Long–term trends of native and non–native fish faunas in the American Southwest

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Olden, J. D. & Poff, N. L., 2005. Long–term trends of native and non–native fish faunas in the American Southwest. *Animal Biodiversity and Conservation*, 28.1: 75–89.

Abstract

Long–term trends of native and non–native fish faunas in the American Southwest.— Environmental degradation and the proliferation of non–native fish species threaten the endemic, and highly unique fish faunas of the American Southwest. The present study examines long–term trends (> 160 years) of fish species distributions in the Lower Colorado River Basin and identifies those native species (*n* = 28) exhibiting the greatest rates of decline and those non–native species (*n* = 48) exhibiting the highest rates of spread. Among the fastest expanding invaders in the basin are red shiner (*Cyprinella lutrensis*), fathead minnow (*Pimephales promelas*), green sunfish (*Lepomis cyanellus*), largemouth bass (*Micropterus salmoides*), western mosquitofish (*Gambussia affinis*) and channel catfish (*Ictalurus punctatus*); species considered to be the most invasive in terms of their negative impacts on native fish communities. Interestingly, non–native species that have been recently introduced (1950+) have generally spread at substantially lower rates as compared to species introduced prior to this time (especially from 1920 to 1950), likely reflecting reductions in human–aided spread of species. We found general agreement between patterns of species decline and extant distribution sizes and official listing status under the U.S. Endangered Species Act. "Endangered" species have generally experienced greater declines and have smaller present–day distributions compared to "threatened" species, which in turn have shown greater declines and smaller distributions than those species not currently listed. A number of notable exceptions did exist, however, and these may provide critical information to help guide the future listing of species (i.e., identification of candidates) and the upgrading or downgrading of current listed species that are endemic to the Lower Colorado River Basin. The strong correlation between probability estimates of local extirpation and patterns of native species decline and present–day distributions suggest a possible proactive conservation strategy of implementing management actions for declining species prior to extreme rarity and imperilment.

Key words: Lower Colorado River, Desert fishes, Extinction, Extirpation, Invasions, Biotic homogenization.

Resumen

Tendencias a largo plazo de la fauna piscícola autóctona y alóctona en el sudoeste americano.— La degradación ambiental y la proliferación de especies de peces alóctonas amenazan la fauna endémica, y única, de peces del sudoeste americano. El presente estudio examina las tendencias a largo plazo (> 160 años) de las distribución de especies de peces en la cuenca inferior del río Colorado e identifica las especies autóctonas (*n* = 28) que exhiben los índices más altos de disminución y las especies alóctonas (*n* = 48) que muestran los índices más altos de dispersión. Entre los invasores de la cuenca que se dispersan más rápido encontramos la carpa roja (*Cyprinella lutrensis*), la carpita cabezona (*Pimephales promelas*), el pez sol (*Lepomis cyanellus*), la perca americana (*Micropterus salmoides*), la gambusia (*Gambussia affinis*) y el pez gato (*Ictalurus punctatus*), especies consideradas las más invasivas por su impacto negativo en las comunidades autóctonas de peces. Las especies alóctonas introducidas recientemente (1950+), en general se han dispersado en tasas substancialmente más bajas que las introducidas con anterioridad (especialmente desde 1920 a 1950), probablemente reflejando una reducción en la dispersión de especies relacionada con el hombre. Encontramos concordancias entre los patrones de disminución de las especies y el tamaño de la zona de distribución existente, y el estatus en

ISSN: 1578–665X

las listas oficiales del Acta de Especies Amenazadas de EE.UU. Las especies "en peligro de extinción", en general, han disminuido más y presentan una área de distribución menor que las especies "amenazadas", que a su vez muestran mayor disminución y menor área de distribución que las especies no incluidas en la lista. Hay, sin embargo, un número de excepciones notable, que pueden proporcionar información crítica para la confección de futuras listas de especies (es decir, identificando candidatos), y para el cambio de estatus de las especies endémicas en la cuenca inferior del río Colorado. La gran correlación entre la probabilidad estimada de extirpación local, y los patrones de disminución de las especies autóctonas y las distribuciones existentes sugieren una estrategia activa de conservación para implementar acciones de control de las especies en disminución antes de que lleguen a ser extremadamente escasas y amenazadas.

Palabras claves: Cuenca inferior del río Colorado, Peces del desierto, Extinción, Extirpation, Invasiones, Homogeneización biótica.

(Received: 22 IV 04; Conditional acceptance: 23 VI 04; Final acceptance: 23 VIII 04)

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Introduction

"The Colorado [River], along the greater part of its lonely and majestic way, shall be forever unvisited and undisturbed."

Lieutenant Joseph C. Ives (1857)

Undeterred by legends of earlier expeditions that had failed, in 1868 John Wesley Powell was successful in his first historic journey down the treacherous Colorado River. Shortly thereafter, he stated his strong belief that, although considerably remote, the western resources were meant to be "redeemed" from a state of idleness for societal use (deBuys, 2001). During the next 130 years Powell's vision was realized, and the waters of the Colorado River played a pivotal role in the settlement, growth and economic development of the American Southwest (Carlson & Muth, 1989). Efforts to tame the Colorado River began soon after the arrival of western Europeans, and today hundreds of dams and diversion structures have created one of the most controlled rivers on Earth (Fradkin, 1981). The Colorado River now provides irrigation water for more than 3.7 million acres (1.5 hectares) of farmland and delivers water and electrical power to 30 million people in the United States and Mexico (Mueller & Marsh, 2002).

The Colorado River ecosystem has been greatly changed during the last century both by environmental alterations and by the introduction and spread of non–native fish species. The construction of water development projects began in the early 1900s (Fradkin, 1981; Carlson & Muth, 1989), and by the 1960s much of the mainstem river had been converted into a system of dams and diversions. Such changes continue to compromise the efficiency of life–history adaptations that have evolved to allow native fishes to thrive in the historically harsh, fluctuating environment of the Colorado River Basin (Miller, 1961; Minckley & Deacon, 1968, 1991). These dramatic environmental alterations have also facilitated the widespread and human–assisted invasion of non–native fish species that prey on and compete with native fishes (Minckley, 1991; Douglas et al., 1994; Marsh & Douglas, 1997; Marsh & Pacey, 2003).

