

Patterns of fish invasions in the Great Plains of North America

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Abstract

A basic step toward controlling invasive species outbreaks is to predict which assemblages or habitats are most susceptible to invasion and effects of invading species on native communities. However, because predictive models may not work across a wide range of conditions it is important to examine processes associated with fish invasions across different regions. In this study, we use data from 949 sites in Oklahoma and Kansas to examine spatial patterns of species invasions in the Great Plains region of the US. Of these sites, 16 were intensively sampled between 1977 and 1994 and used to evaluate temporal patterns of species introductions. We found a trend of increasing introduced species richness without a decline in native species richness over 18 years. However, total abundance and community structure of native assemblages has changed at several of these sites during this time period. Because some of these changes occurred at sites with few or no introduced species, factors other than interactions with introduced fishes may have been responsible for this pattern. A stepwise multiple regression model that included human population size, native species richness, mean annual precipitation and drainage area explained 43% of the variation in the number of non-native species across all sites. Most introduced species in this region have native ranges within the Mississippi River basin and therefore are presumably adapted to regional environmental conditions. Great Plains streams have, to some extent, resisted invasion by introduced species; however, our analysis shows that proximity to dense human populations and importance to humans has largely structured species introductions and can partly explain spatial patterns of species invasions in this region.

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1. Introduction

Introduced species are a major threat to the earth's biota (Soule, 1990; Allan and Flecker, 1993; Lodge, 1993) and controlling species invasions is a priority for conservation of native assemblages (Mack et al., 2000). Although we are currently not able to accurately predict the results of individual invasions (but see Kolar and Lodge, 2002), the ability to demonstrate statistical patterns or probabilities of invasion success and subsequent effects on communities (e.g., Ross, 1991; Williamson and Fitter, 1996) should aid conservation and management decisions. Additionally, predictive models of species invasions (e.g., Li and Moyle, 1981) will help us

understand assembly rules of natural communities because most assemblages are the result of multiple invasions and extinctions over longer time periods (Vermeij, 1991; Lodge, 1993).

A long history of research on species invasions has led to a number of generalizations or predictions. Elton (1958) predicted lower invasion success in communities with greater species richness than in depauperate communities. Experiments manipulating native plant diversity provide some support for this prediction (e.g., Tilman, 1997; Symstad, 2000). However, there is growing evidence that invasibility of assemblages can be independent of native species richness (e.g., Levine and D'Antonio, 1999; Stohlgren et al., 1999; Levine, 2000).

Characteristics of invaders, suitability of the invaded ecosystem and modes of transportation are all important in determining success of introduced species. Successful fish invaders tend to tolerate a broad range of

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conditions, grow rapidly, and have a history of successful invasions (Moyle and Light, 1996a; Moyle and Light, 1996b; Kolar and Lodge, 2002). In addition, human disturbance is thought to predispose habitats to invasion and successful invaders tend to have some value to humans (Moyle, 1986; Lodge, 1993; Meador et al., 2003). These factors likely explain higher numbers of introduced species in heavily populated areas (e.g., McKinney, 2001).

Effects of species invasions are quite variable and range from catastrophic changes in assemblage structure (Kaufman, 1992) to subtle effects on food web interactions (Townsend, 1996). Moyle and Light (1996a) predicted that most species invasions should not have a large effect on an ecosystem, but they emphasized that predicting the magnitude of individual species impacts is difficult. By examining patterns of fish invasions and characteristics of invaders across a variety of habitats we can evaluate general processes associated with invasion success and determine the vulnerability of different systems to alien species.

Stream fish assemblages are ideal for testing patterns of invasions because they are often isolated in drainage basins separated by land or unfavorable conditions in mainstem rivers (Hocutt and Wiley, 1986; Angermeier and Winston, 1998; Matthews and Robison, 1998). Thus, individual sites can be used as independent observations because dispersal among drainages is unlikely, and many introduced species were established through human-assisted dispersal, particularly sport and bait fishes (e.g., Magnuson, 1976; Courtenay and Stauffer, 1984; Moyle, 1986). Streams, however, may have fewer introduced species than other aquatic habitats (lakes and reservoirs) because environmental conditions (e.g., flooding and drought) may repel species invasions more so than in reservoirs and lakes. Moyle and Light (1996b) suggested that streams with variable, but predictable annual discharge resist most alien fish invaders that are not adapted to those conditions.

Studies of fish invasions have largely focused on areas with high numbers of introduced fishes, such as California, the Great Lakes and Florida (Courtenay and Robins, 1973; Mills et al., 1993; Moyle and Light, 1996a; Moyle and Light, 1996b) or at the scale of entire continents (e.g., Ross, 1991; McKinney, 2001). Recently, Meador et al. (2003) found that some factors associated with the success of introduced species varied across regions within the US. In this study, we characterize patterns of fish invasions in the Great Plains, where there have been fewer species introductions and introduced species only comprise a small proportion of the overall assemblage diversity. Our data will help evaluate processes that regulate species invasions in regions where these species have not yet had a drastic effect or become overly abundant. Moreover, stream systems of the Great Plains have quite variable

environmental conditions and a less predictable hydrology. Our objectives were to: (1) describe spatial patterns of fish invasions in the Great Plains; (2) describe temporal patterns of fish invasions in Oklahoma across 18 years; and (3) contrast our finding with those from areas with higher abundance of introduced species. We predict the establishment of introduced species in Great Plains streams is limited by the harsh abiotic conditions and that species which are successful are tolerant of local conditions or occupy disturbed habitats.

