Quantifying Rarity, Losses, and Risks for Native Fishes of the Lower Colorado River Basin: Implications for Conservation Listing

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Abstract: *We examined spatial distributions of fishes native to the lower basin of the Colorado River (25 species) at three scales to determine percent decline from historical distributions based on a regional biodiversity database. We cumulated records from 1843 to 1980 to develop a "historical distribution" for each species and used those occurrences recorded from 1981 to 1998 as "modern" records. We then contrasted historical and modern distributions to (1) quantify losses in spatial distribution; (2) determine how strongly these losses and fragmentation patterns corresponded to the perceived risk of extinction of each species, as represented by its status under the IUCN Red List of Endangered Species; and (3) update extinction risk rankings for 15 fishes endemic to the lower Colorado Basin according to the IUCN criteria. Based on presence and absence data, fish fauna of the lower Colorado Basin have suffered massive distributional losses. On average, ranges of extant species have diminished more than 45% relative to their historical distribution, and 35% of species have lost 50% or more of their occurrences. We provide nine new IUCN rankings and six updates to reflect more accurately the heightened imperilment of these species. Based on our new rankings, 7 of the 15 lower Colorado Basin endemics are critically endangered, 1 is endangered, 2 are vulnerable, and 1 is already extinct. We categorize the remaining 2 endemics as lower risk. This work demonstrates the utility of matching quantitative spatial metrics such as the scale-area slope statistic to extinction risk criteria for species whose persistence is strongly influenced by spatial distribution.*

Key Words: extinction risk, fish distributions, fish spatial distribution, IUCN criteria, quantitative spatial metrics, scale-area slope

Cuantificación de Rareza, Pérdidas y Riesgos para Peces Nativos de la Cuenca Baja del Río Colorado: Implicaciones para las Listas de Conservación

Resumen: *Examinamos la distribución espacial de peces nativos de la cuenca baja del Río Colorado (25 especies) en tres escalas para determinar el porcentaje de declinación de sus distribuciones históricas a partir de una base de datos de biodiversidad regional. Acumulamos registros de 1843 a 1980 para desarrollar una "distribución histórica" de cada especie y consideramos a las ocurrencias de 1981 a 1998 como registros "modernos". Posteriormente contrastamos las distribuciones históricas y modernas para (1) cuantificar pérdidas de distribución espacial; (2) determinar el grado en que estas pérdidas y patrones de fragmentación correspondieron con el riesgo de extinción percibido para cada especie, representado por su estatus en la Lista Roja de Especies en Peligro de IUCN (IUCN, Unión Mundial para la Conservación) y (3) actualizar la clasificación de riesgo de extinción de 15 peces endémicos a la cuenca baja del Río Colorado, de acuerdo con criterios de la IUCN. Con base en datos de presencia y ausencia, la fauna de peces del bajo Rió Colorado ha sufrido reducciones de distribución masivas. En promedio, la distribución de especies actuales ha disminuido más de 45% en relación con su distribución histórica, y 35% de las especies han perdido 50% o más de sus registros.*

Proporcionamos nueve posiciones IUCN nuevas y seis actualizaciones para reflejar el alto grado de peligro de estas especies con más precisión. Con base en nuestra nueva clasificación, 7 de las 15 especies endémicas de la Cuenca del Colorado están en peligro crítico, 1 está en peligro, 2 son vulnerables y 1 esta extinta. Clasificamos en riesgo bajo a las 2 endémicas restantes. Este trabajo demuestra la utilidad de combinar métricas espaciales cuantitativas, como el estadístico pendiente escala-área, con criterios de riesgo de extinción para especies cuya persistencia esta fuertemente influida por la distribución espacial.

Palabras Clave: criterios IUCN, distribución de peces, distribución espacial de peces, métrica espacial cuantitativa, pendiente escala-área, riesgo de extinción

Introduction

For many species extinction risk is directly linked to the absolute number of individuals remaining (Gaston 1994; Morris & Doak 2003), whereas for others extinction risk is more strongly determined by the amount and spatial distribution of habitat occupied (e.g., Hanski 1998). Desert fishes (whose population sizes can fluctuate manyfold over one or a few generations, or whose populations can be locally extirpated because of environmental factors such as droughts, floods, predation, and differential recruitment) fall into this latter category (John 1964; Deacon & Minckley 1974; Meffe & Minckley 1987; Minckley & Meffe 1987). For such species the spatial distribution of populations determines long-term recolonization potential, and changes in spatial distribution can provide direct insights into species status. In these settings biodiversity databases, which draw on museum records and other sources to characterize historical and present-day spatial distributions of species, may be particularly useful as conservation resources (Alberch 1993; Fagan et al. 2002, 2005).

