge, 2000). Land use and water use changes can affect streams in many ways, including increased suspended sediment, nutrients, and stream temperatures (through loss of riparian vegetation), and alteration to flow regimes. As a result of the effects of these disturbances, the quantity and quality of habitats important to native freshwater organisms are altered, and thus native species may be more vulnerable to competition and/or predation by introduced species that may be more tolerant of degraded systems.

Leidy and Fiedler (1985) reported an abundance of introduced fish species in disturbed streams. The use of introduced fish as an ecological indicator of degraded stream systems was first proposed by Karr et al. (1986) and was first used by Hughes and Gammon (1987). The presence of introduced fish has been viewed as a deviation from the original state of the fish community and thus is in itself considered a perturbation of the ecosystem (Bramblett and Fausch, 1991). Though the ecology of individual introduced species is becoming better understood, little or no quantitative analyses have been conducted to describe stream characteristics that tend to be invaded by introduced species (Kolar and Lodge, 2000). Assessment of patterns in such relations could be used to better understand the impacts of introduced species and provide information that could potentially reduce risks to ecosystems.

Fish community structure (species richness and abundance of individual species) is characterized as part of an integrated physical, chemical, and biological assessment of the Nation's water quality in the US Geological Survey's (USGS) National Water-Quality Assessment (NAWQA) Program. Data collected as part of the NAWQA Program provided the opportunity to examine patterns in the ecology of introduced fish species at large geographic scales. The goal of this investigation was to assess patterns in relations among introduced fish species and their abundances, watershed characteristics, stream physicochemistry, and native fish species and their abundances. Specific objectives were to: (1) examine regional patterns in relations among native and non-native fish species and their abundances and (2) examine regional patterns in relations between fish species (introduced and native) and environmental gradients.

2. Methods

The NAWQA Program focuses on major river basins across the United States (Gilliom et al., 1995). Data included in this study were collected from 1993 to 1995 in 20 river basins (Table 1). A total of 157 sites was sampled representing a range of stream sizes across major physiographic regions of the United States. Two types of sites were sampled. Wadeable stream sites were selected at the outlet of drainage basins with relatively homogeneous land use and physiographic conditions. Non-wadeable stream sites were selected to represent environmental conditions resulting from combined multiple small basins, each with different land uses and physiographic conditions.

At each site, stream reaches were established based on the number and diversity of stream habitat types (pools, riffles, and runs), meander wavelengths, and minimum/maximum sampling distances (Fitzpatrick et al., 1998). The sampling reach included, where possible, at least two different stream habitat types. Where this was not possible (for example, a stream that is a continuous run), the length of the sampling reach included one meander wavelength, based on 20 times the distance of the channel width (Leopold et al., 1964). A minimum reach length of 150 m and a maximum reach length of 300 m were established prior to sampling at wadeable sites. Minimum and maximum reach lengths at non-wadeable sites were 500 and 1000 m, respectively.

Table 1
The 20 NAWQA river basins sampled between 1993 and 1995 and sampling details

Region	NAWQA river basin name	River basin abbreviation	Number of sites sampled	Total number of fishes collected
Northeast	Central Nebraska Basins	CNBR	8	4308
	Connecticut, Housatonic, and Thames River Basins	CONN	8	1418
	Hudson River Basin	HDSN	5	3628
	Lower Susquehanna River Basin	LSUS	6	3748
	Potomac River Basin	POTO	9	3066
	Red River of the North Basin	REDN	8	2979
	White River Basin	WHIT	11	6308
	Western Lake Michigan Drainage	WMIC	11	2022
Southeast	Apalachicola-Chattahoochee-Flint River Basin	ACFB	6	2133
	Albemarle-Pamlico Drainage	ALBE	10	2952
	Georgia-Florida Coastal Plain	GAFL	6	1153
	Ozark Plateaus	OZRK	9	7517
	Trinity River Basin	TRIN	10	765
West	Central Columbia Plateau	CCPT	6	1426
	Nevada Basin and Range	NVBR	3	568
	Rio Grande Valley	RIOG	7	773
	San Joaquin-Tulare Basins	SANJ	7	863
	South Platte River Basin	SPLT	10	5549
	Upper Snake River Basin	USNK	11	1456
	Willamette Basin	WILL	6	1530