2. Methods

2.1. Spatial patterns

Two large data sets were used to characterize spatial patterns of fish invasions in the Great Plains; collections from Oklahoma streams made by the Oklahoma Department of Environmental Quality (ODEQ) and collections from Kansas streams made by the Kansas Department of Wildlife and Parks (KDWP) (Fig. 1). The ODEQ collections included 163 sites, sampled between 1977 and 1994 using a standardized sampling effort for each collection. Twenty, 10 m seine hauls were taken at each site with a 3×1.5 m (4.7 mm mesh) heavy leaded seine. Collections were all made under the supervision of J. Pigg and effort was approximately one hour per site. Thus, we had both species abundance (number per 200 m of stream sampled) and incidence data. For analysis of spatial patterns, we only used data from the most recent year sampled for those sites that were visited multiple years. When more than one sample was taken at a site in the same year, abundance of each species was averaged for the year and incidence was

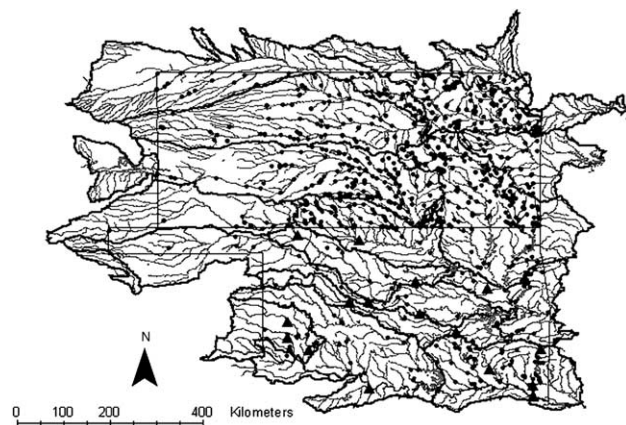


Fig. 1. Location of the 949 study sites in Kansas and Oklahoma streams. Triangles represent 16 sites sampled continuously between 1977 and 1994. Major drainage basins based on 4-digit US GS Hydrologic Unit Codes are outlined with bold lines. Three main river systems drain this region: Kansas/Missouri River, Arkansas River, and Red River.

determined if a species was present during any of the visits. Although species abundance may be quite variable between June and August due to spawning and recruitment, we felt an average of these samples would be most comparable with other sites that were only sampled once, typically during July. Specimens were preserved in 10% formalin and representative collections from 1992 to 1994 are archived at the Sam Noble Oklahoma Museum of Natural History.

Fish surveys in Kansas included 786 sites visited between 1995 and 2000 as part of the KDWP annual stream surveys. These surveys included 786 sample sites throughout the state. At each sample site, a reach that was 40 times the average wetted width of the stream channel (minimum 150 m and maximum 300 m) was sampled with a combination of straight and bag seines (4.7 mm mesh) and a DC-pulsed backpack electrofishing unit.

Collections made with seines and backpack electrofishing units as the sole sampling methods may be biased towards small-bodied fishes that occur near shore. Large-bodied fishes that occur in mid-channel habitats or that were able to avoid capture were likely underestimated in our sampling; however we did catch many juveniles of such species. Moreover, in some of the larger river sites, by sampling ≤ 300 m of shoreline, rare species that would have been caught with greater sampling effort may have been missed (e.g., Angermeier and Smogor, 1995). Thus our results reflect spatial and temporal patterns of relatively common, small-bodied fishes.

Determination of the status (introduced or native) of each species was based on published distributional maps (Cross, 1967; Miller and Robison, 1973; Lee et al., 1980; Page and Burr, 1991; Fuller et al., 1999). We classified fishes as: (1) *Exotic*, which were species introduced from outside North America (e.g., *Cyprinus carpio*), (2) *Regional non-natives*, which are species with native distributions in North America but introduced to Kansas or Oklahoma (e.g., *Morone americana*), and (3) *Drainage basin non-natives*, which are species native to some drainages within Kansas and Oklahoma but introduced to others (e.g., *Cyprinodon rubrofluvialis* and *Pimephales vigilax*).

Because factors that influence species invasions may operate at the scale of major watersheds, we also examined species invasions at the scale of 4-digit US Geological Survey Hydrologic Unit Codes (HUCs). The number of introduced species in each of these basins was determined by the cumulative number of introduced species across all sample sites in that basin.

