

LIFE-HISTORY STRATEGIES PREDICT FISH INVASIONS AND EXTIRPATIONS IN THE COLORADO RIVER BASIN

JULIAN D. OLDEN,^{1,3} N. LEROY POFF,¹ AND KEVIN R. BESTGEN²

¹*Graduate Degree Program in Ecology, Department of Biology, Colorado State University, Fort Collins, Colorado 80523 USA*

²*Larval Fish Laboratory, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, Colorado 80523 USA*

Abstract. Understanding the mechanisms by which nonnative species successfully invade new regions and the consequences for native fauna is a pressing ecological issue, and one for which niche theory can play an important role. In this paper, we quantify a comprehensive suite of morphological, behavioral, physiological, trophic, and life-history traits for the entire fish species pool in the Colorado River Basin to explore a number of hypotheses regarding linkages between human-induced environmental change, the creation and modification of ecological niche opportunities, and subsequent invasion and extirpation of species over the past 150 years. Specifically, we use the fish life-history model of K. O. Winemiller and K. A. Rose to quantitatively evaluate how the rates of nonnative species spread and native species range contraction reflect the interplay between overlapping life-history strategies and an anthropogenically altered adaptive landscape. Our results reveal a number of intriguing findings. First, nonnative species are located throughout the adaptive surface defined by the life-history attributes, and they surround the ecological niche volume represented by the native fish species pool. Second, native species that show the greatest distributional declines are separated into those exhibiting strong life-history overlap with nonnative species (evidence for biotic interactions) and those having a periodic strategy that is not well adapted to present-day modified environmental conditions. Third, rapidly spreading nonnative fishes generally occupy “vacant” niche positions in life-history space, which is associated either with “niche opportunities” provided by human-created environmental conditions (consistent with the environmental-resistance hypothesis of invasion) or with minimal overlap with native life-history strategies (consistent with the biotic-resistance hypothesis). This study is the first to identify specific life-history strategies that are associated with extensive range reduction of native species and expansion of nonnative species, and it highlights the utility of using niche and life-history perspectives to evaluate different mechanisms that contribute to the patterns of fish invasions and extirpations in the American Southwest.

Key words: *attributes; endangered fishes; functional diversity; functional niche; river regulation; traits; trilateral continuum.*

INTRODUCTION

Biological invasions are widely recognized as a significant component of human-caused environmental change (Elton 1958) that often cause substantial ecological, evolutionary, and economic damage (Mack et al. 2000, Pimental et al. 2000, Moritz 2002, Olden et al. 2004). The field of ecology has witnessed considerable empirical and theoretical advances in forecasting invasions (e.g., Kolar and Lodge 2001, but see Hulme 2003), including the use of life-history traits as correlates of invasion success (Sakai et al. 2001) and niche modeling for predicting the geography of species' in-

vasions based on environmental requirements (Peterson 2003). Ecological niche theory posits that invasion success will be mediated by intrinsic biological traits of species that dictate their degree of “pre-adaptation” to habitats in the receiving ecosystem including biotic interactions with resident native species. Despite some recent claims that question the utility of the niche concept in ecology (Hubbell 2001), contemporary ecological niche theory can arguably be considered a very powerful construct for understanding broad-scale patterns and changes in the diversity, distribution, and abundance of species (see Chase and Leibold 2003).

The modern view of the ecological niche is an integration of the original concepts proposed by Grinnell (1917) and Hutchinson (1957) and is pluralistically defined as a combination of a species' “place” and “role” in the environment (Chase and Leibold 2003). In this sense, an ecological niche defines where and under what circumstances a species will exist and how

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³ Present address: Center for Limnology, 680 Park Street N., University of Wisconsin–Madison, Madison, Wisconsin 53706 USA. E-mail: olden@wisc.edu

it interacts with its environment. Life-history and ecological trait attributes can be used to quantify a species' ecological niche, which can be plotted in relation to other species in n -dimensional niche space where axes are different traits (Rosenfeld 2002). Theoretically, the signature of niche differentiation among species and between native and nonnative species' pools provides insight into the biotic and abiotic mechanisms responsible for long-term patterns of species' invasions and extinctions (Crawley et al. 1996). For example, the success of biological invasions may be determined by potential "niche opportunities," which arise when a nonnative species possesses some set of traits that differ from those of native species and that are favored by the environmental template (sensu Shea and Chesson 2002). Consequently, we would expect that the rate of spread of nonnative species will reflect the magnitude and extent of these opportunities (Sax and Brown 2000). The idea that "niche opportunities" can facilitate biological invasions has incited both excitement and disagreement among ecologists (Herbold and Moyle 1986); however, this hypothesis remains untested due to a lack of necessary species' trait information and long-term empirical data. Niche theory is also appealing in that it provides a basis for identifying possible mechanisms behind the range contractions of native species in terms of niche overlap with both nonnative species and fit to the environmental template, both of which have changed dramatically in recent history. In short, contemporary ecological niche theory may provide a useful heuristic tool for understanding past and future distributional changes in native and nonnative species, yet its potential remains largely unexplored in quantitative terms.

A large number of biological traits across a diversity of taxonomic groups have been used to describe a species' ecological niche. For freshwater fishes, attributes related to morphology, behavior, life-history, and habitat and trophic requirements have proven very useful for relating species distributions to environmental variables (e.g., Poff and Allan 1995, Lamouroux et al. 2002, Brazner et al. 2004). Of these attributes, life-history traits have been shown to be particularly good predictors of both fish invasions (e.g., Fausch et al. 2001, Kolar and Lodge 2002, Marchetti et al. 2004, Vila-Gispert et al. 2005) and extirpations (e.g., Angermeier 1995, Parent and Schriml 1995, Reynolds et al. 2005). Life-history traits may represent a critical dimension of a species' ecological niche because life-history strategies are considered to have evolved from constraints among traits that have consequences for reproduction and fitness in different environments. Life-history theory is also considered valuable because it makes explicit predictions about relationships between these strategies and the environment (Pianka 1970, Grime 1977, Southwood 1977, 1988, Stearns 1992).

Comparative studies from a diverse array of fishes in freshwater and marine systems have independently identified three primary life-history strategies that represent the endpoints of a triangular continuum arising from trade-offs among the three basic demographic parameters of survival, fecundity, and onset and duration of reproduction (e.g., Winemiller 1989, Vila-Gispert et al. 2002, King and McFarlane 2003). In a comprehensive study, Winemiller and Rose (1992) examined 216 species (57 families) of North American freshwater and marine fishes and provided the following descriptions of the characteristic biological and habitat environmental attributes associated with each strategy: (i) periodic strategists are large-bodied fishes with late maturation, high fecundity per spawning event, low juvenile survivorship (i.e., no parental care), and that typically inhabit seasonal, periodically suitable environments; (ii) opportunistic strategists are small-bodied fishes with early maturation, low fecundity per spawning event, and low juvenile survivorship, and that typically inhabit highly disturbed and unpredictable environments; (iii) equilibrium strategists are small- to medium-bodied fishes with moderate maturation age, low fecundity per spawning event, and high juvenile survivorship (i.e., greater parental care), and that typically inhabit constant environments. The three primary strategies of North American fishes have some striking similarities with earlier life-history models for animals and plants (reviewed in Southwood 1988), but notably the Winemiller and Rose model (hereafter called W-R model) extends the classic r - K model by splitting the r strategy into the periodic and opportunistic strategies and more narrowly defines the K strategy as the equilibrium strategy.