Fish were collected during summer low-flow periods from 1993 to 1995 using a combination of electrofishing and seining (Meador et al., 1993). Although this combination of methods provides the opportunity to collect nearly all fish species present in the sampling reach, the sampling effort for each method is different and varies regionally (Patton et al., 2000). Electrofishing gear consisted of three types—backpack, towed barge, and boat-mounted units. All electrofishing methods were conducted by using a pulsed direct current waveform. Recommended pulse frequencies ranged from 30 to 60 pulses per second (Meador et al., 1993). Operators of electrofishing gear received training in the sampling protocol (Meador et al., 1993) and in electrofishing principles, such as power transfer theory in order to help standardize electrofishing effort and increase the efficiency of electrofishing operations (Reynolds, 1996). In wadeable streams, backpack and towed barge electrofishing began at the downstream boundary of the sampling reach and two passes were conducted in an upstream direction. Boat electrofishing began at the upstream boundary of the sampling reach and proceeded in a downstream direction, one pass along each shoreline.

Seining was conducted upon completion of two electrofishing passes. In wadeable sampling reaches, seine hauls were conducted in the upper, middle, and lower sections of the reach for a total of three seine hauls per reach. In non-wadeable streams, beach seining was conducted in wadeable shoreline areas. Beach seining was conducted by maintaining one end of the seine stationary on the shore while the remainder of the seine was deployed into the water perpendicular to the shore and pulled in a downstream direction. Three beach seine hauls were taken from the upper, lower, and middle sections of the non-wadeable sampling reach.

Fish from electrofishing and seining were combined as a single sample of fish community structure for a reach. Fish were identified to species and counted. Fish that could not be identified in the field were retained for identification in the laboratory (Walsh and Meador, 1998).

In each river basin, fish species were classified as resident or introduced. The status of the majority of fish species was established on the basis of two national databases—Texas Natural History Collections North American Freshwater Fishes Index

Images, Maps and Information (TMM, 1998), and the non-indigenous aquatic species database (USGS, 2000b). In addition, Lee et al. (1980), and various State and regional fish books were used (Benson, 1982; Laerm and Freeman, 1986; Robison and Buchanan, 1988; Etnier and Starnes, 1993; Jenkins and Burkhead, 1993; Rhode et al., 1994; Cross and Collins, 1995; Mettee et al., 1996). In a few cases, fish species status was determined by consultation with regional experts.

Drainage area (km^2) was determined from watershed boundaries delineated from a 1-km resolution digital elevation model of the conterminous United States. Elevation at each site was also determined from this model. Average annual runoff was calculated for each watershed from Gebert et al. (1987). Tabular data for drainage area, elevation, and runoff were determined from NAWQA digital map products (USGS, 2000a).

Soil-drainage conditions were classified for each watershed by using US Department of Agriculture STATSGO soil hydrologic groups (USDA, 1991). Soil hydrologic groups are groups of soils with the same runoff potential under similar storm and vegetative-cover conditions and included groups A and B (well-drained), group C (moderately drained), and group D (poorly drained). Amounts of soil hydrologic groups in each watershed were determined by overlaying watershed boundaries.

Human-population density per square kilometer in each watershed was estimated by using geographic information system (GIS) polygon coverages of census-block groups processed from 1990 census data (U.S. Census Bureau, 1991). The census-block group coverage was intersected with watershed boundaries, and the percentage of area of each census-block group that was located within each watershed was multiplied by the total number of people in that block group. The total population in all census-block groups within each watershed was summed, and population density was estimated by dividing the total population by drainage area.