The case for conservation for the Lower Colorado River Basin is most urgent as the distributions of native fish species continue to decline at unprecedented rates and the spread of non–native fishes accelerate at an unparalleled speed (Minckley et al., 2003). Of the 31 native fish species in the Lower Colorado Basin, 25 are extinct, extirpated, listed under the US Endangered Species Act (USFWS, 1999), or believed to have suffered significant declines in distribution (Minckley, 1991). Remnant native populations are highly fragmented, compounding the problem of recovery and further elevating the probability of extinction (Fagan et al., 2002). In contrast, the deliberate introduction of non–indigenous fishes in the Lower Colorado River Basin began in the late 1800s (Minckley, 1999) and today more than 90 species have been introduced, over half of which are considered established (Rinne & Janisch, 1995). Long–term conservation and management strategies for the Lower Colorado River Basin require knowledge about rates of change in the distribution of native and non–native species over time. Such strategies should be based on the analysis of large–scale, long–term datasets, which when combined with small–scale experimental studies, will provide complementary approaches to better understanding distributional shifts of native and non–native species and their association with altered environmental regimes. Broad–scale studies provide the foundation for proactive conservation by identifying native species declines prior to extreme rarity so that management efforts can be implemented before imperilment (Anderson et al., 1995; Patton et al., 1998).

To date, evidence for the widespread replacement of native fish communities by non–native species in the Lower Colorado River Basin has been largely anecdotal and has lacked rigourous quantification. This is not to say that species' distributions have not, and are not continuing to change. Rather the extent to which species' distributions have decreased or increased over time has only been investigated for a limited number of species (mainly mainstem "big–river" species) and therefore remains largely unknown (and not quantified) for the majority of the species pool. We address this research need by presenting a historical perspective on long–term trends of native and non–native freshwater fish species distributions in the Lower Colorado River Basin using an unparalleled dataset containing tens of thousands of records collected over a century and a half. By conducting a broad, spatio–temporal assessment of changes in patterns of species' occurrences, we shed important insight into rates of native species decline and non–native species expansion for the entire, present–day species pool of Lower Colorado River Basin. We address the question of whether long–term distribution trends can act as a surrogate for local extirpation risk of native species and "test" the biological component of the United States Endangered Species Act by comparing these trends to species' official status. This comparison may help address the question of whether governmental legislation is, in fact, helping identity (and conserve) those rare, endemic species that have experienced substantial declines in their distributions and are currently rare in the Lower Colorado River.

Material and methods

The Colorado River is the primary waterway and lifeline of the American Southwest. Our study focused on the lower basin of the Colorado River (hereafter called Lower CR Basin), which includes ca. 26,000 km of streams and rivers between Glen Canyon Dam (located at the border between Arizona and Utah, U.S.A.) and the Gulf of California, and drains ca. 362,750 km^2 from five states of the

United States and northwestern Mexico (fig. 1). To examine long–term temporal trends in native and non–native freshwater fish faunas we used the SONFISHES database (Desert Fishes Council, http://www.desertfishes.org/na/gis/index.html). This database was developed by the tireless efforts of the late ichthyologist W. L. Minckley and contains > 38,000 occurrence records for 132 freshwater fish species from over 150 years of research throughout the Lower CR Basin. SONFISHES contains incidence, identity, and collection data for the complete holdings of major regional museum collections, numerous smaller holdings, and records from peer–reviewed and gray literature sources. Records are geo–referenced to within 1 km of their collecting site in a Geographic Information System (see Unmack, 2002 for details).

Using ArcGIS (Environmental Services Research Inc., v. 8.3) we plotted 28,755 locality records from 1840 to 2000 (excluding occurrence records resulting from artificial translocations and reintroductions) for 28 native species and 48 non–native species from the SONFISHES database onto a digital coverage of streams and rivers in the Lower CR Basin (U.S. Geological Survey Enhanced River Reach File 2.0: http://www.usgs.gov/). We summarized the dataset in several ways to address the objectives of the study. Based on the large size and high temporal frequency of locality records in the dataset (see table 1) we were able to examine species patterns for 5 time periods: pre–1960; 1960–69; 1970–79; 1980–89; and 1990–1999. Following Fagan et al. (2002), historical locality records for native species were considered to be those collected prior to 1980, whereas modern (or extant) native records were collected between 1980 and 1999. For native species, historical presences and extant absences constitute true extirpation events because modern records in the dataset are almost exclusively the result of intensive efforts by federal or state agencies to determine species' complete distributions prior to listing decisions under the U.S. or Mexican Endangered Species Acts (Fagan et al., 2002).

For each time period, we calculated the total river kilometres that each species was present by summing the length of the river segments (defined as a section of river delineated by two confluences) in which the species was recorded. Importantly, if a species was collected multiple times in the same river segment in the same time period, the length of the river segment was counted only once when calculating total river kilometres. Species' distributions were estimated by dividing the total river kilometres that a species was present by the total river kilometres where all species were present during the specified time period (see table 1). This approach attempts to account for the influence of differential sampling effort (assumed to be proportional to the number of records) through time. Distributions were represented as a percentage and are assumed to provide an approximation for the total size of the species distribution in the entire Lower CR Basin.

For native species, distributional changes were calculated by subtracting extant range size (1980–1999) from historical range size (pre–1980) and dividing by historical range size. Regression analyses with curve estimation (SPSS, v.11) were conducted to assess relationships between extant distribution size (%), percent distributional change and the estimated probability of local extirpation (as given for 25 species in table 1 of Fagan et al., 2002). Pairwise *t*–tests were used to compare distributional change and extant distributions between species with different official statuses under the U.S. Endangered Species Act (data obtained from the United States Fish and Wildlife Service: Threatened and Endangered Species System, http://endangered.fws.gov, as of July 2004). For non–native species, dates of introduction were estimated using both table 6 of Mueller & Marsh (2002) and year of first occurrence in the SONFISHES database. Extant distributions were divided by the number of years since introduction (calculated from 2000) to estimate the rate of non–native species spread in the basin ($km \cdot year^{-1}$). Regression analyses were conducted to assess relationships between date of introduction, extant distribution size, and rate of spread for each species.

Results

Temporal patterns of native fish distributions

Over the past century and a half, native fishes have predominantly decreased in their spatial distributions throughout the Lower CR Basin. Native fish species typically showed dramatic declines in the size of their distributions; a trend, however, that varied among species from 100% range reduction to 14% range expansion (table 2). In total, the distribution of 23 species decreased and 5 species slightly increased. Distribution trends over time illustrate that species have exhibited differential patterns of change. Gila trout, Virgin River spinedace and Gila topminnow, for example, have shown gradual reductions in their distribution, whereas Colorado pikeminnow, bonytail, razorback sucker, spikedace and Gila chub (among others) have shown punctuated declines. Other species appear to be occupying relatively constant ranges in the basin, including roundtail chub, bluehead sucker and Sonora sucker. Extant native fishes range from being completely absent (i.e., 0%) to occupying an estimated two–fifths of the basin (table 2). According to our results using modern locality records, five species have been extirpated (only Santa Cruz pupfish is truly extinct) and 15 species currently occupy extremely small distributions in the basin (< 5%), whereas other species still exhibit relatively broad distributions (> ca. 30%), e.g., specked dace, longfin dace, desert sucker and Sonora sucker.