The life-history strategies of the W-R model can be interpreted as being adaptive with respect to the relative intensity and predictability of temporal and spatial variation in abiotic environmental conditions, food availability, and predation pressure (Winemiller 2005). This model was envisioned to have strong implications for understanding and predicting fish population responses to changing environments; however, it has only once been applied in the literature for this purpose (i.e., VanWinkle et al. 1993) and it has never been used to study the geography of fish invasions and extinctions. In this paper, we ask the question, "Can ecological niche theory together with the life-history model of Winemiller and Rose (1992) be used to explain long-term trends of nonnative fish spread and native fish range contraction in the Colorado River Basin?" The highly endemic ichthyofauna of this basin is adapted to the harsh and fluctuating environmental conditions typical of the American Southwest (Minckley and Deacon 1968, 1991), but, since European settlement, it has become increasingly threatened both by significant environmental degradation associated with dam building and irrigation works and by the introduction of nu-



PLATE 1. Aerial view of the Yampa River upstream of its confluence with the Green River, Colorado, USA. Photo credit: Jeremy B. Monroe.

merous nonnative species (Fradkin 1981, Carlson and Muth 1989).

The present paper couples fish life-history theory and ecological niche theory to examine the underlying mechanisms of distributional changes for native and nonnative fishes over the last 150 years in the Colorado River Basin (see Plate 1). Specifically, we develop a comprehensive database of morphological, behavioral, physiological, trophic and life-history traits (22 in total) for the extant freshwater fish fauna of the Colorado River (90 species in total) to test several hypotheses. (1) Differences in the total ecological niche space of the native and nonnative species pools will strongly reflect environmental changes in the Colorado River Basin over the past century. We expected that, although some nonnative species will overlap in niche space with native species, many nonnatives will possess ecological traits that allow them to occupy niche space associated with conditions of hydrologically stable flow regimes created by the recent construction of numerous dams throughout the basin. (2) Native and nonnative species pools will populate different areas in the life-history adaptive surface bounded by the periodic, opportunistic, and equilibrium life-history strategies identified in the W-R model. (3) Rates of nonnative species spread and native species decline over the past 150 years will reflect the differential selection of life-history strategies under contrasting environmental and biological regimes.

Our first expectation was that nonnative equilibrium strategists would spread most rapidly because of niche opportunities created by extensive environmental

change and minimal niche overlap with native species that are less well adapted to the altered conditions. Second, we expected rapidly declining native species to be either opportunistic or periodic strategists. According to the W-R model, declining ranges for opportunistic strategists would be consistent with a mechanism of biotic interactions (and therefore should show high life-history overlap with rapidly spreading nonnative species), whereas declining ranges for periodic strategists would reflect environmental alteration (and therefore should show minimal overlap with nonnative species). Using these series of hypotheses and expectations, we hoped to gain insight into the mechanisms of nonnative fish spread and native fish range contraction in the Colorado River Basin over the past century.

METHODS

Fishes of the Colorado River Basin

The Colorado River travels southwest from the Rocky Mountains to the Gulf of California and drains approximately 632 000 km² of land from seven states in the United States and northwestern Mexico. For water management purposes, Glen Canyon Dam is the demarcation between the upper and lower basins. The upper basin produces most of the river's discharge with snowmelt runoff, whereas discharge in the lower basin is generated mostly by winter rainstorms and late summer monsoons (except for the mainstem Colorado River). As a result of long isolation and fluctuating environmental conditions, the basin has some of the most unique ichthyofauna in North America (Evermann and

TABLE 1. Freshwater native ($n = 28$) fish species of the Colorado River Basin examined in our study.

Family and species	Common name	Species code
Catostomidae		
<i>Catostomus clarkii</i>	desert sucker	A
<i>Catostomus discobolus</i>	bluehead sucker	B
<i>Catostomus insignis</i>	Sonora sucker	C
<i>Catostomus latipinnis</i>	flannelmouth sucker	D
<i>Catostomus platyrhynchus</i>	mountain sucker	E
<i>Xyrauchen texanus</i>	razorback sucker	F
Cottidae		
<i>Cottus bairdii</i>	mottled sculpin	G
<i>Cottus beldingii</i>	Paiute sculpin	H
Cyprinidae		
<i>Gila cypha</i>	humpback chub	I
<i>Gila elegans</i>	bonytail	J
<i>Gila intermedia</i>	Gila chub	K
<i>Gila nigra</i>	headwater chub	L
<i>Gila robusta</i>	roundtail chub	M
<i>Lepidomeda mollispinis</i>	Virgin River spinedace	N
<i>Lepidomeda vittata</i>	Little Colorado River spinedace	O
<i>Meda fulgida</i>	spikedace	P
<i>Moapa coriacea</i>	Moapa dace	Q
<i>Plagopterus argentissimus</i>	woundfin	R
<i>Ptychocheilus lucius</i>	Colorado pikeminnow	S
<i>Agosia chrysoaster</i>	longfin dace	T
<i>Rhinichthys osculus</i>	speckled dace	U
<i>Rhinichthys cobitis</i>	loach minnow	V
Cyprinodontidae		
<i>Cyprinodon macularius</i>	desert pupfish	W
Poeciliidae		
<i>Poeciliopsis occidentalis</i>	Gila topminnow	X
Salmonidae		
<i>Oncorhynchus gilae apache</i>	Apache trout	Y
<i>Oncorhynchus clarkii</i>	cutthroat trout	Z
<i>Oncorhynchus gilae gilae</i>	Gila trout	AA
<i>Prosopium williamsoni</i>	mountain whitefish	BB

Note: Nomenclature follows Nelson et al. (2004).

Rutter 1895) while, at the same time, one of the most endangered (Minckley and Deacon 1968, 1991). We compiled a present-day list of the native and established nonnative freshwater fishes of the Colorado River Basin for which adequate trait data was available (Tables 1 and 2) using species lists from state accounts and other sources from the primary literature (Appendix A).

Ecological and life-history traits

We used the scientific literature, electronic databases, and expertise from regional fish biologists to provide a comprehensive functional description of the native ($n = 28$) and nonnative ($n = 62$) fish species of the Colorado River Basin (see Olden 2004 for details). We collated data for 22 ecological and life-history attributes (collectively referred to as biological traits) that could be justified on the basis of our current state of knowledge and information available for the entire pool of species (Appendix B). These traits allow each species to be characterized according to its unique relation with the environment (“place”) and other spe-

cies (“role”). These 22 traits were divided into five categories, as follows. Body morphology included (1) maximum total body length (cm), (2) shape factor (the ratio of total body length to maximum body depth), (3) swim factor (the ratio of minimum depth of the caudal peduncle to the maximum depth of the caudal fin, where small factors are indicative of strong swimmers [calculated following Webb 1984]). Behavior included (4) water temperature preference (cold [10–17°C], cool [18–26°C], or warm water [$>26^\circ\text{C}$] based on species distributions and perceived physiological optima), (5) substrate preference (rubble [including cobble and gravel], sand, silt/mud, or general), (6) fluvial dependence (reliance on flowing waters for completing life cycle, e.g., flow required for feeding or reproduction [classified as yes or no]), (7) current velocity preference (slow, slow-moderate, moderate, moderate-fast, or fast current velocity), (8) vertical position (benthic or non-benthic based on species morphology and behavior). Physiology included (9) critical thermal tolerance (low [$<30^\circ\text{C}$], moderate [30–35°C], high [35–40°C], or very high [$>40^\circ\text{C}$] critical water temperature for survival).