Surface-water samples were collected according to protocols established for the NAWQA Program (Shelton, 1994). Water-column physicochemical data collection at each site included suspended sediment (mg/l), total nitrogen (mg/l), total phosphorus (mg/l), pH, dissolved oxygen (mg/l), and dissolved organic carbon (mg/l). Sites were sampled approximately monthly for 1 or 2 years. Discharge (m^3/s), specific conductance (μS/cm), and water temperature (°C) were measured continuously over the same time period. To facilitate comparisons of total nitrogen and total phosphorus among sites that might be biased by varying streamflow and sampling frequencies, flow-weighted concentrations were determined (Clark et al., 2000). The rating curve method was used to estimate a concentration value for each day of a common period of streamflow record, and a mean annual flow-weighted concentration was computed for each site based on these daily estimates.

Five fish metrics were analyzed—(1) number of introduced species captured, (2) number of native species captured, (3) total number of species captured, (4) percentage of total species captured that were introduced species, and (5) percentage of total fish abundance consisting of introduced species. These variables are commonly used indicators of environmental conditions in the development of bioassessment procedures from various geographic regions of the US.

Environmental data collected for this study (watershed characteristics and stream physicochemistry) were examined for normality using normal probability plots. Variables were transformed to improve normality by using $\log_{10}(x + 1)$ or arcsine square root when necessary.

The four soil hydrologic group variables combined added to 100% for each watershed. To maximize independence of soil hydrologic group variables, the number of soil hydrologic group variables was reduced to soil hydrologic groups C (moderately drained) and D (well-drained).

Sites were a priori divided into the three regions: northeast, southeast, and west (Table 1). Sites were divided into eastern and western regions at the 100th meridian except the south Platte River Basin, which was considered to be in the western region even though a small portion of the river basin appears in the eastern region. The east–west division was made to account for major longitudinal differences in precipitation and runoff (Foxworthy and Moody, 1986) that occur at approximately the 100th meridian and large-scale zoogeographic patterns in fish communities (McAllister et al., 1986). Eastern sites were further divided into northeastern and southeastern regions at the 38th parallel. This division was made to account for latitudinal limits of Pleistocene glaciation (Reed and Bush, 2001) and related zoogeographic patterns in fish communities (McAllister et al., 1986). The northeastern region included 66 sites in 8 river basins, the southeastern region included 41 sites in 5 river basins, and the western region included 50 sites in 7 river basins (Table 1).

Because fish metrics are correlated with stream size and because an assessment of relations between fish metrics and environmental variables independent of stream-size effects is desired, standardized residuals were used in analyses (Smogor and Angermeier, 1999). Within each of the three regions, residuals were obtained from regression models of log-transformed drainage area and fish metrics. Pearson correlation analysis was used to assess all pair-wise correlations among these residuals, representing fish metrics normalized for stream size. Relations among the environmental variables were summarized using principal components (PC) analysis of the correlation matrix. Regression analyses were then conducted to examine relations between residuals for the number of introduced fish species and the number of native fish species and principal component axes describing environmental variables. Statistical significance was declared at the 0.05 level. Significance was determined based on the Bonferroni correction for multiple pair-wise comparisons and a P-value of less than 0.05.

3. Results

Of the 325 fish taxa (species and hybrids) collected from 157 sites across all 20 river basins, 58 taxa (18%) were introduced. Introduced fish species were collected in all 20 river basins. On average, introduced species comprised 45% of the total species richness in the western region, compared to 15 and 7.2% in the northeastern and southeastern regions, respectively. Moreover, the largest number of introduced species (19) was collected in the San Joaquin-Tulare Basins, California, representing 70% of the total species richness in that river basin (Fig. 1). Introduced species represented greater than 25% of total fish species richness in all river basins in the western region and for the Central Nebraska Basin and the Connecticut, Housatonic, and Thames River Basin river basins in the northeastern region. Common carp (*Cyprinus carpio*), largemouth bass (*Micropterus salmoides*), and green sunfish (*Lepomis cyanellus*) were the most frequently captured introduced species, respectively, occurring in more than 20% of all sites nationwide (Table 2). Common carp was the most frequently collected introduced fish species in the northeastern and western regions whereas green sunfish was the most frequently collected introduced species in the southeastern region (Table 2).