With respect to identifying those species that warrant special concern and targeted conservation efforts, it is necessary to examine associations

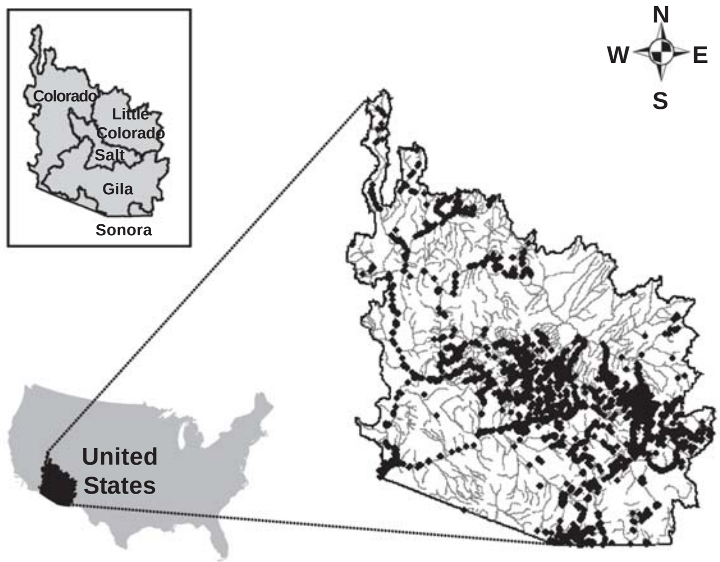

Fig. 1. Map of the Lower Colorado River Basin showing the 28,755 locality records from the SONFISHES database used in this study. Inset shows locations of major river drainages.

Fig. 1. Mapa de la cuenca inferior del río Colorado mostrando los 28.755 registros de localidades de la base de datos SONFISHES utilizada en este estudio. El recuadro muestra la situación de los principales drenajes del río.

between the probability of local extirpation and broad–scale temporal trends in their distributions. We obtained estimates of local extirpation for 25 native species from table 1 of Fagan et al. (2002), who calculated these probabilities using the SONFISHES database as the proportion of historic records at a 5–km reach scale having no modern records (e.g., if an extinct species was present in 50 of 1000 pre–1980 records, its extinction probability would be 0.95). We found a significant positive and linear relationship between percent distributional decline and the probability of extirpation ($R^2 = 0.807$, $P < 0.001$), indicating that native species exhibiting greater declines in their distributions at the whole basin scale also have a greater risk of local extirpation (fig. 2A). By examining deviations from this relationship we see that humpback chub (code X) and Virgin River spinedace (L), for example, have a higher estimated local extirpation risk compared to what is expected according to their basin–level decline over time (large positive residual). In contrast, desert pupfish (B), spikedace (N), loach minnow (R) and desert sucker (U) have a much lower extirpation risk as predicted from their level of distributional decline (large negative residual). Additionally, we found a significant negative and non–linear relationship between extant distribution size and the probability of local extirpation ($R^2 = 0.571$, $P < 0.001$, quadratic curve), indicating that species with smaller present–day distributions have a greater estimated risk of local extirpation (fig. 2B). Species such as roundtail chub (V) and

Table 1. Diagnostic properties of the SONFISHES database used in this study. Reported fields include the number of locality records (i.e., fish observations) and total river kilometres during different time periods (T): N. Native; nN. Non–native; TRkm. Total river kilometres where all species were observed.

Tabla 1. Propiedades de diagnóstico de la base de datos SONFISHES utilizada en este estudio. Los campos que se presentan incluyen el número de registros de localidad (observaciones de peces) y el total de kilómetros de río a lo largo de distintos períodos de tiempo (T): N. Autóctonos; nN. Alóctonos; TRkm. Kilómetros totales de río donde se observaron todas las especies.

	Records		
T	N	nN	TRkm
Pre–1960	1,463	462	6,496
1960–1969	3,106	1,671	6,875
1970–1979	2,772	1,400	7,839
1980–1989	3,033	4,125	7,918
1990–1999	5,389	5,334	6,491
Total	15,763	12,992	14,380

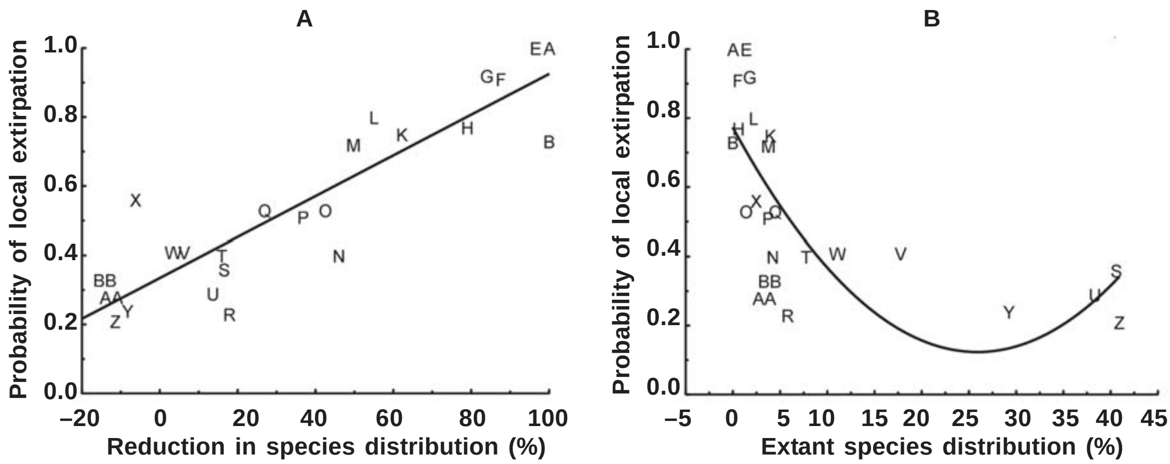

Fig. 2. Comparisons of percentages of distributional decline (A), extant distribution size (B) and probability of local extirpation of native fishes in the Lower Colorado River Basin. Least–squares regression lines are represented. Letter codes refer to native species in table 2.

Fig. 2. Comparaciones entre porcentajes de disminución distribucional (A), tamaño de la distribución existente (B) y probabilidad de extirpación local de peces autóctonos en la cuenca inferior del río Colorado. Se representan las líneas de regresión de mínimos cuadrados. Los códigos de letras se refieren a las especies autóctonas de la tabla 2.

Sonora sucker (Y) have greater probability of extirpation than that expected from their present distributions in the basin, whereas the local extirpation probabilities of loach minnow (R), headwater chub (AA) and Little Colorado spinedace (BB) are much lower than is suggested from their current distributions. Visual examination of this figure suggests a threshold relationship where species with extant distributions greater than 10% are at much lower risk to local extirpation (probability < 0.5) compared to those species will extremely small distributions.