Trophic traits included (10) trophic guild (adult feeding mode based on published diet analyses and classified as herbivore–detritivore [approximately > 25% plant matter], omnivore [approximately < 5% plant matter], invertivore, or invertivore–piscivore), (11) diet breadth (total number of major diet items consumed at any time during a fish’s lifetime, including inorganic material, vegetative material, plankton, aquatic/terrestrial insects, oligochaetes/crustaceans/molluscs, fish/fish eggs, and amphibians/mammals/birds [range 1–7]). Life history included (12) longevity (maximum potential life span [years]), (13) age at maturation (years), (14) length at maturation (cm), (15) fecundity (total number of eggs or offspring per breeding season, represented on a logarithmic [base 10] scale), (16) egg size (mean diameter of mature [fully yolked] ovarian oocytes [mm]), (17) spawning temperature (temperature at which spawning is typically initiated [°C]), (18) parental care (metric representing the total energetic contribution of parents to their offspring [calculated following Winemiller 1989]), (19) reproductive guild (nonguarders [open substratum spawners, brood hidens], guarders [substratum choosers, nest spawners], or bearers [internal, external] [calculated following Balon 1975]), (20) spawning substrate (mineral substrate, vegetation, pelagic, or various), (21) time to hatch (mean time to egg hatch within the range of average post-spawning water temperatures [days]), (22) larvae length at hatching (mean total length of larvae at hatching [mm]).

Trait assignments were based on a multitiered data collection procedure. First, trait data were collected from species accounts in the comprehensive texts of the state fish faunas (Appendix A). Second, we used species descriptions from the primary literature, state agency reports, university reports, and graduate theses. Third, we obtained data from electronic databases available on the World Wide Web, including FishBase (*available online*),⁴ Arizona’s Heritage Data Management System, and Biota Information System of New Mexico. Fourth, expert knowledge of regional specialists was used to assign values to a small number of trait states that could not be obtained from the previous methods (mainly inferred from congeners). To account for interdemic variation in biological traits we recorded trait values based on research conducted in the Colorado River Basin or the closest geographic proximity. Trait values were represented by ordinal, nominal or continuous data. Ordinal and nominal traits were assigned a single state based on a majority of evidence rule according to adult preferences, and median values for continuous traits were used when ranges were presented.

Fish distributional trends over the past 150 years in the Lower Colorado River Basin

Our objective was to compare patterns of species’ distributional changes for native and nonnative fishes

across the life-history continuum model proposed by Winemiller and Rose (1992). The data for such an empirical analysis need to be long-term and spatially extensive, and for our study they were provided by the SONFISHES database (*available online*).⁵ This database was developed over a eight-year period by the tireless efforts of the late ichthyologist W. L. Minckley and colleagues, and contains >38 000 occurrence records for freshwater fish species from over 150 years of research conducted throughout the Lower Colorado River Basin. Records include incidence, identity, and collection information for the complete holdings of major regional museum collections, numerous smaller holdings, and records from peer-reviewed and gray literature sources, and they are georeferenced to within 1 km of their collection site in a Geographic Information System (Unmack 2002). While we recognize the potential limitations associated with analyzing compiled data that was not systematically collected, such as museum-based specimen data (Graham et al. 2004), this database was constructed with a high level of quality control. Records from published, peer-reviewed literature were typically cross-referenced with voucher specimens from museums, and records from agency/institutional reports and other sources of “gray literature” were only used after being individually reviewed by specialists with ichthyological and historical expertise (primarily W. L. Minckley). A number of studies have already illustrated the utility of the SONFISHES database for ecological applications (e.g., Fagan et al. 2002, 2005) and we recently used these data to quantify long-term changes in fish distributions in the lower basin (Olden and Poff 2005).

Using ArcGIS (version 8.3; Environmental Services Research, Inc., Redlands, California, USA) we plotted 28 755 locality records from 1840 to 2000 (excluding occurrence records resulting from artificial translocations and reintroductions) for 23 native species and 47 nonnative species (i.e., species present in the lower basin) from the SONFISHES database onto a digital stream network (*available online*).⁶ Following Fagan et al. (2002), we defined historical records as those collected between ca. 1840 and 1979 and extant records as those collected between 1980 and 1999, a robust breakpoint for comparing temporal trends in this data (see Fagan et al. 2005). For both historical and extant time periods we calculated the total river kilometers occupied by each species by summing the length of the river segments (defined as a section of river delineated by two confluences) in which the species was recorded present. Species’ distributional decline (percentage) was then calculated by subtracting extant range size from historical range size and dividing by historical range size. While we recognize that estimates of species decline will differ depending the particular method

⁴ (<http://www.fishbase.org>)

⁵ (<http://www.desertfishes.org/na/gis/index.html>)

⁶ (<http://nhd.usgs.gov/>)

TABLE 2. Freshwater nonnative ($n = 62$) fish species of the Colorado River Basin examined in our study.

Family and species	Common name	Species code
Catostomidae		
<i>Catostomus ardens</i>	Utah sucker	1
<i>Catostomus catostomus</i>	longnose sucker	2
<i>Catostomus commersonii</i>	white sucker	3
<i>Catostomus plebeius</i>	Rio Grande sucker	4
<i>Ictiobus bubalus</i>	smallmouth buffalo	5
<i>Ictiobus cyprinellus</i>	bigmouth buffalo	6
<i>Ictiobus niger</i>	black buffalo	7
Centrarchidae		
<i>Ambloplites rupestris</i>	rock bass	8
<i>Lepomis gulosus</i>	warmouth	9
<i>Lepomis cyanellus</i>	green sunfish	10
<i>Lepomis gibbosus</i>	pumpkinseed	11
<i>Lepomis macrochirus</i>	bluegill	12
<i>Lepomis microlophus</i>	reardear sunfish	13
<i>Micropterus dolomieu</i>	smallmouth bass	14
<i>Micropterus punctulatus</i>	spotted bass	15
<i>Micropterus salmoides</i>	largemouth bass	16
<i>Pomoxis annularis</i>	white crappie	17
<i>Pomoxis nigromaculatus</i>	black crappie	18
Cichlidae		
<i>Herichthys cyanoguttatus</i>	Rio Grande cichlid	19
<i>Archocentrus nigrofasciatus</i>	convict cichlid	20
<i>Oreochromis aureus</i>	blue tilapia	21
<i>Oreochromis mossambica</i>	Mozambique tilapia	22
<i>Tilapia zilli</i>	redbelly tilapia	23
Clupeidae		
<i>Dorosoma cepedianum</i>	gizzard shad	24
<i>Dorosoma petenense</i>	threadfin shad	25
Cyprinidae		
<i>Carassius auratus</i>	goldfish	26
<i>Ctenopharyngodon idellus</i>	grass carp	27
<i>Cyprinella lutrensis</i>	red shiner	28
<i>Cyprinus carpio</i>	common carp	29
<i>Gila atraria</i>	Utah chub	30
<i>Hybognathus hankinsoni</i>	brassy minnow	31
<i>Notemigonus crysoleucus</i>	golden shiner	32
<i>Notropis stramineus</i>	sand shiner	33
<i>Pimephales promelas</i>	fathead minnow	34
<i>Rhinichthys cataractae</i>	longnose dace	35
<i>Richardsonius balteatus</i>	redside shiner	36
<i>Semotilus atromaculatus</i>	creek chub	37
Esocidae		
<i>Esox lucius</i>	northern pike	38
Fundulidae		
<i>Fundulus sciadicus</i>	plains topminnow	39
<i>Fundulus zebrinus</i>	plains killifish	40
Gasterosteidae		
<i>Culaea inconstans</i>	brook stickleback	41
Ictaluridae		
<i>Ameiurus melas</i>	black bullhead	42
<i>Ameiurus natalis</i>	yellow bullhead	43
<i>Ameiurus nebulosus</i>	brown bullhead	44
<i>Ictalurus punctatus</i>	channel catfish	45
<i>Pylodictis olivaris</i>	flathead catfish	46
Moronidae		
<i>Morone chrysops</i>	white bass	47
<i>Morone mississippiensis</i>	yellow bass	48
<i>Morone saxatilis</i>	striped bass	49
Percidae		
<i>Perca flavescens</i>	yellow perch	50
<i>Sander vitreus</i>	walleye	51