For all three regions, significant positive correlations occurred between the percentage of introduced fish and the number of introduced species, the percentage of introduced fish and the percentage of introduced species, the number of introduced species and the percentage of introduced species, and the numbers of native species and total species (Table 3). Additional correlations were significant in the western region. In the western region, a significant negative correlation was also observed between the percentage of introduced fish and number of native species, and a significant positive correlation was observed between the number of introduced species and the total number of species. No other significant correlations were detected.

In the northeastern region, the first three principal components had Eigen values greater than one and together accounted for 62.9% of the variance in the environmental data (Table 4). The first principal component (PRIN1_NE) summarized increasing suspended sediment with decreasing runoff. The second principal component (PRIN2_NE) summarized a gradient of increasing total nitrogen and population density with decreasing elevation and poorly drained soils. The third principal component (PRIN3_NE) summarized a gradient of increasing population density associated with increasing poorly drained soils, specific conductance, and pH. Stream size normalized number of introduced fish species in the northeast was not significantly related to PRIN1_NE ($P = 0.342$) but was significantly positively related to PRIN2_NE ($P = 0.0002$, $r^2 = 0.20$) and to PRIN3_NE ($P = 0.021$, $r^2 = 0.08$). Stream size normalized number of native fish species in the northeast was not significantly related to PRIN1_NE ($P = 0.489$), PRIN2_NE ($P = 0.078$), or PRIN3_NE ($P = 0.921$).

In the southeastern region, the first three principal components had Eigen values greater than one