Comparisons of species distributional change and extant distribution size with categories of official status under the U.S. Endangered Species Act (provided in table 2) also revealed interesting findings (fig. 3). With increasing risk category (i.e., not listed–threatened–endangered), we found average distributional decline to become larger and extant distribution size to become markedly smaller. Endangered species exhibit significantly greater distributional declines compared to threatened species ($t_{1,15}$ = 2.93, P = 0.01) and to those species not listed ($t_{1,20}$ = 4.33, P < 0.001). Similarly, endangered species exhibit significantly smaller extant distributions compared to threatened species ($t_{1,15}$ = –4.78, P < 0.001) and to those species not listed ($t_{1,20}$ = –4.30, P < 0.001). Extant distributions of threatened species were marginally smaller than species not listed ($t_{1,11}$ = –1.90, P = 0.08), although the rate of distributional decline did not differ.

For illustrative purposes figure 4 shows historical and extant distributions of three native species that exhibit markedly different % decline over time and have different ESA statuses – bonytail (Endangered, 87.5% decline), spikedace (Threatened, 45.9% decline) and specked dace (Not Listed, 16.5% decline). Historical populations of bonytail in the Salt River, Gila River and mainstem Colorado River have been lost, and present–day distributions are restricted to Lake Mohave above Davis Dam. Spikedace populations were once present in the rivers Salt, Verde, Gila and San Pedro, but are now confined to only small stretches of the Gila River and Verde River. Specked dace was historically abundant and continuous throughout the basin, but its present–day distribution is greatly reduced and highly fragmented (e.g., Virgin River).

Temporal patterns of non–native fish distributions

In contrast to native fishes, the majority of non–native fishes showed substantial increases in the size of their distributions over time (table 3). At the extreme, fathead minnow, green sunfish and red shiner exhibit the greatest rates of invasion, spreading at over 50 km·year^{-1} since their dates of introduction. As expected, we found a strong, positive relationship between the rate of spread and extant distribution size (R^2 = 0.874, P < 0.001), indicating that fast spreading non–native species are generally more broadly distributed in the basin (fig. 5A). A number of non–native species are much more broadly distributed in the basin as what is expected based their rate of spread, e.g., channel catfish (code 8), yellow bullhead (10) and common carp (11) (all introduced prior to 1900). In contrast, the

Table 2. Temporal patterns of native fish distributions in the Lower Colorado River Basin expressed as a percentage of the total kilometres of rivers where all species were observed for each time period. Nomenclature follows Nelson et al. (2004): C. Code, labels in figure 2; S. Species' official federal status under the U.S. Endangered Species Act (X. Extinct; E. Endangered; T. Threatened; PE. Proposed for listing as endangered; and no status means it is a species not listed); ER. Extant range, species distribution percentaje based on 1981–1999 records; and D. Decline, percent change in species' distribution. Note that *P. lucius*, *C. macularius*, *M. coriacea* and *G. robusta jordani* are not extinct from the lower basin, but are estimated as exhibiting a 100% decline because the database does not contain recent records of their occurrence.

Tabla 2. Patrones temporales de distribución de peces autóctonos en la cuenca inferior del río Colorado, expresadas en porcentajes del total de kilómetros de río donde se observaron todas las especies durante cada periodo de tiempo. La nomenclatura es según Nelson et al. (2004): C. Código, letras en la figura 2; S. Estatus federal oficial según el Acta de Especies Amenazadas de EE.UU. (X. Extinguida; E. En peligro de extinción; T. Amenazada; PE. Propuesta para que conste como especie en peligro; si no hay estatus la especie no se encuentra en la lista); ER. Rango existente en porcentaje de distribución de las especies basada en registros entre 1981–1999; D. Disminución, cambio de porcentaje en la distribución de las especies. Nótese que P. lucius, C. macularius, M. coriacea *and* G. robusta jordani *no están extinguidos en la cuenca inferior del río, pero se estima que presentan una disminución del 100% debido a que la base de datos no contiene registros recientes de su presencia.*

			Temporal trends						
Species	C	S	<1960	1960s	1970s	1980s	1990s	ER	D
Colorado pikeminnow (*Ptychocheilus lucius*)	A	E	4.4	0.0	0.0	0.0	0.0	0.0	100.0
Desert pupfish (*Cyprinodon macularius*)	B	E	3.2	0.0	0.0	0.0	0.0	0.0	100.0
Moapa dace (*Moapa coriacea*)	C	E	1.0	0.9	0.0	0.0	0.0	0.0	100.0
Pahranagat roundtail chub (*Gila robusta jordani*)	D	E	1.2	1.1	1.0	0.0	0.0	0.0	100.0
Santa Cruz pupfish (*Cyprinodon arcuatus*)	E	X	0.7	0.7	0.0	0.0	0.0	0.0	100.0
Bonytail (*Gila elegans*)	F	E	8.1	2.4	2.0	0.6	0.8	0.5	87.7
Gila trout (*Oncorhynchus gilae gilae*)	G	E	1.9	2.0	1.7	0.4	0.0	0.3	84.0
Woundfin (*Plagopterus argentissimus*)	H	E	3.5	2.0	0.8	0.5	0.2	0.6	78.9
White River spinedace (*Lepidomeda albivallis*)	I	E	4.2	1.9	0.0	0.7	0.0	0.6	74.3
White River springfish (*Crenichthys baileyi*)	J	E	5.5	6.1	0.0	1.2	0.0	1.0	71.1
Flannelmouth sucker (*Catostomus latipinnis*)	K		5.5	7.3	11.0	4.0	1.1	4.0	62.2
Virgin River spinedace (*Lepidomeda mollispinis*)	L		4.9	5.0	5.9	2.2	1.4	2.2	55.1
Razorback sucker (*Xyrauchen texanus*)	M	E	11.9	2.4	4.0	3.5	2.9	3.7	49.7
Spikedace (*Meda fulgida*)	N	T	12.9	2.8	4.5	3.4	4.9	4.2	45.9
Virgin River roundtail chub (*Gila seminuda*)	O	E	2.6	2.8	1.0	0.7	1.6	1.4	42.5
Gila topminnow (*Poeciliopsis occidentalis*)	P	E	8.3	2.5	1.7	3.6	3.9	3.7	36.8
Apache trout (*Oncorhynchus gilae apache*)	Q	T	4.0	6.1	5.7	2.1	4.6	4.5	26.9
Loach minnow (*Rhinichthys cobitis*)	R	T	9.8	3.8	7.0	5.3	6.8	5.8	17.9
Speckled dace (*Rhinichthys osculus*)	S		52.8	50.3	42.6	32.2	40.6	40.6	16.5
Gila chub (*Gila intermedia*)	T	PE	14.0	4.0	4.6	6.2	10.4	7.7	15.9
Desert sucker (*Catostomus clarkii*)	U		45.4	43.6	39.8	40.4	37.0	38.3	13.5
Roundtail chub (*Gila robusta*)	V		18.4	16.2	12.9	16.6	15.6	17.7	6.2
Bluehead sucker (*Catostomus discobolus*)	W		5.6	7.9	13.2	6.0	13.0	11.1	3.5
Humpback chub (*Gila cypha*)	X	E	0.6	1.5	3.0	3.0	1.4	2.5	–6.1
Sonora sucker (*Catostomus insignis*)	Y		25.9	28.5	25.4	28.5	29.5	29.3	–8.2
Longfin dace (*Agosia chrysogaster*)	Z		34.9	28.1	33.5	45.4	46.2	40.9	–11.4
Headwater chub (*Gila nigra*)	AA		3.1	2.2	1.9	2.3	2.3	2.3	–12.6
Little Colorado spinedace (*Lepidomeda vittata*)	BB	T	1.5	3.0	1.4	3.0	3.9	3.6	–14.1

two latest invaders to the basin, blue tilapia (9) and flathead catfish (6), were found to have very fast rates of spread, although they are still limited in their distribution due to their short invasion history.