2.2. Correlates with introduced species

Stepwise multiple regression ($P < 0.05$ for variable inclusion) was used to estimate which combination of

variables best predicted the observed number of introduced species at each site. This analysis was performed for both the total number of introduced species and the number of exotic species. Exotic species were separated because their evolutionary history on other continents may alter their response to environmental conditions relative to regional or drainage basin non-natives. However, because of the widespread occurrence of *C. carpio*, the analysis of exotic species is largely driven by incidence of this species. A number of variables were examined for correlations with the number of introduced species across the 949 sample sites. Because human disturbance is thought to favor introduced species, we used information from a continent-wide water-use survey by Solley et al. (1993) to characterize human disturbances at sites and watersheds. Solley et al. (1993) listed water-use parameters for subdrainages in the US that correspond to US Geological Survey 8-digit Hydrologic Unit Codes. From this survey, we chose six characteristics of subdrainages that we considered potential disturbances to fish assemblages: human population density (number/km²), total groundwater withdraws (m³/d), total surface water withdraws (m³/d), reservoir surface area (km² within a basin), and livestock water withdrawals (m³/d; as an index of grazing density). Several variables that may affect fish assemblages were excluded from the analysis because they were highly correlated with the variables listed above. Wastewater input (m³/d) was positively associated with population density ($r = 0.851$, $P < 0.001$) and irrigated land (km²) was associated with total groundwater withdraws ($r = 0.930$, $P < 0.001$). Two series of analyses were conducted; one at the scale of individual sites and one by major drainage basin. Because variables reported by Solley et al. (1993) were given for watersheds, we assigned values for sites based on the subdrainage in which the site occurred. For analyses at the scale of major drainage basins (4-digit HUCs), data from all subdrainages were averaged within a basin.

Because non-native fishes may spread into stream sites from reservoirs, we included proximity of sites to reservoirs as a potential predictor of introduced species richness. Minimum distance up and downstream to a reservoir was calculated as the watercourse distance to the nearest reservoir as measured on a 1:100,000 USGS map. To illustrate differences above and below reservoirs, we plotted the number of introduced species as a function of distance from a reservoir. We omitted sites that were not directly in line with a reservoir (i.e., unimpounded tributaries or main river sites that have unimpeded flow to the ocean), but calculated the mean number of introduced species at these sites as a comparison. Direction was not included in our regression analysis because the above results showed a similar pattern of introduced species occurrences up and downstream from reservoirs (regardless of distance).

Two climate variables were included in the model. Precipitation, which varies from west to east, was calculated using 12.7 cm/year isoclines (1961–1990, National Resource Conservation Service, Spatial Climate Analysis Service, Corvallis, Oregon) and latitude, which was used as an index of thermal regime. In addition, drainage area was calculated from 1:100,000 USGS maps.

Native species diversity was included in our regression models because they may reduce the success of introduced species through interspecific interactions (Elton, 1958). Because sampling gear and effort varied across sites and states, and there was significantly greater species richness in collections with greater numbers of individuals ($r^2 = 0.164$, $P < 0.001$), a rarefaction estimate of species richness (Gotelli and Entsminger, 2001) was calculated for each site. Rarefaction estimates are based on the random selection of a set number of individuals ($N = 100$ for this study), from a given collection and calculating the expected number of species if only that number of individuals was collected at all sites. Because rarified richness values can mask variation attributed to environmental conditions rather than sampling effort, we ran our statistical analyses with both actual and rarified data.

2.3. Temporal data

Trends in the numbers and abundance of introduced species were examined at the 16 sites in Oklahoma sampled annually between 1977 and 1994. Sample reaches were in approximately the same area, so depending on the stability of the stream channel, similar habitats were sampled during each visit. We contrasted changes in introduced species occurrence and abundance with those of native species to test the hypothesis that introduced species can have negative effects on native species. If introduced species have an adverse effect on native fishes we would expect an overall negative trend in the number and abundance of native species or changes in community composition across time that was coincident with an increase in the number and abundance of introduced species. We examined trends in abundance and species occurrences at each site and with all sites pooled using product–moment correlations. Abundance data were $\log(x + 1)$ transformed prior to analysis to better approximate normality. To evaluate potential changes in community structure of native fish assemblages, we calculated a dissimilarity matrix for assemblages among years using a chord distance coefficient (Orlóci, 1967). This metric was used because it normalizes abundances and places equal emphasis on rare and abundant taxa (Legendre and Legendre, 1998). The dissimilarity matrix of assemblage structure was compared to a matrix representing time differences among samples using a Mantel test (Mantel,

1967). A significant concordance among these two matrices indicates a directional change in assemblage structure across the 18 years. Mantel statistics and P -values, based on 1000 random permutations, were calculated in NTSYSpc ver 2.1. Alpha levels for analyzing temporal trends were subjected to a Bonferroni correction to decrease the chance of type I errors that would occur by calculating independent correlations for each of the 16 sites; we only present corrected P -values for these analysis.

3. Results

3.1. Spatial patterns

Stepwise regression models to predict the number of introduced species across the 949 sites included native species richness, precipitation, human population density and drainage area, regardless if actual or rarified native species richness values were used. Because the explained variance in total number of introduced species was only slightly different with the use of rarified or actual richness values (36% versus 43%, respectively) we only present data from models with actual native species richness (Table 1). A plot of the observed versus predicted values based on this model resulted in a wedge-shaped pattern (Fig. 2), suggesting that the selected variables may adequately predict sites with relatively high numbers of introduced species, but not areas with low numbers. A similar analysis using only exotic species was significant ($R^2 = 0.301$, $P < 0.001$), but included more variables and explained a smaller proportion of the variance across sites (Table 1). Livestock withdraws was the only variable included in a model to predict the number of introduced species in major drainage basins (4-digit HUCs) ($R^2 = 0.372$, $P = 0.009$), and had a positive association with the number of introduced species. None of the variables examined at the scale of major drainage basins could be used to significantly predict the number of exotic species.