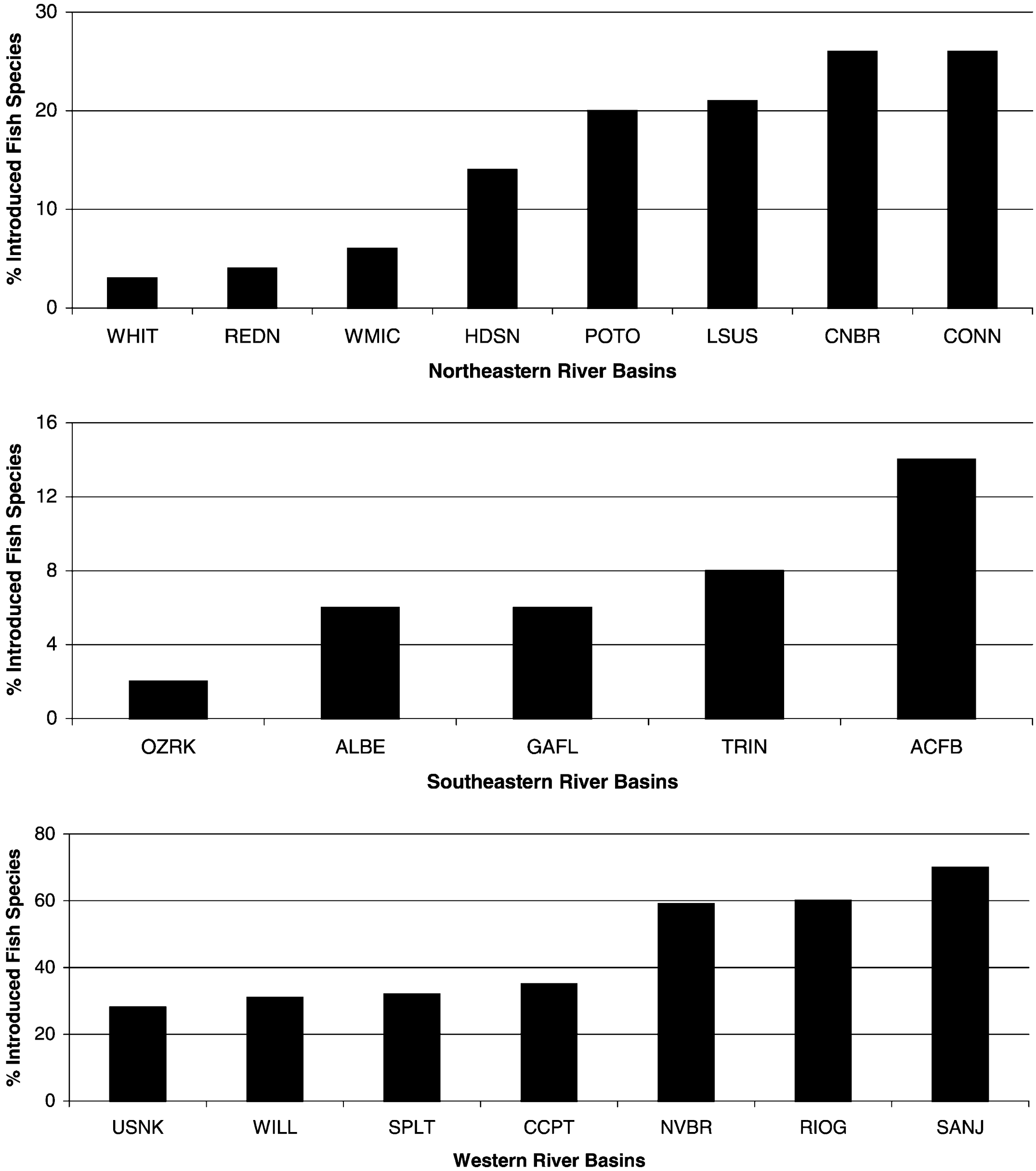

Fig. 1. Percentages of introduced fish species in NAWQA river basins in northeastern, southeastern, and western regions of the US. See Table 1 for river basin abbreviations.

and together accounted for 63.7% of the variance in the environmental data (Table 5). The first principal component (PRIN1_SE) summarized a gradient of increasing elevation, dissolved oxygen, and pH, and decreasing dissolved organic carbon. The second principal component (PRIN2_SE) summarized a gradient of increasing total phosphorous, population density, water temperature, and specific conductance. The third principal component (PRIN3_SE) summarized sites characterized by moderately drained soils. Stream size normalized number of introduced fish species in the southeast was not significantly related

Table 2
Introduced fish species collected at 10 or more sites, number of sites where collected, and percentage of occurrence at all sites ($N = 157$), northeastern sites ($N = 66$), southeastern sites ($N = 41$), and western sites ($N = 50$)

Common name	Scientific name	Number of sites where collected	Percentage of occurrence
All sites			
Common carp	*Cyprinus carpio*	76	48.4
Largemouth bass	*Micropterus salmoides*	46	29.3
Green sunfish	*Lepomis cyanellus*	32	20.4
Bluegill	*Lepomis macrochirus*	29	18.5
Smallmouth bass	*Micropterus dolomieu*	29	18.5
Brown trout	*Salmo trutta*	28	17.8
Mosquitofish	*Gambusia affinis*	16	10.2
Rainbow trout	*Oncorhynchus mykiss*	12	7.6
Goldfish	*Carassius auratus*	11	7.0
Yellow perch	*Perca flavescens*	11	7.0
Rock bass	*Ambloplites rupestris*	10	6.4
Northeastern sites			
Common carp	*Cyprinus carpio*	37	56.1
Largemouth bass	*Micropterus salmoides*	22	33.3
Bluegill	*Lepomis macrochirus*	18	27.3
Smallmouth bass	*Micropterus dolomieu*	16	24.2
Brown trout	*Salmo trutta*	16	24.2
Green sunfish	*Lepomis cyanellus*	10	15.2
Southeastern sites			
Green sunfish	*Lepomis cyanellus*	32	78.0
Common carp	*Cyprinus carpio*	11	26.8
Western sites			
Common carp	*Cyprinus carpio*	29	58.0
Largemouth bass	*Micropterus salmoides*	16	32.0
Smallmouth bass	*Micropterus dolomieu*	14	28.0
Mosquitofish	*Gambusia affinis*	13	26.0
Brown trout	*Salmo trutta*	13	26.0
Bluegill	*Lepomis macrochirus*	11	22.0
Green sunfish	*Lepomis cyanellus*	11	22.0

to PRIN1_SE ($P = 0.828$), but was significantly positively related to PRIN2_SE ($P = 0.006$, $r^2 = 0.18$) and negatively related to PRIN3_SE ($P = 0.016$, $r^2 = -0.14$). Stream size normalized number of native fish species in the southeast was significantly positively related to PRIN1_SE ($P = 0.0003$, $r^2 = 0.29$) but was not significantly related to PRIN2_SE ($P = 0.110$) or to PRIN3_SE ($P = 0.154$).