Although we expected the positive relationship in figure 5A because extant distribution size was used to calculate spread, the unexplained variation in this relationship can be attributed, in part, to the lack of a significant negative relationship between the year of introduction and rate of spread ($R^2 = 0.051$, $P = 0.124$) (fig. 5B). Interestingly, we found a significant negative relationship between year of introduction and extant distribution size ($R^2 = 0.243$, $P < 0.001$) (fig. 5C). Visual examination of this figure suggests a threshold relationship where non–native species introduced after 1950 have limited distributions (< 10%) whereas species will longer invasion histories in the basin have a broad range of distribution sizes (10–45%). Further, a number of species deviate from this relationship, indicating that species with long invasion histories do not necessarily have large extant distributions in the basin, e.g., yellow bass (35), white crappie (36), brown bullhead (42). Of note is that the top 5 fastest spreading non–native species (species 1–5 in table 3) were all introduced between 1920 and 1950 (fig. 5B) and have much greater present–day distributions than expected based on their length of invasion history (fig. 5C).

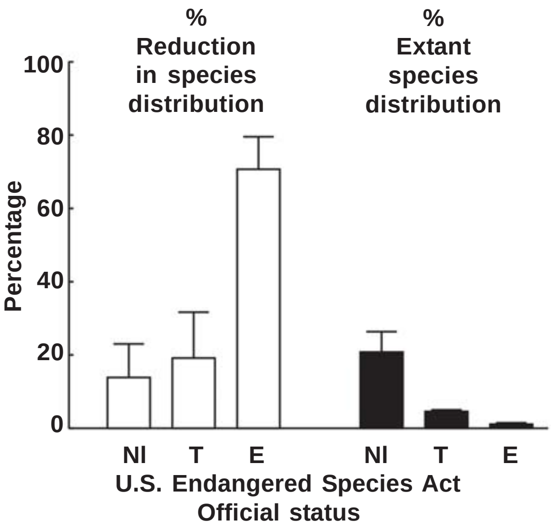

Fig. 3. Comparisons of percentages of distributional decline and extant distribution size of native species classified as classified under the U.S. Endangered Species Act: NI. Not listed; T. Threatened; E. Endangered. (Bars represent means and whiskers represent 1 standard error.)

Fig. 3. Comparaciones entre los porcentajes de disminución y de tamaño de la distribución existente de peces autóctonos clasificados según el Acta de Especies en peligro de Extinción de EE.UU.: NI. No están en la lista; T. Amenazadas; E. En peligro. (Las barras representan las medias y las prolongaciones representan un error estándar igual a 1.)

Discussion

Distributions of native and non–native fishes have changed dramatically over the past century (Courtenay et al., 1984; Moyle, 1986; Gido & Brown, 1999), resulting in the biotic homogenization of fish faunas throughout North America (Rahel, 2000; Olden & Poff, 2004; Taylor, 2004). Biogeographic studies that explore long–term trends in species distributions can provide important insight into predicting the identity of those species declining in their distribution and under risk of extinction (e.g., Williams et al., 1989; Reinthal & Stiassny, 1991; Anderson et al., 1995; Patton et al., 1998). More generally, such studies can help understand how temporal changes in native species distributions relate to patterns of non–native species distributions, thus providing correlative insight into broad–scale implications of biological invasions.

Temporal patterns of native fish distributions

The American Southwest contains among the most threatened aquatic systems in North America, and despite early warnings (Dill, 1944; Miller, 1946), the unique, highly endemic, native fish fauna of the Lower Colorado River Basin have become increasingly imperilled over time. Our study provides quantitative estimates of distributional trends in native fishes and show significant declines of many species over both historical and recent times. These findings provide empirical support for the observational hypothesis of Mueller & Marsh (2002) who postulated that native fishes rapidly declined between 1890 and 1935 because of intensive water management practices and the introduction of common carp, bullhead and channel catfish, which was then followed by a prolonged period when remnant communities gradually disappeared after the construction of Roosevelt, Hoover, Imperial, and a number of other dams that caused remarkable hydraulic and physical change to the basin.

Our results indicate the highest rate of declines in a number of native fish species that have previously identified as imperilled in the basin, including a number of "big–river" fishes such as Colorado pikeminnow, razorback sucker, bonytail and flannelmouth sucker; and species inhabiting marginal spring and stream habitats such as the desert pupfish and Gila topminnow (Minckley & Deacon, 1991; Mueller & Marsh, 2002). The last wild Colorado pikeminnow was caught in 1975 in the Lower Colorado River; bonytail likely persist only in Lake Mohave; and although annual spawning occurs, razorback sucker populations consist largely of old

Table 3. Temporal patterns of non–native fish distributions in the Lower Colorado River Basin expressed as the percentage of the total kilometres of rivers where all species were observed for each time period. Nomenclature follows Nelson et al. (2004): C. Code, labels in figure 5; I. Year of introduction or first observed in the basin; ER, Extant range, percentage of species distribution based on 1980–1999 records; S. Rate of spread in km/year.

Tabla 3. Patrones temporales de distribución de peces alóctonos en la cuenca inferior del río Colorado expresadas como el porcentaje del total de kilómetros de río donde se observaron todas las especies en cada período. La nomenclatura es según Nelson et al. (2004): C. Código, números en la figura 5; I. Año de introducción o primera observación en la cuenca; ER. Rango existente, porcentaje de distribución de las especies basada en los registros de 1980–1999; S. Tasa de dispersión en km/año.