Presence and absence biodiversity databases, however, have received less attention in conservation than other assets (such as time series of population counts) because of methodological difficulties. In particular, estimates of extinction risk derived from spatial data often rely on indices that depend on—and are often sensitive to—the scale of analysis (discussed in Thomas & Abery 1995; Fagan et al. 2002; Hartley & Kunin 2003). Scale-independent or multiscale metrics such as the scale-area curve (Kunin 1998) afford new opportunities to quantify how attributes of species spatial distributions are linked to extinction risk (Fagan et al. 2002, 2005; Hartley & Kunin 2003). Explicit consideration of spatial scale can alter dramatically perceptions of species rarity, rate of decline, and range fragmentation. Therefore, established systems for categorizing species with regard to the relative risks of extinction, such as the IUCN Red List categories and criteria (IUCN [World Conservation Union] 2001), need to incorporate spatial scale more directly (Hartley & Kunin 2003).

We used a multiscale strategy to quantify changes in spatial distribution for 25 species of native fishes within the Colorado River system (southwestern United States and northwestern Mexico) (Minckley & Deacon 1968;

Minckley 1973, 1991). Using a biodiversity database of presence and absence data, we quantified distributional losses of fishes over a 155-year period and characterized future risk potential for this diverse assemblage of native fishes. Our goal was to explore how strongly the observed changes in spatial distributions correspond to the perceived risks of extinction for each species, as represented by their current status under the IUCN Red Lists. We asked two questions: (1) Are species that have suffered greater distributional losses (relative to their historical distributions) ranked higher on the red list than those species that suffered smaller losses? and (2) Is range fragmentation—which constitutes a key threat to persistence of many lower Colorado Basin fishes (Fagan et al. 2002, 2005)—reflected in the threat rankings for these species? The answers to these two questions were generally no, and as a result we developed an updated set of red-list extinction risk rankings for 15 endemic fishes based on the spatial database.

Methods

SONFISHES

The Sonoran Fishes (or SONFISHES) database, initially developed by the late ichthyologist W. L. Minckley, contains extensive distributional data for native freshwater fishes in the southwestern United States and northwestern Mexico. Much of this landscape lacks perennial water because of the interplay among precipitation, discharge, and substrate and more recently as a result of diversion and desiccation through human activities (Brown et al. 1981). The SONFISHES database has 155 years (from 1843 to 1998) of data; it contains incidence, identity, and collection data from the complete holdings of the major museum collections from this region and numerous smaller collections of southwestern fishes and records from the Non-Game Branch of the Arizona Game and Fish Department and peer-reviewed and gray literature sources. Because of the intensity and time span of sampling, SONFISHES summarizes virtually all that is known about past and present distributions of fishes in the region and represents an unusually comprehensive resource for examining changes in species spatial distributions over time.

We focused on 25 native species of stream- and river-dwelling fishes from the lower Colorado Basin, which includes both Mexican and U.S. reaches, including all tributaries between Glen Canyon Dam (northern Arizona) and the Gulf of California, except the Salton Sea. A total of 25,970 km of stream drains 331,500 km^2 of landscape. Fifteen of the 25 native species are endemic to the lower Colorado Basin; thus our database covers their global range. The remaining 10 native species also occur outside the lower Colorado Basin (Table 1). The SONFISHES database contains more than 20,000 georeferenced locality records of these 25 native freshwater fishes (representing millions of specimens). Only natural occurrences of native fishes were included. Known translocations were excluded because of their low survivorship and reproduction and their dependence on artificial habitats (Hendrickson & Brooks 1991).

In a database of the scope of SONFISHES, sampling intensity varies over time. The first major collections (1843–1860) were associated with the United States-Mexican border survey (1843–1860) (Emory 1857). From 1920 to 1980 surveys were conducted by academic scientists (Miller & Hubbs 1960; Miller 1961; Minckley & Deacon 1968; Minckley 1973; Miller et al. 1991). After 1980 intense surveys were conducted by state and federal agencies to document the remnant distributions of native fishes. Consequently a convenient break in the SONFISHES database occurs around 1980, when survey efforts by academicians gave way to extensive and systematic sampling by state and federal agencies. Although the pre- and post-1980 time periods differ in temporal length, they are comparable in sampling effort because of the intense sampling adopted after 1980. Indeed, 61% of the database records in SONFISHES were taken after 1980.

Temporally heterogeneous sampling is a problem in analyses of biodiversity databases (Dobyns 1997; Gibbons et al. 1997; Moreno & Halffter 2000; Brose et al. 2003). By dividing the database into two broad time frames rather than focusing on year-to-year transitions, however, we diminished inherent biases. Specifically, we cumulated occurrence records from 1843 through 1980 to develop a "historical distribution" and from 1981 through 1998 to develop a "modern distribution" for each species (Fig. 1; see also Fagan et al. 2002). The two exceptions were the trouts *Oncorhynchus gilae* and *O. apache*, whose modern distributions were determined after 1999 (Brown et al. 2001; L. Ruiz, personal communication, respectively), based on distributional changes revealed after catastrophic wildfires. Our conclusions about extinction losses are insensitive to the use of 1980 as the breakpoint between the historical and modern periods (Fagan et al. 2005; see also Results).