A plot of native versus introduced species richness revealed a triangular pattern with the greatest number of introduced species occurring at sites with moderate to high native species richness (Fig. 3). Because sites with high native species richness occur in southeast Oklahoma, where precipitation is also greatest, this illustrates the interaction of these factors in our regression model.

The exclusion of proximity to reservoirs in our models that predicted total introduced species richness could have been due to a non-linear relationship between these factors, as there is a wider range in the number of introduced species near reservoirs relative to those far away (Fig. 4). Of the 428 sites that occurred directly above a reservoir, the mean number of intro-

Table 1

Results from stepwise multiple regression analyses of the effects of abiotic and biotic factors on the number of introduced species in Great Plains streams

Source	df	F-value	P-value	R ²	Variable	df	Standardized parameter estimate	t	P-value
<i>Total introduced species by site</i>									
Model	4	102.0	<0.001	0.431	Native richness	1	0.605	16.10	<0.001
Error	944				Precipitation	1	-0.423	-11.30	<0.001
Total	948				Drainage area	1	0.169	4.83	<0.001
					Population density	1	0.139	4.01	<0.001
<i>Exotic species by site</i>									
Model	6	39.9	<0.001	0.301	Ground water withdraws	1	0.304	6.37	<0.001
Error	942				Native richness	1	0.365	8.79	<0.001
Total	948				Precipitation	1	-0.176	-3.63	<0.001
					Drainage area	1	0.161	4.18	<0.001
					Livestock withdraws	1	-0.160	-3.76	<0.001
					Distance to reservoir	1	0.116	2.84	0.008
<i>Total introduced by HUC4</i>									
Model	1	8.89	0.009	0.372	Livestock withdraws	1	0.610	2.98	0.009
Error	15								
Total	16								

Dependent variables for these models are total number of species by site and 4-digit HUC, and number of exotic species by site. The model for number of exotic species by 4-digit HUC was not significant.

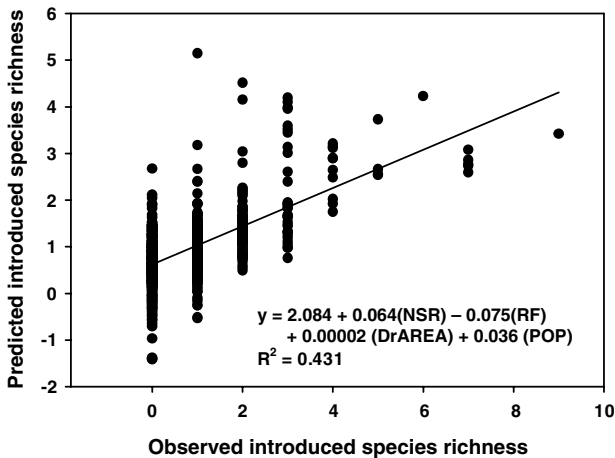


Fig. 2. A plot of the observed number of introduced species across the 949 sample sites (x-axis) and the predicted number of introduced species (y-axis) based on a stepwise multiple regression including native species richness (RNSR), human population size (HUMPOP), mean annual rainfall (RF), and drainage area (DrAREA).

duced species per site was 1.15 (±1.26 SD), versus a mean of 0.74 (±1.05 SD) for sites without a reservoir downstream. Similarly, of the 138 sites below reservoirs, the mean number of introduced species was 1.70 (±1.70 SD) versus 0.88 (±1.03 SD) for sites without a reservoir upstream.

3.2. Temporal patterns

When individual sites were examined for temporal trends in the number of introduced species, we found that one of the 16 sites had a significant (Bonferroni

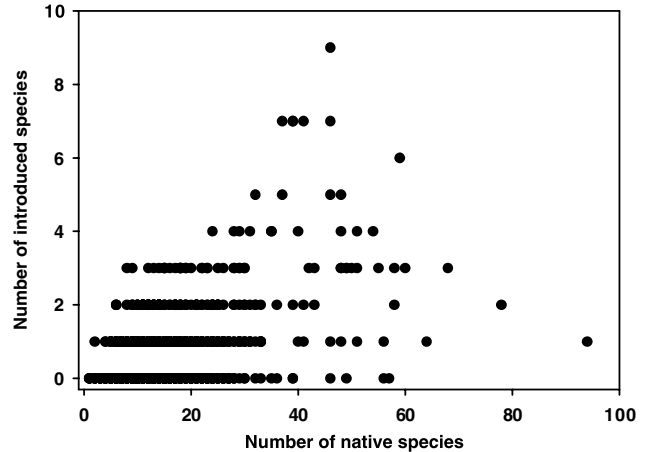


Fig. 3. Relationship between the number of introduced species and native species richness across the 949 sample sites.

adjusted $P < 0.05$) increase in the number of introduced species between 1977 and 1994 (Table 2). There was no significant relationship between native species richness and time at any of the sites. When the 16 sites were pooled for each year, there was a highly significant positive association ($r = 0.651$, $P = 0.003$) between mean number of introduced species and time (Fig. 5). On average, each site gained approximately 0.5 introduced species in the 18 years of this study. Mean native species richness showed no association with time ($r = 0.280$, $P = 0.260$). Thus, there has been a general trend of increasing total number of species at stream sites in Oklahoma.