TABLE 2. Continued.

Family and species	Common name	Species code
Poeciliidae		
<i>Gambusia affinis</i>	western mosquitofish	52
<i>Poecilia latipinna</i>	sailfin molly	53
<i>Poecilia mexicana</i>	shortfin molly	54
<i>Poecilia reticulata</i>	guppy	55
Salmonidae		
<i>Oncorhynchus mykiss</i>	rainbow trout	56
<i>Oncorhynchus mykiss aguabonita</i>	golden trout	57
<i>Oncorhynchus nerka</i>	kokanee	58
<i>Salmo trutta</i>	brown trout	59
<i>Salvelinus fontinalis</i>	brook trout	60
<i>Salvelinus namaycush</i>	lake trout	61
<i>Thymallus arcticus</i>	arctic grayling	62

Note: Nomenclature follows Nelson et al. (2004).

of quantification, e.g., point data versus range size based on atlas data (see Telfer et al. 2002), our estimate of the percentage of decline was highly correlated with the probability of local extirpation ($R = 0.90$, $P < 0.05$) reported by Fagan et al. (2002). Nonnative species' rate of spread (km/yr) was calculated as the species' extant distribution divided by the number of years since introduction (calculated from 2000 and estimated from Table 6 of Mueller and Marsh (2002) or alternatively defined as the year of first occurrence in the SON-FISHES database). These estimates of spread reflect both natural and human-aided dispersal for several recreational and bait fish species; the relative roles of which are difficult to differentiate. We refer the reader to Olden and Poff (2005) for additional methodological details.

Statistical analyses

Phylogenetic history and shared ancestral characters may mean that related species are not independent sampling units, and therefore the potential effect of phylogeny on ecological patterns should be accounted for prior to analyzing comparative data (Fisher and Owens 2004). Given the broad taxonomic diversity of the species pool examined in this study (15 families, 49 genera), ecological constraint is much more likely to explain geographical patterns than phylogenetic constraint (Westoby et al. 1995). Therefore, rather than employing phylogenetic contrasts (Felsenstein 1985) for this diverse group, we followed Grafen (1989) and calculated phylogenetic relatedness by ranking fish families by the degree of derived characters from most ancient to the most derived based on Nelson (1994) and Lee et al. (1980), and then used this information to compute a phylogenetic distance matrix (see Kolar and Lodge 2002). Next, a matrix of trait similarities for the 90 fish species according to the 22 biological attributes was calculated using Gower's similarity coefficient, a multivariate similarity index able to accommodate mixed data types (Legendre and Legendre 1998). Using a modified version of the technique pre-

sented by Diniz-Filho et al. (1998), we partitioned the total variance in the biological trait distance matrix into its phylogenetic and specific components using a Mantel test, which essentially correlates two distance matrices that have been unfolded into single column vectors. We regressed the phylogenetic matrix against the trait matrix to derive a residual matrix that represents trait similarities among species after controlling for phylogenetic similarities. The Mantel test showed a non-significant correlation between the trait and phylogenetic distance matrices (Mantel's standardized $R = 0.25$, $P = 0.08$), indicating only a marginal degree of phylogenetic constraint. Principal coordinate analysis (PCoA) was then performed on the residual similarity matrix to summarize the dominant patterns of variation among the biological traits and examine functional similarities and differences among native and nonnative species. In all cases only the first two principal components were statistically significant (based on the broken-stick rule: Legendre and Legendre 1998), and they were used to facilitate visual interpretation of the resulting plots.

To evaluate the fish life-history continuum model we followed Winemiller and Rose (1992) by plotting species' positions in relation to three life-history axes: (1) \log_e maturation size (a surrogate of maturation age that is highly correlated with maturation size in our study, $R^2 = 0.81$); (2) \log_e mean fecundity; and (3) investment per progeny (calculated as the sum of \log_e [egg diameter] and \log_e [parental care]). Our analysis was twofold. First, we visually assessed the association between species' positions in trivariate life-history space and empirical estimates of native distributional declines and nonnative rates of spread. Second, linear regression analysis was conducted to assess the relationship between life-history overlap and species' distributional changes. A measure of life-history overlap was calculated as the inverse of the Euclidean distance in trivariate life-history space between each species' position and the centroid of the opposing species pool (e.g., each nonnative species in relation to the entire

native species pool, and vice-versa). This calculation was based on z -scored trait values (i.e., standardized range between 0 and 1 for each trait) to ensure equal contributions of the three life-history axes. To examine the interaction between life history overlap and fit to the changing environment (i.e., control for “new” niche opportunities provided by historically recent reservoirs) we ran separate analyses for species preferring slow current velocities and species preferring moderate to fast current velocities.

RESULTS

Ecological niches of native and nonnative fishes

In support of our first hypothesis, the ecological niches (according to all biological traits) for the native and nonnative fish species pools differed substantially (Fig. 1). The first two principal components of the PCoA explained 35.5% of the total trait variation; additional (nonsignificant) axes did not alter the interpretation of results. The most striking pattern was that the nonnative species pool occupied most of the ordination space and therefore exhibited much greater niche diversity compared to the native species pool. The first principal axis identified a trait gradient that contrasted the native fishes occurring mostly in the right-hand side of the ordination from the majority of nonnative fishes that occurred in the left-hand side of the ordination ($t_{88} = 2.54$, $P = 0.01$; Fig. 1B). With the exception of the razorback sucker and bonytail, the entire lower-left quadrant of the ordination space was comprised of nonnative species that exhibit unique functional attributes, including species of buffalo, channel catfish, common carp, red shiner, and northern pike (Fig. 1A, see Table 2 for scientific names). This “new” niche space occupied by nonnatives can largely be characterized by a number of traits, including lack of dependence on fluvial conditions to complete the life cycle, preference for slow currents and warm water, omnivory, variable spawning substrate requirements, maturation at an early age and smaller size, production of smaller eggs that hatch quickly, and larger swim factors (Fig. 1C).