			Temporal trends						
Species	C	I	<1960	1960s	1970s	1980s	1990s	ER	S
Fathead minnow (*Pimephales promelas*)	1	1950	1.9	7.7	21.8	28.7	39.2	39.3	74.1
Green sunfish (*Lepomis cyanellus*)	2	1937	11.4	16.9	19.8	30.9	44.1	42.0	62.9
Red shiner (*Cyprinella lutrensis*)	3	1950	0.9	17.4	18.7	27.4	27.9	28.9	54.6
Western mosquitofish (*Gambusia affinis*)	4	1922	15.4	16.5	19.2	28.1	27.5	31.3	37.9
Largemouth bass (*Micropterus salmoides*)	5	1935	9.2	15.3	11.6	20.6	19.9	23.6	34.2
Flathead catfish (*Pylodictis olivaris*)	6	1962	1.0	0.6	3.1	9.3	9.3	9.5	23.7
Bluegill (*Lepomis macrochirus*)	7	1937	8.0	8.2	7.2	12.8	12.7	15.6	23.4
Channel catfish (*Ictalurus punctatus*)	8	1892	11.2	15.1	14.6	27.5	15.4	25.2	22.0
Blue tilapia (*Oreochromis aureus*)	9	1978	0.0	0.0	0.3	5.9	1.0	4.8	20.7
Yellow bullhead (*Ameiurus natalis*)	10	1899	5.7	7.6	10.9	16.3	21.8	21.9	20.4
Common carp (*Cyprinus carpio*)	11	1881	14.0	16.5	15.8	21.7	21.2	25.1	19.9
Smallmouth bass (*Micropterus dolomieui*)	12	1942	2.8	3.5	5.2	10.8	10.1	11.1	18.0
Rainbow trout (*Oncorhynchus mykiss*)	13	1900	12.4	18.7	23.3	16.7	20.3	19.1	18.0
Threadfin shad (*Dorosoma petenense*)	14	1953	1.3	6.3	3.5	8.4	2.3	7.9	15.8
Golden shiner (*Notemigonus crysoleucus*)	15	1953	0.3	2.4	2.3	4.0	7.0	6.3	12.7
Striped bass (*Morone saxatilis*)	16	1959	0.4	0.8	1.6	5.6	1.5	5.2	11.9
Brown trout (*Salmo trutta*)	17	1924	2.4	7.3	8.6	7.1	10.3	8.9	11.0
Goldfish (*Carassius auratus*)	18	1944	0.1	6.8	1.4	5.5	2.4	6.3	10.6
Plains killifish (*Fundulus zebrinus*)	19	1950	0.0	1.3	4.6	4.3	2.2	4.8	9.0
Black crappie (*Pomoxis nigromaculatus*)	20	1936	7.5	2.5	4.4	4.7	2.9	5.6	8.3
Black bullhead (*Ameiurus melas*)	21	1904	9.3	11.2	6.8	7.7	6.7	8.2	8.1
Sailfin molly (*Poecilia latipinna*)	22	1950	1.0	2.7	1.4	5.1	0.7	4.2	7.9
Brook trout (*Salvelinus fontinalis*)	23	1920	2.6	4.2	3.9	4.3	7.6	6.3	7.4
Walleye (*Sander vitreus*)	24	1971	0.0	0.1	0.3	0.8	1.5	1.8	5.7
Rio Grande cichlid (*Herichthys cyanoguttatus*)	25	1996	0.0	0.0	0.0	0.0	0.3	0.2	5.5
Arctic grayling (*Thymallus arcticus*)	26	1965	0.0	0.9	0.8	0.8	2.2	2.0	5.3
Cutthroat trout (*Oncorhynchus clarkii*)	27	1937	1.3	1.3	0.6	2.2	3.2	3.3	5.0
Northern pike (*Esox lucius*)	28	1969	0.0	0.0	1.3	1.5	0.1	1.3	4.0
Redside shiner (*Richardsonius balteatus*)	29	1950	0.0	0.8	1.1	2.4	0.0	2.0	3.8
Redear sunfish (*Lepomis microlophus*)	30	1951	2.2	1.7	2.7	1.8	0.7	1.9	3.6
Mozambique tilapia (*Oreochromis mossambica*)	31	1965	0.0	1.0	3.4	1.5	0.0	1.2	3.2
Redbelly tilapia (*Tilapia zilli*)	32	1965	0.0	0.0	0.3	1.4	1.0	1.1	3.1
Rock bass (*Ambloplites rupestris*)	33	1962	0.0	0.0	0.0	0.4	0.5	0.7	1.8

Table 3. (Cont.)

Species	C	I	Temporal trends <1960	1960s	1970s	1980s	1990s	ER	S
Guppy (*Poecilia reticulata*)	34	1950	0.0	1.3	0.5	0.8	0.4	0.9	1.6
Yellow bass (*Morone mississippiensis*)	35	1931	0.4	0.4	0.3	1.2	0.1	1.1	1.5
White crappie (*Pomoxis annularis*)	36	1934	1.8	0.4	0.0	0.1	0.7	0.6	0.8
Shortfin molly (*Poecilia mexicana*)	37	1950	0.0	3.7	0.5	0.3	0.0	0.2	0.4
Rio Grande sucker (*Catostomus plebeius*)	38	1950	1.9	0.9	0.8	0.0	0.2	0.1	0.3
White bass (*Morone chrysops*)	39	1960	0.0	0.1	0.0	0.1	0.0	0.1	0.2
Bigmouth buffalo (*Ictiobus cyprinellus*)	40	1964	0.0	0.5	0.2	0.1	0.1	0.1	0.2
Smallmouth buffalo (*Ictiobus bubalus*)	41	1950	0.0	0.5	0.3	0.0	0.1	0.1	0.1
Brown bullhead (*Ameiurus nebulosus*)	42	1910	6.6	1.5	0.0	0.0	0.0	0.0	0.0
Convict cichlid (*Archocentrus nigrofasciatus*)	43	1955	0.0	1.5	0.0	0.0	0.0	0.0	0.0
Grass carp (*Ctenopharyngodon idellus*)	44	1976	0.0	0.0	1.8	0.0	0.0	0.0	0.0
Black buffalo (*Ictiobus niger*)	45	1966	0.0	0.4	0.2	0.0	0.0	0.0	0.0
Warmouth (*Lepomis gulosus*)	46	1958	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Spotted bass (*Micropterus punctulatus*)	47	1956	0.6	0.5	0.1	0.0	0.0	0.0	0.0
Yellow perch (*Perca flavescens*)	48	1951	0.6	0.2	0.0	0.0	0.0	0.0	0.0

adults with no evidence of recruitment (Minckley, 1991). Other, comparatively less studied, species also experienced significant declines over time, including spikedace and woundfin. Similarly, loach minnow has seen dramatic declines when compared to historical records, although there is some evidence that its distribution has remained fairly constant over the recent decades. This finding is supported by recent work showing the local stability of remnant loach minnow populations in Arizona (Marsh et al., 2003). In contrast to the many species that have exhibited significant declines in their distributions, longfin dace, desert sucker and Sonora sucker are presently abundant throughout the basin and appear to have maintained relatively stable distributions over time. Finally, temporal trends and present–day sizes of species' distributions were highly correlated to estimates of local extirpation risk for the native fishes. This suggests that long–term studies conducted at the drainage scale might provide a coarse–level surrogate for identifying those species that are most likely to extirpated at the local reach scale.