Abundance and assemblage structure data yielded a different pattern. Introduced species abundances were

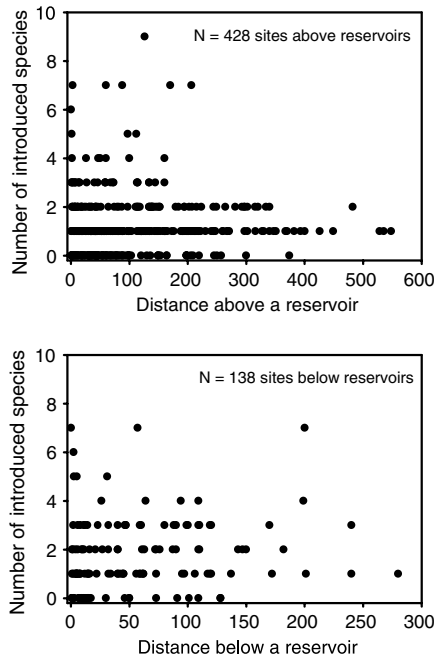


Fig. 4. Relationship between total number of introduced species and distance upstream (top) and downstream (bottom) from a reservoir. Only sites in which water flowed directly to or from a reservoir were used in these plots.

not associated with time at individual sites (Table 2) or with all sites combined ($r = 0.19$, $P = 0.443$). In contrast, native species abundance significantly declined in 4 of the 16 sites and overall showed a significant decline in

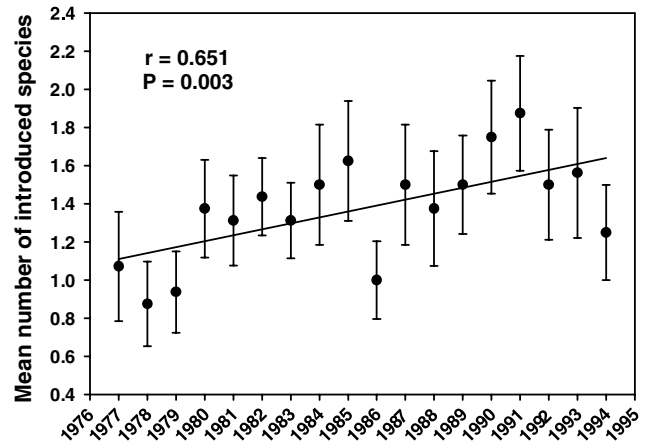


Fig. 5. Relationship between mean number of introduced species across 18 years of sampling 16 stream sites in Oklahoma between 1977 and 1994. Vertical bars represent one standard error.

abundance when all sites were pooled ($r = -0.69$, $P = 0.002$, Fig. 6). In addition, Mantel tests suggest that assemblage structure significantly changed over time at 2 of the 16 sites; neither of which showed a significant change in native species abundance.

Although we show a general decline in abundance of native fishes across all sites, data from individual sites suggest that factors other than introduced species were responsible for this pattern. Introduced species may be responsible for the decline in native species abundance at site 1, where four introduced species accounted for

Table 2

Pearson coefficients and Bonferroni corrected P -values (i.e., actual $P \times 16$, in parentheses) for correlations between time and the number and abundance of native and introduced species for the 16 intensively sample sites in Oklahoma

Site#	Number of native species	Number of introduced species (percent of total individuals)	Native species richness	Introduced species richness	Native species abundance	Introduced species abundance	Mantel statistic
1	32	4 (34.0)	0.082 (>0.50)	0.043 (>0.50)	-0.659 (0.048) ^a	0.243 (>0.50)	0.241 (0.208)
2	22	2 (55.1)	-0.183 (>0.50)	0.281 (>0.50)	0.144 (>0.50)	0.326 (>0.50)	0.164 (>0.50)
3	39	6 (61.3)	0.176 (>0.50)	0.113 (>0.50)	-0.355 (>0.50)	-0.369 (>0.50)	0.395 (0.003) ^a
4	46	4 (0.4)	0.015 (>0.50)	0.139 (>0.50)	-0.402 (>0.50)	0.152 (>0.50)	-0.066 (>0.50)
5	30	3 (1.0)	0.228 (>0.50)	0.720 (<0.001) ^a	-0.347 (>0.50)	-0.164 (>0.50)	0.243 (0.066)
6	48	2 (0.2)	0.324 (>0.50)	-0.043 (>0.50)	-0.469 (>0.50)	-0.131 (>0.50)	0.125 (>0.50)
7	32	4 (11)	0.012 (>0.50)	0.491 (>0.50)	-0.265 (>0.50)	0.565 (0.240)	0.312 (0.006) ^a
8	32	6 (7.1)	0.354 (>0.50)	-0.063 (>0.50)	-0.100 (>0.50)	-0.424 (>0.50)	0.065 (>0.50)
9	33	3 (2.3)	0.073 (>0.50)	0.370 (>0.50)	-0.285 (>0.50)	0.462 (>0.50)	-0.006 (>0.50)
10	27	1 (2.5)	0.365 (>0.50)	-0.244 (>0.50)	-0.165 (>0.50)	-0.500 (>0.50)	0.078 (>0.50)
11	38	2 (0.8)	0.601 (0.128)	0.209 (>0.50)	-0.246 (>0.50)	0.157 (>0.50)	-0.011 (>0.50)
12	47	5 (1.1)	0.261 (>0.50)	0.527 (>0.50)	-0.793 (0.002) ^a	0.209 (>0.50)	0.192 (>0.50)
13	48	0 (0)	0.088 (>0.50)	-	-0.389 (>0.50)	-	0.047 (>0.50)
14	57	1 (<0.1)	0.147 (>0.50)	-0.301 (>0.50)	-0.123 (>0.50)	-0.135 (>0.50)	-0.072 (>0.50)
15	85	3 (0.1)	0.212 (>0.50)	0.534 (0.384)	-0.658 (0.048) ^a	0.406 (>0.50)	0.178 (0.400)
16	91	0 (0)	-0.369 (>0.50)	-	-0.655 (0.016) ^a	-	0.015 (>0.50)
Means	44.2	2.9 (11.0)	0.280 (0.260)	0.651 (0.003) ^a	-0.690 (0.001) ^a	0.193 (0.442)	0.119