Comparative life-history strategies of native and nonnative fishes

Positions of the Colorado River fishes in relation to the three demographic axes of the life-history continuum model provided strong evidence for the basic form of the triangular adaptive surface and were found to span the numeric range of life-history values presented by Winemiller and Rose (1992) for North American fishes. As predicted by our second hypothesis, native and nonnative species pools occupied very different positions on the adaptive surface anchored by the periodic, opportunistic, and equilibrium strategy endpoints (Fig. 2). The native species pool, with the exception of *Gila topminnow* and *cutthroat trout*, occu-

ried intermediate positions within the life-history continuum rather than the endpoint regions defining the distinct life-history strategies (see Appendix C for triplot with species' labels). In fact, the majority of native fishes were located along a linear axis connecting the opportunistic endpoint and the midpoint of the edge connecting the periodic and equilibrium endpoints. Notable exceptions included species that showed closer, albeit weak, affiliations to the equilibrium endpoint, including trout species, loach minnow, and speckled dace. In contrast, nonnative species were represented across the entire adaptive surface and occupied all three endpoints—the periodic (e.g., common carp, striped bass), opportunist (e.g., guppy, western mosquitofish), and equilibrium (e.g., bullhead species, channel catfish, lake trout, smallmouth bass) strategies. Of particular interest was that the positions of nonnative fishes strongly defined the edge joining the opportunist and periodic strategies (Fig. 2).

Life-history strategies and fish distributional trends in Lower Colorado River Basin

In agreement with our third hypothesis, rates of native species decline and nonnative species spread over the past 150 years varied across the life-history strategies. Native species located closest to the periodic, opportunistic, and equilibrium strategies showed relatively large declines compared to native species occupying more intermediate positions in life-history space (Fig. 3A). Species exhibiting the greatest distributional declines include Colorado pikeminnow, desert pupfish, Moapa dace, and bonytail (Appendix D). For nonnative species, equilibrium strategists and species positioned along the life-history axis joining the opportunistic and equilibrium endpoints exhibited the highest rates of spread (Fig. 3B). This included the three fastest spreading species: fathead minnow, green sunfish, and red shiner (Appendix D). In contrast, nonnative species located in closer proximity to the periodic strategy region tended to show relatively lower rates of spread.

Three striking patterns emerged when comparing distributional trends of native and nonnative species to their positions in life-history space (Fig. 3). First, along the axis joining the opportunistic and equilibrium life-history strategies, we found strong concordance between those native species exhibiting the greatest declines and those nonnative species exhibiting the fastest rates of spread. Second, native species near the periodic endpoint had the greatest distributional declines, but they showed no life-history overlap with fast spreading, nonnative fishes, which were generally absent from this area of adaptive space. Regression analysis revealed no relationship between percent native decline and the degree of life-history overlap with the nonnative species pool for native species preferring slow water habitats (slope = -0.25 , $F_{1,1} = 0.07$, $P = 0.84$, $R^2 = 0.06$; Fig. 4A), but a significant negative relationship for na-

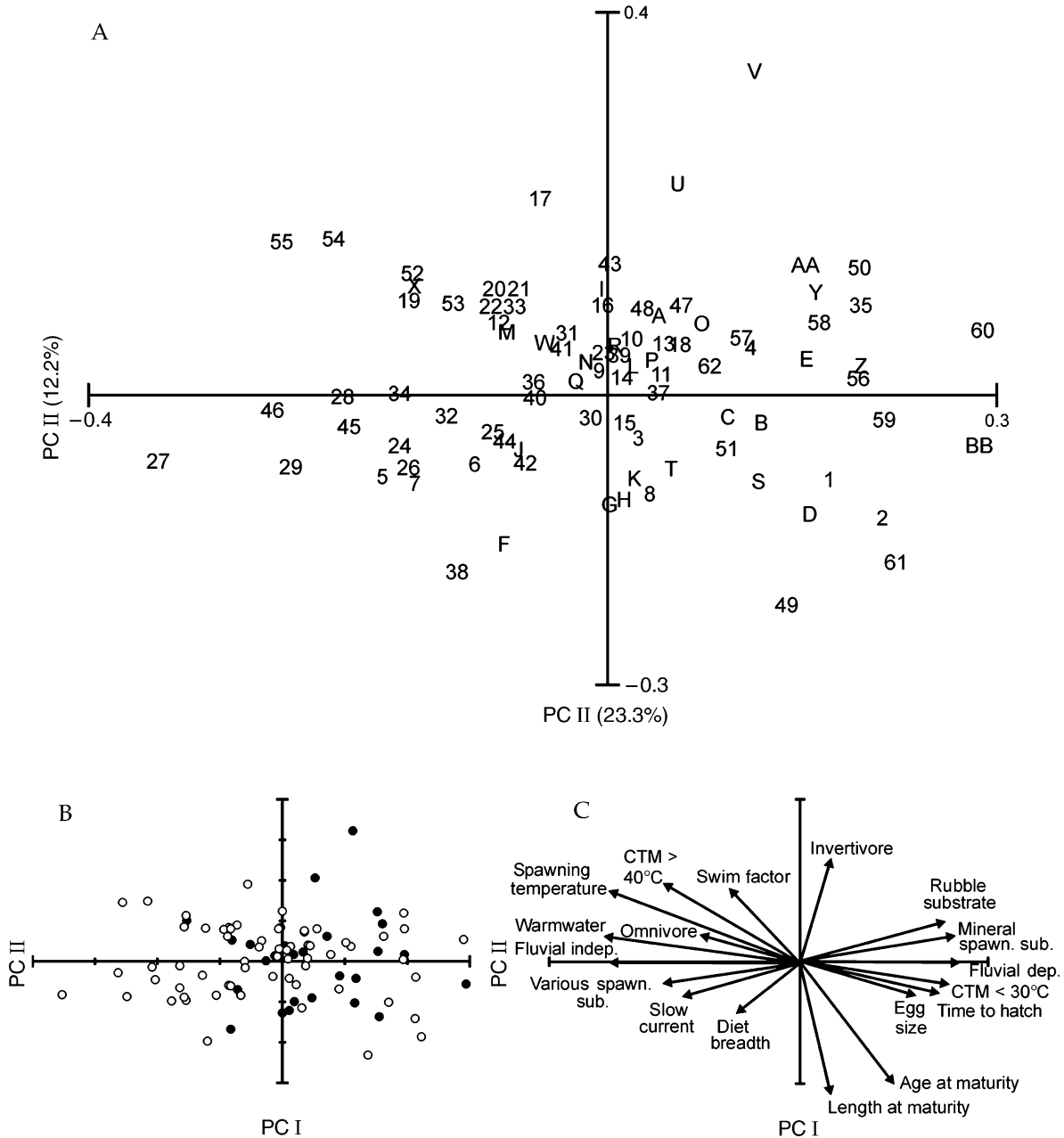


FIG. 1. Two-dimensional ordination plots resulting from the principal coordinate analysis on the 22 biological traits for the 90 fish species comprising the native and nonnative fish species pools of the Colorado River Basin: (A) fish species biplot where letter and number codes refer to native and nonnative species, respectively (identified in Tables 1 and 2); (B) fish species biplot where solid circles represent native species and open circles represent nonnative species; (C) eigenvector plot of the traits with the highest combined loadings (>0.50) on the first two principal components (see *Methods* for full trait descriptions).

tive species preferring moderate-fast water habitats (slope = -0.55, $F_{1,18} = 7.85$, $P = 0.01$, $R^2 = 0.30$). Third, nonnative opportunists exhibited the highest rates of spread, which also corresponded with a volume of life-history space that was completely devoid of native species. For nonnative species preferring slow current velocities (i.e., presumably those species provided

niche opportunities in historically recent reservoirs) we found no relationship between rate of spread and life-history overlap with native species (slope = 0.15, $F_{1,24} = 0.57$, $P = 0.46$, $R^2 = 0.02$; Fig. 4B), whereas we found a significant negative relationship for nonnative species preferring moderate-fast current velocities (slope = -0.46, $F_{1,19} = 5.02$, $P = 0.04$, $R^2 = 0.21$).