In the western region, the first three principal components had Eigen values greater than one and together accounted for 64.6% of the variance in the environmental data (Table 6). The first principal component (PRIN1_WE) summarized a gradient of increasing total nitrogen, total phosphorous, water temperature, and dissolved organic carbon. The second principal component (PRIN2_WE) summarized a gradient of increasing pH and suspended sediment and decreasing runoff. The third principal component (PRIN3_WE) summarized sites characterized by high poorly drained and low moderately drained soils. Stream size normalized number of introduced fish species in the west was significantly positively related to PRIN1_WE ($P = 0.0004$, $r^2 = 0.24$) and negatively related to PRIN2_WE ($P = 0.0009$, $r^2 = -0.21$), but was not significantly related to PRIN3_WE ($P = 0.067$). Stream size normalized number of native fish species in the west was not significantly related to PRIN1_WE ($P = 0.593$) or PRIN2_WE ($P = 0.334$) but was significantly related to PRIN3_WE ($P = 0.0001$, $r^2 = 0.27$).

Table 3
Pearson product moment correlations between fish metrics for northeastern ($N = 66$), southeastern ($N = 41$), and western ($N = 50$) sites sampled during 1993–1995

Variable	Mean	I_FISH%	I_SPP	N_SPP	T_SPP	I_SPP%
Northeast						
I_FISH%	7.9	–				
I_SPP	2.4	**0.71**	–			
N_SPP	17.9	−0.31	−0.01	–		
T_SPP	20.3	−0.13	−0.23	**0.97**	–	
I_SPP%	12.1	**0.77**	**0.91**	−0.25	−0.04	–
Southeast						
I_FISH%	2.2	–				
I_SPP	1.1	**0.77**	–			
N_SPP	23.7	−0.07	0.13	–		
T_SPP	24.8	0.03	0.26	**0.99**	–	
I_SPP%	4.6	**0.79**	**0.97**	0.04	0.16	–
West						
I_FISH%	31.3	–				
I_SPP	4.2	**0.71**	–			
N_SPP	5.8	**−0.56**	−0.28	–		
T_SPP	10.0	0.20	**0.70**	**0.40**	–	
I_SPP%	37.8	**0.79**	**0.83**	−0.36	0.38	–

Significant correlations are in bold. Significance was determined based on the Bonferroni correction for multiple pair-wise comparisons and a P-value of less than 0.05. I_FISH%, percentage of introduced fish; I_SPP, number of introduced species; N_SPP, number of native species; T_SPP, total number of species; I_SPP%, percentage of introduced species.

Table 4
Principal components analysis loadings for environmental variables on the first three principal components from northeastern ($N = 66$) sites

Variable	PC1	PC2	PC3
Elevation (m)	–	−0.37	–
Runoff (cm)	−0.36	–	–
Population density (per km^2)	–	0.41	0.36
Percentage moderately drained soils	–	–	–
Percentage poorly drained soils	–	−0.40	0.40
Discharge (m^3/s)	–	–	–
Nitrogen, total (mg/l)	–	0.41	–
Phosphorus, total (mg/l)	–	–	–
Mean daily water temperature (°C)	–	–	–
Mean daily specific conductance (μS/cm)	–	–	0.59
Mean monthly dissolved oxygen concentration (mg/l)	–	–	–
Mean monthly pH	–	–	0.36
Mean monthly dissolved organic carbon (mg/l)	–	–	–
Mean monthly suspended sediment (mg/l)	0.41	–	–
% variances explained by component	32.9	19.4	10.5

Loadings less than \|0.35\| are indicated by (–).