In summary, a number of explanations are possible to describe the distributional changes observed in our study. By explicitly linking patterns of environmental degradation and non–native species distributions to patterns of native species distributions, we could gain greater insight into potential mechanisms of native imperilment and thus better tease apart the synergistic manner in which these stresses are threatening native faunas in the Lower Colorado River Basin (Olden et al., in press).

Temporal patterns of non–native fish distributions

The establishment of non–native fish species has substantially changed native fish community structure in southwestern rivers (Minckley & Deacon, 1968, 1991; Meffe, 1985; Rinne & Minckley, 1991). While the total number of non–native fishes continues to increase across the U.S. (Gido & Brown, 1999; Rahel, 2000; Meador et al., 2003), quantitative estimates of distributional changes are lacking for most fish, and such analyses are rarely conducted at large temporal and spatial scales that are required to properly understand these processes. Our study contributes to a better understanding of the shear magnitude in which non–native species have spread throughout the Lower Colorado River Basin over the past century and points to those invaders that have exhibited considerable rates of expansion since their introduction. This information provides a scientific basis for the management of fast spreading species and enhanced education targeted specifically to reducing their future introduction by humans.

Perhaps our most striking result is that red shiner, fathead minnow, green sunfish, largemouth bass, western mosquitofish and channel catfish are the among the fastest expanding invaders in the basin, and these species have also been identified by expert ichthyologists as having the greatest negative impacts on native fish communities (Hawkins & Nesler, 1991; J. D. Olden, unpublished survey data). Recent studies have further supported the significant ecological effects of these

Fig. 4. Maps of historical and extant distributions of three native fishes exhibiting markedly different percentage of decline over time and having different statuses under U.S. Endangered Species Act: A. Bonytail (*Gyla elegans*), endangered, 87.7% decline; B. Spikedace (*Meda fulgida*), threatened, 45.9% decline; C. Specked dace (*Rhinichthys osculus*), not listed, 16.5% decline. Thicker lines represent river segments where the species was recorded present during the time period. See inset of figure 1 for locations of major river drainages.

*Fig. 4. Mapas de las distribuciones históricas y existentes de tres peces autóctonos mostrando porcentajes distintos de disminución a lo largo del tiempo y con distintos estatus reconocidos en el Acta de Especies Amenazadas de EE.UU.: A. Carpita elegante (*Gyla elegans*), en peligro, 87,7% de disminución; B. Charal espinoso (*Meda fulgida*), amenazado, 45,9% de disminución; C. Carpa pinta (*Rhinichthys osculus*), no listada, 16,5% de disminución. Las líneas gruesas representan las secciones del río donde se registró la especie a lo largo del periodo de estudio. Ver el recuadro de la figura 1 para las localizaciones de los principales drenajes del río.*

non–native species on native fishes (e.g., Courtenay & Meffe, 1989; Douglas et al., 1994; Marsh & Douglas, 1997; Dudley & Matter, 2000; Marsh & Pacey, 2003), in addition to their role as vectors of exotic parasites, including the Asian fish tapeworm (Clarkson et al., 1997).

Of particular interest is that non–native species introduced after 1950 have generally spread at substantially lower rates as compared to non–native introduced prior to this time (especially 1920–1950), and consequently occupy much smaller distributions. The most optimistic explanation for this threshold pattern is that recent decades have seen declines in U.S. government–sanctioned introductions of gamefish or forage species outside their native ranges (Courtenay & Moyle, 1996), a pattern that reflects both a saturation of gamefish species in many drainages and a heightened awareness by fisheries biologists of the problems associated with non–native species (Rahel, 1997). However, inadvertent introductions (e.g., aquarium trade releases: Padilla & Williams, 2004) and unauthorized introductions (Rahel, 2004) by the public continue, which likely explain the notable exceptions to this general pattern – blue tilapia and flathead catfish – both species exhibiting very high faster rates of spread since its introduction in recent decades.

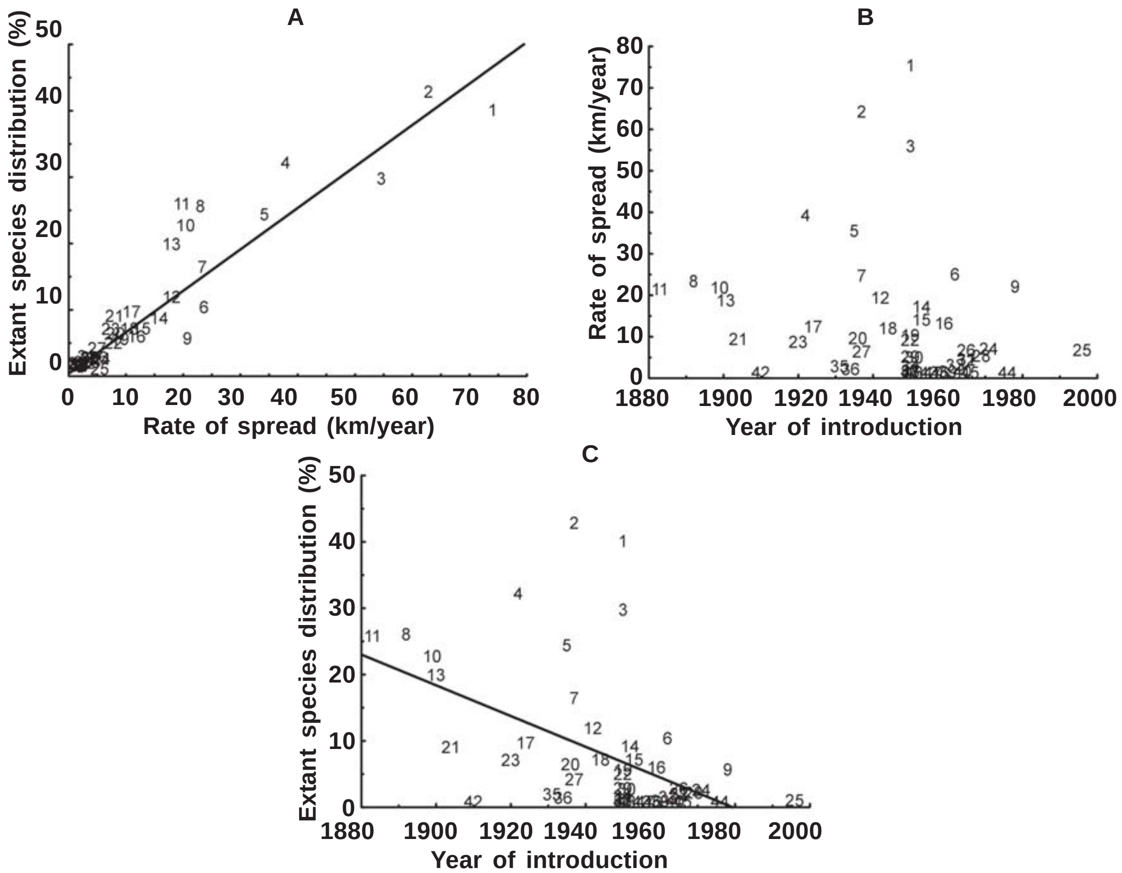

Fig. 5. Comparisons of extant distribution size percentages, rate of spread (km/year) and year of introduction of non–native fishes in the Lower Colorado River Basin. Least–squares regression lines are represented. Numbers refer to non–native species in table 3.