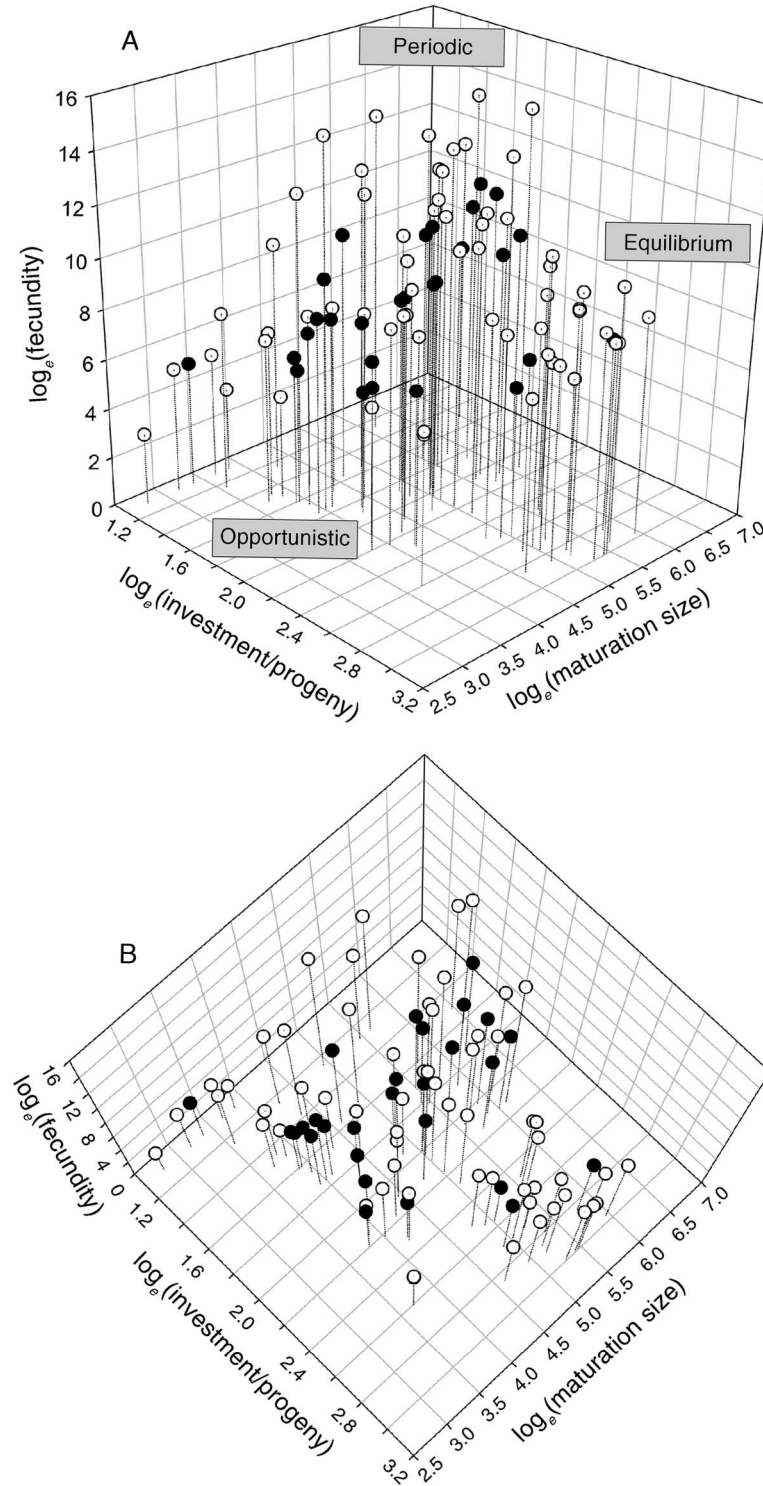


FIG. 2. Three-dimensional plot of $\log_e(\text{maturation length})$, $\log_e(\text{mean fecundity})$, and relative investment per progeny (a surrogate of juvenile survivorship that was equal to $\log_e[(\text{egg diameter} + 1)(\text{parental care} + 1)]$) for the fishes of the Colorado River Basin according to the trilateral continuum model of fish life histories (Winemiller and Rose 1992). Native species are represented by solid symbols, and nonnative species are represented by open symbols; the positions of the periodic, opportunistic, and equilibrium strategies are also shown. Panels (A) and (B) are the same plots from different vertical perspectives. Appendix C contains the plot with species' labels according to Tables 1 and 2.