The last column presents Mantel statistics as an indication of the temporal autocorrelation between change in native assemblage structure and time; significant values indicate a directional change in assemblage structure across time.

^a Bonferroni adjusted $P < 0.05$.

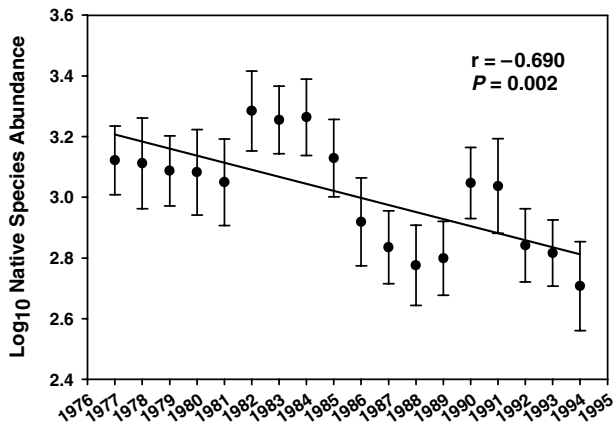


Fig. 6. Relationship between mean abundance of native species across 18 years of sampling 16 stream sites in Oklahoma between 1977 and 1994.

>34% of the total individuals captured at that site, but site 26 also had a significant decline in abundance of native species during this time period and no introduced species. Introduced species represented 61% and 11% of the total individuals captured at the two sites (sites 3 and 7) that showed a significant change in assemblage structure.

4. Discussion

4.1. Spatial patterns

Human population density was found to be a significant predictor of introduced species abundance across sample sites; sites with the highest numbers of introduced species occurred in watersheds with high population densities. Although habitat modification of streams (i.e., bridges, artificial riprap, impoundments, increased nutrient loads, etc.) may be associated with large population densities (Meador et al., 2003), there also may be a greater number of potential introductions (e.g., bait-bucket and sport fish) in highly populated areas. Thus, the greater number of introduced species at sites near densely populated areas may simply be caused by higher propagule pressure rather than habitat modifications that benefit invasive species. This pattern is consistent with a larger scale analysis by McKinney (2001), who reported a positive association of non-native fish diversity with increasing human population size across the contiguous 48 United States.

Other factors included in the stepwise analysis were native species richness, annual rainfall and drainage area. A combination of these factors can explain the triangular relationship between native and introduced species diversity, in which the highest numbers of introduced species occur at sites with intermediate native species diversity. In general, both native species and

introduced species richness was greatest in large rivers in southern watersheds, thus explaining the positive association between drainage area (i.e., a correlate with river size) and native richness. However, streams in the lower Red River basin had the highest native species diversity along with low numbers of introduced species. Because this area also received the most precipitation in the region, precipitation was negatively associated with introduced species richness in the regression model. Although it is impossible to determine causation from these associations, the reduced numbers of introduced species in south-eastern Oklahoma may simply be attributed to the greater number of sport and bait fishes that are native to this region, rather than the ability of native assemblages to resist invasion.

Surprisingly, distance to reservoirs only had a weak influence on numbers of introduced species in that it was only included in the model for exotic species, and was positively associated with exotic species richness, suggesting exotics were more common further away from reservoirs. In many streams, impoundments are considered disturbances favoring introduced species because they create additional habitats up- and downstream of the impoundments (Baxter, 1977; Moyle, 1986; Ligon et al., 1995). In addition, they are typically stocked with game or forage fishes that become quite abundant in these systems (e.g., Gido et al., 2000). Assuming most reservoirs have a higher number of introduced species than our stream sites, the lack of a strong association between distance to reservoirs and numbers of introduced species suggests a generally localized effect of reservoir introductions on stream fish assemblages. Although approximately 40% of our study sites were within 20 km of a reservoir, the majority of these sites did not seem to be markedly influenced by introduced reservoir fishes. Streams entering Lake Texoma on the Oklahoma-Texas border, which has a minimum of 9 introduced species (K. Gido, unpublished data), provides an example of this localized effect in that only four introduced species occurred at our intensively sampled site on the Red River near Gainesville, OK which is within 20 km of Lake Texoma. Moreover, Lienesch et al. (2000) found little introgression of reservoir fishes at sites on Buncombe Creek <10 kilometers from its confluence with Lake Texoma. Although proximity to reservoirs was not associated with increased numbers of introduced species richness in most sites, the range in total number of introduced species at sites within 200 km of a reservoir was greater than at sites further away (Fig. 4). This pattern of high variance in numbers of introduced species near reservoirs is likely attributed to differences in species introductions among reservoirs. Because even a single reservoir species may have a strong influence on stream fish assemblages, further examination of species composition and abundances at finer spatial and temporal scales may be

necessary to evaluate the zone of influence reservoirs have on persistence of introduced species in streams near reservoirs.