Table 5
Principal components analysis loadings for environmental variables on the first three principal components from southeastern ($N = 41$) sites

Variable	PC1	PC2	PC3
Elevation (m)	0.36	–	–
Runoff (cm)	–	–	–
Population density (per km^2)	–	0.36	–
Percentage moderately drained soils	–	–	0.45
Percentage poorly drained soils	–	–	–
Discharge (m^3/s)	–	–	–
Nitrogen, total (mg/l)	–	–	–
Phosphorus, total (mg/l)	–	0.45	–
Mean daily water temperature (°C)	–	0.42	–
Mean daily specific conductance (μS/cm)	–	0.36	–
Mean monthly dissolved oxygen concentration (mg/l)	0.43	–	–
Mean monthly pH	0.43	–	–
Mean monthly dissolved organic carbon (mg/l)	−0.43	–	–
Mean monthly suspended sediment (mg/l)	–	–	–
% variance explained by component	29.5	19.0	15.2

Loadings less than \|0.35\| are indicated by (–).

Table 6
Principal components analysis loadings for environmental variables on the first three principal components from western ($N = 50$) sites

Variable	PC1	PC2	PC3
Elevation (m)	–	–	–
Runoff (cm)	–	−0.41	–
Population density (per km^2)	–	–	–
Percentage moderately drained soils	–	–	−0.58
Percentage poorly drained soils	–	–	0.41
Discharge (m^3/s)	–	–	–
Nitrogen, total (mg/l)	0.38	–	–
Phosphorus, total (mg/l)	0.36	–	–
Mean daily water temperature (°C)	0.37	–	–
Mean daily specific conductance (μS/cm)	–	–	–
Mean monthly dissolved oxygen concentration (mg/l)	–	–	–
Mean monthly pH	–	0.49	–
Mean monthly dissolved organic carbon (mg/l)	0.39	–	–
Mean monthly suspended sediment (mg/l)	–	0.35	–
% variance explained by component	31.9	20.4	12.3

Loadings less than |0.35| are indicated by (–).

4. Discussion

Based on the percentage of introduced fish species, the fish communities most altered by the presence of introduced fish occurred in the western and northeastern parts of the US. Similar patterns were noted by Rahel (2000). In the present study, more than half of the total fish species collected in the San Joaquin-Tulare Basin, Nevada Basin and Range, and Rio Grande Valley river basins were composed of introduced species. The percentage of introduced species ranged from 20 to 49% in other western river basins and river basins in the northeastern US. This pattern of alteration is largely a reflection of the relatively small number of native fish species in these areas compared to the southeast (McAllister et al., 1986).

Native fish species richness was not a broad-scale indicator of introduced fish species richness. Rathert et al. (1999) reported that Oregon native fish species richness and introduced species richness were positively correlated. Willams and Meffee (1998) indicated that successful introduced species tend to have certain characteristics that further their establishment, such as being habitat generalists and tolerant of a wide range of environmental conditions. Rathert et al. (1999) proposed that areas of relatively low species richness might favor survival of some introduced fishes and coexistence of introduced and native species, particularly in relatively benign environmental conditions. However, results of the present study indicate that native species richness was not related to introduced species richness for the northeastern, southeastern, or western parts of the US.

Introduced fish species richness was related to total fish species richness in the west. More than 50% of total fish species richness was accounted for by introduced species in three river basins in the west. Guido and Brown (1999), in a study of 125 watersheds across North America, reported that introduced fish species richness was often associated with increased total fish species richness. Introduced species are thought to contribute to the extinction of many native fish species (Miller et al., 1989) thereby reducing biodiversity. However, introduced fish species richness can contribute to an increase in total fish species richness at large scales. Baltz and Moyle (1993) noted that native California stream fishes can demonstrate an ability to resist invasion by introduced fishes under certain conditions. However, total species richness may also increase at large scales when the number of introduced species becoming naturalized is greater than the number of native species becoming extinct (Sax et al., 2002).