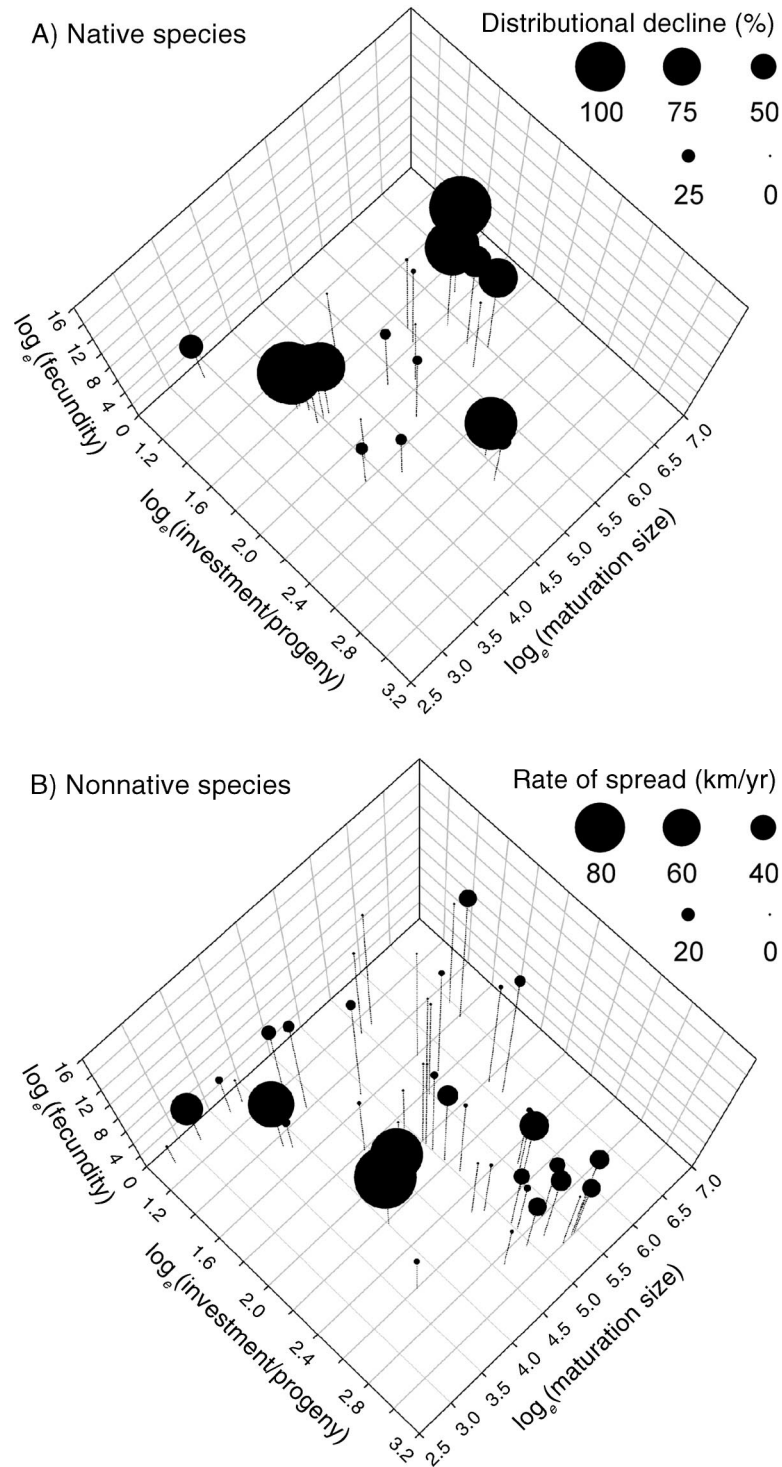


FIG. 3. Three-dimensional plot of $\log_e(\text{maturation length})$, $\log_e(\text{mean fecundity})$, and relative investment per progeny (a surrogate of juvenile survivorship that was equal to $\log_e[(\text{egg diameter} + 1)(\text{parental care} + 1)]$) for (A) native and (B) nonnative fishes of the Colorado River Basin. The size of the symbols is scaled to the percentage of distributional decline for native species and rate of spread for nonnative fishes. See Fig. 2 for the position of the periodic, opportunistic, and equilibrium strategies.

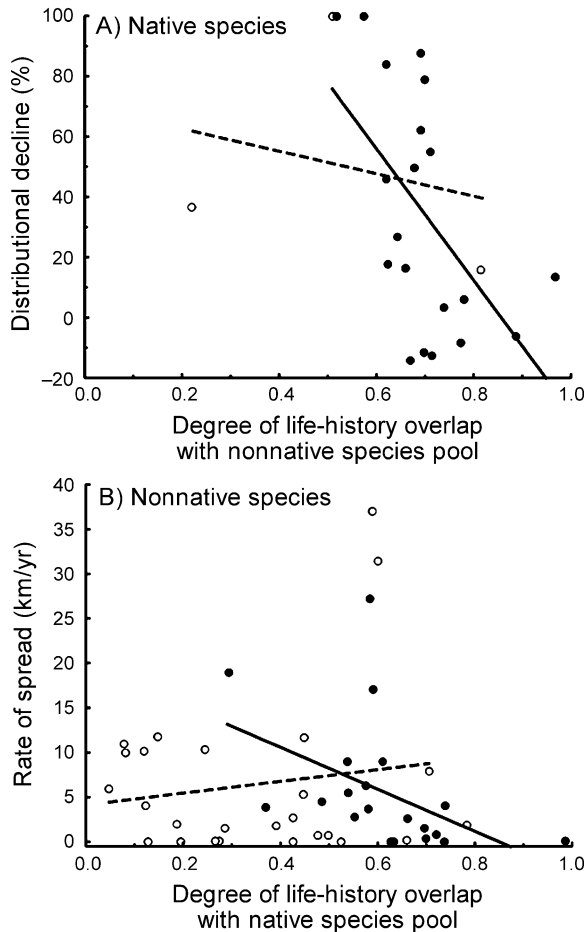


FIG. 4. Relationships (A) between the distributional decline of native species and the degree of life-history overlap with the nonnative species pool and (B) between the rate of spread of nonnative species and the degree of life-history overlap with the native species pool. Life-history overlap was calculated as the inverse of the Euclidean distance in trivariate life-history space between each species' position and the centroid of the opposing species pool. Species preferring slow current velocities are represented by open symbols and a dashed line; species preferring moderate to fast current velocities are represented by solid symbols and a solid line. According to linear regression analysis, for both native and nonnative species preferring moderate/fast water habitats there was a significant negative relationship ($P = 0.01$ and $P = 0.04$, respectively), whereas no significant relationship existed for species preferring slow water habitats ($P = 0.84$ and $P = 0.46$, respectively).

DISCUSSION

The present study utilizes contemporary ecological niche theory and fish life-history theory to explore the mechanisms responsible for patterns and rates of fish invasions and extirpations in the Colorado River Basin over the past century and a half. Although species' traits have been used as correlates of introduction success (e.g., Kolar and Lodge 2002, Marchetti et al. 2004) and extirpation events (e.g., Angermeier 1995, Reyn-

olds et al. 2005), our study takes a comparative trait approach of the entire contemporary fish species pools. With this approach we are able to make strong inferences regarding the roles of biotic and abiotic drivers in shaping long-term distributional trends of native and nonnative fishes in the Colorado River Basin.

Our findings illustrate the utility of the "niche opportunity" construct (Shea and Chesson 2002) to interpret historical changes in the species pool. In the context of adaptations for alternative environments, we found that traits expressed by members of the nonnative fish species pool (but not the native pool) provide a distinct, functional signature that likely reflects niche opportunities arising from long-term environmental changes in the Colorado River Basin. Specifically, these nonnative fishes include many that prefer slow-moving, warm waters, that are trophic generalists, and that are generally weaker swimmers not requiring fluvial conditions to complete their life cycle. This finding is consistent with the transformation of a substantial portion of the surface waters in the Colorado River Basin from lotic habitat to lentic reservoirs and associated stabilization of flow regimes below dams (Carlson and Muth 1989, Mueller and Marsh 2002). Niche opportunities for these nonnative fishes are further enhanced by river regulation because native species are less well adapted and largely absent from these "novel" environments. Thus, while many nonnatives occupy similar habitats with native species, the overall functional breadth of the contemporary species pool has been increased by fish invasions. These findings have a number of important ramifications for linking patterns of anthropogenic alteration to functional aspects of community structure, including functional redundancy (Rosenfeld 2002), diversity (Petchey et al. 2004), and regularity (Mouillot et al. 2005). Research in this area is currently in progress.

Our findings support the value of using the W-R model for studying fish invasions and extinctions, insofar as a species' position in this life-history continuum can be interpreted in terms of adaptation to the relative intensity and predictability of temporal and spatial variation in abiotic environmental conditions, food availability, and predation pressure. In agreement with our predictions, the relative positions of the native and nonnative species in life-history space reflected those life-history strategies that are differentially favored in historical versus contemporary (and highly altered) environments of the Colorado River Basin. The majority of native fishes were located along a life-history axis connecting the opportunistic endpoint to the midpoint of the edge attaching the periodic and equilibrium endpoints. This axis presumably defines a gradient of evolutionary "bet-hedging" considered adaptive in highly unpredictable environments where conditions are occasionally so bad that recruitment fails entirely (Cohen 1966, Stearns 1992). Historical conditions of the lower basin could be broadly character-

ized as extreme and often unpredictable (Fradkin 1981), contributing to the bet-hedging strategies long noted for many native species (e.g., Minckley and Deacon 1968). In contrast, nonnative species were found to occupy the entire life-history space that included an extended coverage into the three endpoint regions. A striking pattern was that several nonnative species were conspicuously located in the equilibrium region of the adaptive surface that was vacant of native species. The equilibrium strategy, largely synonymous with the traditional *K* strategy of adaptation to life in resource-limited or density-dependent environments (Pianka 1970), is considered advantageous in environments with low variation in habitat quality and strong direct and indirect biotic interactions (Winemiller and Rose 1992), conditions that are arguably more typical of present-day environmental conditions.