With the exception of the most species rich assemblages in the lower Red River, our data supported the prediction that all assemblages are invulnerable regardless of native species richness (Moyle and Light, 1996a). Thus, at the scale of our study native species diversity does not appear to limit the number of introduced species. However, there are two important considerations. First, it is likely the relationship between introduced and native species richness is non-linear or there is greater variation in the number of species at sites with few natives (e.g., a constraint envelope, Gido and Brown, 1999). For example, two sites, the upper Kiamichi (site 22) and Little rivers (site 26), both had no introduced species and high native species diversity (48 and 91 species, respectively). However, the Beaver River (site 9), in northwestern Oklahoma, had the lowest native species richness ($n = 20$) and only one introduced species. This example suggests that factors other than native diversity can limit the success of introduced species and these confounding factors may limit our ability to detect patterns of invasion using conventional statistics.

A second consideration is that we do not know if colonization opportunities were equal across sites. Although we might assume the available pool of colonists was greater for less speciose regions, there could be as many or more colonization attempts at species rich sites due to their close proximity to other speciose drainage basins (e.g., Little and Kiamichi rivers). Thus we might expect more interbasin transfer (i.e., drainage basin non-natives) in regions with high species richness, particularly through the baitfish trade which is thought to be responsible for the range expansions of many species (Litvak and Mandrak, 1999). Unfortunately, data on the number of colonization attempts are difficult or impossible to obtain.

Although our data show that reservoirs and water-use variables were only weakly associated with the success of introduced species, we only considered present disturbances (occurring after colonization). Moyle and Light (1996a,b) suggest that disturbances may be particularly important during the initial colonization phase on introduced species. Thus, if the disturbances that allowed fish invasions in Great Plains stream were transient our analysis would not have detected these effects. We did, however, find a positive association of groundwater withdraws and exotic species richness across sites and a positive association between livestock water withdraws and total introduced species richness at the scale of major drainages (4-digit HUCs). We do not suggest these factors as a direct mechanism, but landscape level processes that are associated with grazing and groundwater withdraws, such as geology and agri-

culture, may influence fish assemblage composition at larger spatial scales.

4.2. Temporal patterns

Temporal patterns of fish invasions at 16 intensively sampled sites in Oklahoma suggest an overall increase in numbers of introduced species between 1977 and 1994 without a decline in native species richness. This pattern suggests that fish communities in the Great Plains are not saturated with species (sensu Cornell and Lawton, 1992) and that fish assemblages can be invaded without a reciprocal loss of native species (Angermeier and Winston, 1998; Gido and Brown, 1999; Moyle and Light, 1996a). However, because extinction processes may occur over longer time periods than our study, we must use caution while interpreting these results and continue close monitoring of these systems to track trends in native species abundances.

Whereas native species diversity has not declined during our study period, there has been a decline in native species abundances and some changes in assemblage structure. Because effects of introduced species on native fishes may be subtle and mediated through lower trophic levels (e.g., Flecker and Townsend, 1994; Townsend, 1996), they may have only caused a shift in abundance of native species, rather than complete extirpation (e.g., Fisher Huckins et al., 2000). Our data does not provide unequivocal support to the general conclusion that introduced species affect native fish assemblages, because some of these changes occurred at sites with no introduced species. Moreover, because many introductions occurred prior to the initiation of this study in 1977, major effects of introduced species on native species may have occurred prior to our study and are underestimated with this data set.

5. General considerations

Previous studies have identified several characteristics that favor the successful invasion of fishes including: pre-adaptation to environmental conditions (e.g., hydrology), broad tolerance, invasion success in other regions, and value to humans (Moyle and Light, 1996a,b; Kolar and Lodge, 2002). Because we didn't have data on unsuccessful invasions, we could not evaluate favorable characteristics of species during the invasion process. However, we did have incidence and abundance data and could evaluate potential for success after colonization. *C. carpio* were by far the most widespread introduced species occurring at approximately half (473) of the sample sites (Table 3). Other introduced species only occurred at fewer than 6% (<45) of the 949 sample sites. With the exception of *C. carpio*, most of the common introduced species are likely the result of sport or bait

Table 3
List of introduced fish abundance and incidence collected across 949 sample sites in Oklahoma and Kansas