Fig. 5. Comparaciones entre el porcentaje del tamaño de distribución existente, la tasa de dispersión (km/año) y año de introducción de peces alóctonos el la cuenca inferior del río Colorado. Se representan las líneas de regresión de mínimos cuadrados. Los números indican las especies alóctonas de la tabla 3.

Results from our study show both similarities and differences to other long–term studies of fish invasions conducted in Great Plains streams of Wyoming (Patton et al., 1998) and Oklahoma and Kansas (Gido et al., 2004). Great Plains stream are similar to desert streams in the American Southwest in that they present harsh environmental conditions and disturbance regimes (Dodds et al., 2004), and they have been invaded by a relatively large number of non–native species as compared to other regions of the United States (Gido & Brown, 1999), thus making it suitable to compare rates of spread between these regions. Based on species common to all three regions, our study found that red shiner, fathead minnow, green sunfish, largemouth bass, channel catfish and black bullhead exhibit relatively high rates of spread, whereas Patton et al. (1998) found that these species' distributions were declining in Wyoming. However, similar patterns were found for common carp (range expansion) and white crappie, rock bass and yellow perch (range declines or low rates of spread). In contrast to distributional changes, comparisons of extant distribution sizes showed remarkable similarity for 15 species shared by the Lower Colorado River basin and plain streams in Oklahoma and Kansas (Gido et al., 2004). In summary, these comparisons suggest that a number of non–native species exhibit similar distribution sizes in these different ecoregions, yet the rate at which they have spread to obtain their distributions differs (likely a result of different rates and timing of human introductions).

Conservation and management implications for native fishes

The United States Endangered Species Act (ESA) of 1973, together with other environmental legislation, has played an important role in the effort to conserve native fishes in the Lower Colorado Basin (Minckley et al., 2003). Although in principle ESA decisions are based on the best biological information, many factors other than biology, including socioeconomic and political issues, influence most plans and projects. We believe our study provides some new insight into the biological component of the listing process for the Lower Colorado River by relating long–term species' distributional trends to their federal status under the ESA. This comparison may help address the question of whether the ESA is, in fact, helping identity (and conserve) those rare species experiencing substantial declines in their distributions. Our results show good agreement between patterns of species decline and extant distribution sizes and expectations based on their official status. "Endangered" species have generally experienced greater declines in their distributions compared to "threatened" species, which in turn have shown greater declines than those species not currently listed. Likewise, non–listed species have three times larger extant distributions than "threatened" species, which in turn have two time larger distributions than "endangered" species. These patterns are reassuring, in that they support the biological underpinnings of the ESA for the native species of this region.

Interestingly, although general patterns were in agreement we did find a number of notable exceptions, which we believe can provide critical information to help guide the future listing of species (i.e., identification of candidates) and the upgrading or downgrading of current listed species that are endemic to this region. For example, based on temporal trends and extant distribution sizes alone, our results suggest that 3 non–listed species might merit consideration for listing under ESA: headwater chub could be a candidate for threatened status (on the basis of extant distribution), and flannelmouth sucker and Virgin River spinedace could be candidates for endangered status. Our results also suggest that Apache trout have experienced significant declines and exhibit extant distributions that correspond more closely with "endangered" species and therefore could be considered for upgrading from its threatened status. Other factors not evident from distributional data support these ideas, e.g., Apache trout are also at high risk to the effects of intensive hybridization with non–native trout (Dowling & Childs, 1992) as well as those arising from hatchery practices. It is very interesting to note that Apache trout was formerly listed as endangered but was downlisted in 1975 to threatened status to facilitate a management program that included recreational angling (Behnke, 1992). This is an excellent example where socioeconomic issues have likely outweighed species biology in the ESA listing process.

Concerning potential data limitations

When analyzing compiled data that has not been systematically collected, as is the case in this study, it is important to consider the effects of sampling bias, spatial scale and data resolution when interpreting the results. Sampling intensity (i.e., as indicated by the number of records) increased through time for both native and non–native species. Consequently, our study provides minimum estimates of native species decline because sampling intensity in recent decades always exceeded that of previous decades, whereas the opposite is true for non–native species where rates of spread may be over–estimated. Spatial scale must also be considered when using historic data to examine species declines. Patton et al. (1998) found greater changes in species distributions at the reach scale compared to the drainage scale for 37 species in Wyoming, which suggests that smaller–scale analyses of temporal trends may provide an over–estimates of species declines. Lastly, although species presence data are not as informative as abundance data for assessing temporal trends, local population fluctuations may confound trend interpretations, especially in for highly variable desert streams characteristic of the American Southwest (Eby et al., 2003). While we acknowledge the above data limitations and issues of sampling and spatial scale, we believe our analyses are appropriate for this region at a scale of study relevant to broad–scale conservation and management planning. Indeed, a number of studies have already illustrated the utility of the SONFISHES database for addressing pressing fish conservation issues in the American Southwest (e.g., Fagan et al., 2002; Unmack & Fagan, 2004) and our study is the first to use this powerful dataset to address broad–scale changes in fish distributions.

Conclusion

The extensive regulation of the Lower Colorado River Basin threatens native fish faunas by drastically altering natural flow, temperature and sediment regimes, and promoting the establishment and spread of non–native species. Results from this study provide a reach–scale examination of distributional trends of the fishes of the Lower Colorado River Basin over the past century. These trends indicate high priorities for conservation and management efforts by identifying declining species before they are lost forever. However, before management plans can be implemented we must first recognize and quantify the degree to which native species are declining and non–native species are spreading across riverine landscapes.

Acknowledgements

This research would not of been possible without the tireless efforts of the late W. L. Minckley, who dedicated his life to the conservation of desert fishes in the American Southwest. We thank Peter Unmack for graciously providing the SONFISHES database and Kevin Bestgen for his continued insights on Colorado

River fishes. Comments from the Editor and an anonymous reviewer greatly improved the final paper. Funding for this research was provided by the American Museum of Natural History (Theodore Roosevelt Memorial Scholarship), the American Fisheries Society (William Trachtenberg Scholarship) and Ocean Journey (Conservation Grant) to JDO, and U.S. EPA STAR Grant #R828636 to NLP.

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