In the west, the percentage of introduced fish was negatively correlated with native fish species richness. Abundant introduced fishes may impact native fish species richness through competition, predation, and recruitment. In the desert southwest, characterized by low native fish richness and high endemism, native species such as pupfishes (*Cyprinodon* spp.) are directly threatened by abundant predaceous introduced fishes (Williams and Meffe, 1998). Predation of larvae and juveniles by introduced fishes has been suggested to impact recruitment of other native fish species in the southwest (Scoppettone, 1993; Marsh and Douglas, 1997). Baltz and Moyle (1993) noted that though native California stream fishes resist invasion through both environmental and biotic factors, a combination of competition and predation seem to be particularly important.

In the northeast, introduced fish species richness was related to factors including increased population density and increased total nitrogen. Whittier and Kincaid (1999) also noted that the intensity of human disturbance in watersheds in the northeastern US was positively associated with introduced fish species richness. The authors indicated that a number of factors including intentional stocking to meet angler preferences related to non-native centrarchids, distance from population centers, and road density contributed to patterns of introduced fish species richness in the northeast. Introduced species such as the common carp, abundant in the northeast, are reported to typically occur in streams enriched with sewage or with substantial runoff from agricultural land but rare or absent in clear, cold waters and high-gradient streams (Trautman, 1981).

In the southeast, the number of introduced fish species was related to factors including increased population density, total phosphorous, and water temperature. Scott and Helfman (2001) noted that land-disturbing activities in the southeastern US have resulted in the removal of riparian vegetation and promoted invasion by introduced fishes because of elevated stream temperatures. Scott and Helfman (2001) also noted that land-use disturbances in the southeast have led to a homogenization of stream habitats, which may contribute to the homogenization of fish faunas (Rahel, 2000).

In the west, introduced fish species richness was related to factors including increased total nitrogen and total phosphorous, and water temperature. Introduced species richness has been reported to be associated with anthropogenically-altered stream systems in the west (Moyle and Light, 1996; Hughes et al., 1998). In California, introduced fish abundance is reported to be a function largely of the ability to adapt to altered flow regimes (Brown and Moyle, 1997, Marchetti and Moyle, 2001, Brown and Ford, 2002). For example, the San Joaquin river system has been intensively converted to agricultural land use, with nearly all available flow substantially altered by dams, diversions, and irrigation return flows (Brown, 2000). As a result, agricultural land use in the San Joaquin river system is associated with altered flows, often containing high concentrations of nutrients and pesticides (Brown et al., 1999; Brown, 2000). Though examining the affects of flow alterations was beyond the scope of the present study, relations among watershed characteristics, stream water chemistry, and introduced species may be enhanced in the presence of an altered flow regime.

Although relations between introduced fish species and environmental factors varied among regions, introduced fish species richness was related in general to factors associated with disturbance at large geographic scales. Some relations between introduced fish species and environmental factors were common between regions. For example, increased introduced fish species richness was directly related to increased population density in the northeast and southeast; increased total nitrogen in the northeast and west; and increased total phosphorous and water temperature in the southeast and west. A nationwide study of nitrogen and phosphorous concentrations in streams concluded that human activities, including agricultural and urban uses of fertilizer, agricultural use of manure, and combustion of fossil fuels, have caused widespread increases in total nitrogen and total phosphorous in streams across the nation (USGS, 1999). The study suggested that concentrations of total nitrogen in streams were greatest in the northeast and west, compared to the southeast. Although the broad geographical pattern observed for total nitrogen appeared similar to that for total phosphorus, total phosphorus concentrations tended to be particularly high in the west (USGS, 1999).

Species patterns result from a hierarchy of natural and anthropogenic processes acting across multiple spatial scales. Levin (1992) explained how analytical scale and the observed patterns are related, emphasizing that a focus on large geographic scales often means a loss in detail but a gain in predictability. In the present study, regional patterns in relations between introduced fish species and watershed- and local-scale environmental conditions revealed that introduced fish species richness is associated with disturbance at large geographic scales across a wide range of streams in the US. These results support the use of introduced fish species richness as a broad-scale indicator of disturbed stream systems. However, local-scale processes determining introduced fish species success are undoubtedly complex. Byers (2002) argued that rapid anthropogenic alteration at a large scale alters spatial and temporal scales of competition and predation. Thus disturbance at large scales may enhance and accelerate invasion success through alteration of biotic factors at local scales.

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