Species	Abundance (# per/sample)	Number of sites introduced	Status
<i>Cyprinus carpio</i> L.	13.3	473	E
<i>Lepomis macrochirus</i>	12.4	47	DBNN
<i>Micropterus salmoides</i>	6.8	44	DBNN
<i>Menidia beryllina</i> (Cope)	33.9	44	DBNN
<i>Gambusia affinis</i>	6.6	33	DBNN
<i>Morone chrysops</i>	6.3	34	DBNN
<i>Pomoxis nigromaculatus</i> (Lesueur)	3.6	29	DBNN
<i>Morone saxatilis</i> (Walbaum)	5.6	28	RNN
<i>Carassius auratus</i>	12.3	28	E
<i>Notropis bairdi</i> Hubbs and Ortenburger	8.8	28	DBNN
<i>Stizostedion vitreum</i>	2.4	24	DBNN
<i>Dorosoma petenense</i> (Gunther)	3.4	19	DBNN
<i>Pimephales vigilax</i>	12.1	19	DBNN
<i>Morone americana</i>	21.3	15	RNN
<i>Lepomis microlophus</i> (Gunther)	3.2	15	RNN
<i>Ambloplites rupestris</i>	4.1	11	DBNN
<i>Micropterus dolomieu</i>	7.8	10	DBNN
<i>Ctenopharyngodon idella</i>	1.4	8	E
<i>Micropterus punctulatus</i>	4.3	7	DBNN
<i>Scardinius erythrophthalmus</i>	1	6	E
<i>Cyprinodon rubrofluviatilis</i> Fowler	5.3	4	DBNN
<i>Oreochromis aurea</i> (Steindachner)	13.5	2	E
<i>Ictalurus furcatus</i>	1.5	2	DBNN
<i>Stizostedion canadensis</i>	1	1	DBNN
<i>Xiphophorus helleri</i>	1	1	E
<i>Perca flavescens</i>	1	1	RNN

Status indicates origin, E = exotic, RNN = regional non-native, and DBNN = drainage basin non-native.

fish introductions within the last 50–100 years. Sixteen of the 24 introduced species captured at the 949 sites were drainage basin non-natives and had native distributions within the spatial extent of this study. Thus, many of the introductions were from areas of high native species diversity (e.g., south-eastern regions) to those of low species diversity (e.g., northeastern regions). For example, the Kansas River basin has received several species native to the adjacent Arkansas River basin; most notably *P. vigilax* and *Gambusia affinis*. Whereas there has been a general pattern of species moving from southern to more northern drainages, some species invasions may have been limited because of cold temperatures. For example, introduced populations of *Dorosoma petenense* and *Menidia beryllina* are widespread and locally abundant in the Red and Arkansas River basins, but do not occur in the Kansas River basin. Because these species have been intentionally introduced throughout this region, it is likely they have been introduced in the Kansas River basin, but were unable to survive the cold winters.

With the exception of cold tolerance, the success of drainage basin non-natives in the Great Plains may be attributed to an evolutionary history in similar climatic conditions. For example, Brown and Moyle (1997) showed that Sacramento pikeminnow (*Ptychocheilus grandis*) and California roach (*Hesperoleucus symmetricus*), which have native distributions in California, were

able to persist in high abundance when introduced into the Eel River, California despite a highly variable and seasonal flow regime. In Virginia, Angermeier and Winston (1998) also suggested that low abundance of introduced species relative to natives was due to poor adaptation to local conditions. Although flows at our study sites are not as seasonal as in California (i.e., consistent spring run-off events), these streams are highly variable and can be quite stressful for many fishes (Matthews and Zimmerman, 1990; Matthews, 1998). Thus, the harsh abiotic conditions at many of these sites may limit the success of potential invaders to those adapted to conditions of the Great Plains.

6. Conclusions

Comparative studies that examine patterns across multiple regions provide an understanding of the complete array of processes that organize communities (Angermeier and Winston, 1998). In general, Great Plains streams appear to be gaining introduced species at a rate of about 0.5 species every 18 years and most of these fishes tend to be native to the Mississippi River basin with some value to humans as sport or bait fish. Similar to other correlative studies of species introductions, it is difficult to isolate causative factors influencing success of introduced species (Rejmánek, 2003), but

large rivers in watersheds with dense populations seems to be most vulnerable. Nevertheless, the overall low numbers of introduced species and weak association with proximity to reservoirs, suggests that Great Plains streams may have some capacity to resist species invasions.

Our results point to areas that need further investigation. For example, our data on species occurrences supports the prediction that species invasions have little effect on native species richness, but we also found either a decline in native species abundance or change in community structure at six sites and an overall trend of decreased abundance of natives between 1977 and 1994. Even though introduced species may have been responsible for these changes at 3 of those sites, the absence or low abundance of introduced species at other sites clearly shows that other factors are responsible for declines in native fish assemblages. More detailed investigations that include potentially interacting factors at finer spatial and temporal scales may increase our predictive ability regarding success of invaders or invasibility of assemblages. In particular, more data on failed invasions (e.g., Meffe, 1991) will greatly aid in refining these predictions.

The ability to predict the causes and consequences of species invasions is of global importance. It is equally important to test these predictions at a variety of spatial and temporal scales to assess their applicability across a broad range of habitats and geographic regions. Future studies that examine the relationship between biotic resistance and environmental variability will improve our ability to predict the patterns and consequences of species invasions in this region. Considering the cases in which introduced species have had drastic effects on local assemblages (e.g., zebra mussel, Stewart and Haynes (1994); Nile perch, Kaufman (1992)), we concur with Moyle and Light (1996a,b) that it is best to assume a worst case scenario until our predictive ability is improved to a point that is useful for ecosystem managers.

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