We found that long-term distributional trends for native and nonnative fishes in the Lower Colorado River Basin varied substantially among life-history strategies and that the direction of change was strongly concordant with fish life-history theory (Winemiller and Rose 1992). While no species can simultaneously maximize all three life-history axes, the fastest spreading nonnative species were distinctly positioned along the opportunistic-equilibrium continuum, suggesting that species optimizing the trade-off between maturation size and progeny investment at the expense of maximizing fecundity have generally had greater rates of population expansion. These species can be interpreted as having traits enhancing the ability to withstand periods of unfavorable environmental conditions and allow for better recruitment (i.e., opportunistic strategy), while still exhibiting more stable populations within constant environmental regimes (i.e., equilibrium strategy). The fact that equilibrium strategists have shown the fastest rates of invasion also support the predictions of McCann (1998) who used a series of stage-structured competition models to suggest that this strategy should be competitively dominant in environments promoting high juvenile density dependence (e.g., low juvenile resource densities and high levels of predation). Indeed, the present-day conditions of the Lower Colorado River are generally characterized by high juvenile predation pressure associated with greater numbers of piscivorous fishes (predominantly nonnatives) and increased resource limitation resulting from reduced inundation of floodplains due to river regulation (Minckley et al. 2003).

Theoretical and empirical evidence suggest that invasions are most likely to occur in areas exhibiting either low environmental resistance or low biological resistance (Case 1991). The relative roles of these processes have been a topic of lively debate in ecology (e.g., Kennedy et al. 2002), and limited evidence for freshwater fishes suggest that environmental resistance may play a more important role (e.g., Baltz and Moyle 1993, Moyle and Light 1996, Gido and Brown 1999).

Our study offers a unique functional perspective on this hypothesis by combining predictions from life-history theory with long-term data on species' distributional trends. We found that invasion rates of nonnative species presented with "niche opportunities" (i.e., those preferring newly created slow-current habitats associated with reservoirs) were independent of life-history overlap with the native species pool. In contrast, spread of nonnatives preferring more lotic habitat (moderate to fast current velocities) showed a strong negative relationship with life-history overlap with native species. These findings suggest that biotic resistance may be particularly important for nonnative species' spread when ecological niche overlap with natives is taken into account. Such "context dependent" biotic resistance may help explain the highly variable and complex nature by which species diversity influence the invasion resistance of communities (Levine and D'Antonio 1999, Levine et al. 2004). Specifically, Shea and Chesson (2002) predicted a negative association between native species and exotic species richness after controlling for covarying extrinsic factors. Here, we argue that the "extrinsic factors" are enhanced niche opportunities for invaders in reservoirs, and when matched for similar environmental requirements (riverine habitats), rates of exotic spread are reduced by native species.

In terms of the native ichthyofauna, fishes exhibiting the greatest historical declines in the Lower Colorado River Basin were confined primarily to two distinct regions in life-history adaptive space. The first group of native species fell along the axis connecting the opportunistic and equilibrium strategies, the same axis dominated by rapidly spreading nonnative species. This pattern is consistent with the hypothesis that these native and nonnative species are, in a sense, vying for this shared life-history space, thus establishing a potential for predation and competition with nonnative species to play an important role in population decline. The second group of declining native species was located in close proximity to the periodic endpoint, an area in life-history space that conspicuously lacks nonnative species. Compared to the other strategies, periodic life-histories are considered to be the least adapted to present-day environmental conditions that have become temporally stable (i.e., nonseasonal) and are subjected to high levels of predation from nonnative species and low resource availability due to decreased inundation of floodplains from damming.

A particularly interesting pattern was the negative relationship between native species decline and life-history overlap with nonnative species. This relationship, however, likely reflects the fact that our analysis is based on adult traits and therefore does not account for overlap that may occur at early life stages where interactions (primarily predation) between native and nonnatives are evident (Minckley 1991). This observation emphasizes the point that there is a clear need

to consider many different ecological mechanisms in broad-scale studies that attempt to explain patterns of species occurrence (Peres-Neto et al. 2001). For example, to better understand the mechanisms responsible for the positive association between riverine fragmentation and native species rarity in the Colorado River as shown by Fagan et al. (2002), we need to carefully consider species' niche requirements and their relation to both changing environmental templates and their niche relations with other species in the regional pool. In support of this idea, our research suggests that ecological and life-history traits may differentially predispose native fish species to rarity, probability of extirpation, and extinction risk from different sources of threat (Olden 2004).

In this study, we used ecological niche theory and the life-history model of Winemiller and Rose (1992) as complementary tools for understanding the mechanisms responsible for long-term trends in fish invasions and extirpations in the Colorado River Basin. The life-history approach emphasizes key processes of reproduction and survivorship in broad environmental settings, whereas the ecological niche approach more explicitly links species traits to specific environmental conditions, both abiotic and biotic. By combining these two approaches, we identified fish species having similar life-history strategies and broad environmental requirements and then made inferences about potential interactions with regard to competition and predation. We believe this approach shows general promise for invasion ecology, and its success will likely reflect the precision with which life history and ecological attributes of entire species pools can be quantified.

In conclusion, life-history theory and the ecological niche concept provide a basis to develop conceptual models to help conserve native species and create risk-assessment protocols for nonnative fishes based on generalized population dynamics and responses to environmental conditions (Winemiller 2005; see King and McFarlane 2003 for an example in marine fisheries). Present-day conservation plans for native fishes of the lower Colorado River focus on demographic principles and minimizing interactions with nonnative fishes (Minckley et al. 2003). Our results are not inconsistent with this view; however, they further emphasize the importance of how biotic and abiotic factors may interact to place native species at risk to extinction. Indeed, for some species such as periodic strategists, restoration of natural habitat templates (in particular, flow regimes; Poff et al. [1997]), may be required, as suggested by recent research (Osmundson et al. 2002). Despite the complexities of managing for native fishes with disparate life-histories, ecological requirements and varying susceptibilities to nonnative fishes (Rinne and Stefferud 1999), we believe application of life history theory and the ecological niche concept to the fields of conservation and invasion biology will permit a broader understanding of how to

reconcile the many, and often conflicting, requirements for the conservation of imperiled fishes in the American Southwest.

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APPENDIX A

A list of sources of literature for compiling the present-day fish species list of the Colorado River Basin (*Ecological Archives* M076-002-A1).

APPENDIX B

Trait values for the freshwater native and nonnative fish species of the Colorado River Basin examined in our study (*Ecological Archives* M076-002-A2).

APPENDIX C

A three-dimensional plot of $\log_e(\text{maturation length})$, $\log_e(\text{mean fecundity})$, and relative investment per progeny for the fishes of the Colorado River Basin according to the trilateral continuum model of fish life histories presented by Winemiller and Rose (1992) (*Ecological Archives* M076-002-A3).

APPENDIX D

Distributional changes for native ($n = 23$) and nonnative ($n = 47$) fishes of the lower Colorado River Basin estimated using the SONFISHES database (*Ecological Archives* M076-002-A4).