Evaluating Distributional Change from Museum Data

Many methods have been proposed for evaluating species extirpation probabilities from museum data (Kuno 1986;

Mace & Lande 1991; Alberch 1993; McCarthy 1998). Those developed by Solow (1993*a*, 1993*b*), based on the time intervals between resightings, are among the most widely used (e.g., Burgman et al. 1995). Because of the spatial and temporal scope of SONFISHES, the lack of repeated sampling at certain collection sites, and the shift in sampling strategy after 1980, we approach extirpation probabilities differently. We estimated extirpation probabilities by dividing the database into historical and modern distributions (as described above) and then quantifying the frequency of disappearances of species from localities, with localities defined at a series of three nested hierarchical scales: 5-, 100-, and 2500-km reaches (Fig. 2). Conducting the analyses on several spatial scales provided complementary insights into how the system has changed. For example, analyses on the 5-km scale provide insight into local-scale changes in distribution and correspond to the scale on which most management actions (such as translocations [Hendrickson & Brooks 1991; Minckley 1995] or creation of off-channel habitats [Minckley et al. 2003]) would be targeted in this system. In contrast, the 2500-km scale corresponds roughly to the scale of major river basins, where watershed-wide problems would most clearly manifest. The 100-km scale provides an intermediate value on a logarithmic axis.

To determine the extent to which occurrences of each species (at the 5-, 100-, and 2500-km scales) have been extirpated, we contrasted the historical and modern distributions (Fagan et al. 2002, 2005). Calculations of extirpation probabilities yielded four possible scenarios. First, a species could occur at a site in both historical and modern times, in which case it was deemed extant. Second, a species could be absent at a locality in both historical and modern times. We treated this second case as true absences. Third, a species could be present historically at a locality but be absent in the modern period. We treated such cases as actual extirpation events. Fourth, a species could be absent historically but present in modern times. We assumed this case indicates insufficient historical sampling; thus we treated these reaches as occupied historically (see Results).

Characterizing Current Distributions and Losses

By examining spatial distributions on three scales we obtained estimates of the extent of species extirpations, both locally and regionally. Likewise, scale-area slope statistics (Kunin et al. 2000; Fagan et al. 2002, 2005; Hartley & Kunin 2003) based on the modern (i.e., after 1980) distributional data provided estimates of present-day range fragmentation. This statistic, which has values from 0 to 1, provides a scale-independent measure of the extent of fragmentation of species distributions. Scale-area slopes for the 25 Sonoran Desert fishes were calculated by Fagan et al. (2002, 2005), who also detail the use of this methodology in the context of a riverine landscape.

Table 1. Spatial rarity and listing status of native freshwater fishes in the lower Colorado Basin with proposed revisions to global IUCN rankings for fishes endemic to the lower Colorado Basin, based on distributional data from the SONFISHES database.

Taxon	Number of current occurrences			Occurrence decline from historical distribution[a] (%)			Area of occupancy[b] (km²)	Current fragmentation score[c]	Current IUCN ranking[d]	Proposed IUCN ranking	Nature of shift in IUCN ranking	Current status US[e]	Mexico[f]
	5 km	100 km	2500 km	5 km	100 km	2500 km							
Lower basin endemics[g]													
Catostomus insignis	284	65	6	25	18	0	63.0	0.49	5	4	new	5	1
Catostomus sp. (Little Colorado R.)[b]	66	16	2	8	0	0	5.1	0.44	5	4	new	5	N
Cyprinodon macularius	1	1	1	90	86	67	1.5	0.86	5	1	new	5	1
Cyprinodon arcuatus	0	0	0	100	100	100	0.0	na	5(X)	extinct	new	5(X)	N
Gila intermedia	51	19	4	39	44	20	3.7	0.70	5	1	new	5(C)	1
Gila nigra	39	9	4	33	40	0	4.3	0.68	5	1	new	5	N
Gila seminuda	17	5	1	15	17	0	2.2	0.71	5	1	new	1	N
Lepidomeda mollispinis	19	7	1	37	13	0	1.6	0.71	5	1	new	5	N
Lepidomeda vittata	35	10	2	33	23	0	2.6	0.53	3	3	no change	2	N
Meda fulgida[i]	37	11	2	52	61	50	12.9	0.66	3	2	up	2	N
Oncorhynchus apache[i]	33	6	1	46	33	67	1.7	0.63	1	3	down	2	N
Oncorhynchus gilae	6	4	1	74	50	50	0.3	1.00	2	1	up	1	N
Pantosteus clarki	396	78	8	27	17	0	70.9	0.48	5	4	new	5	5
Plagopterus argentissimus	9	3	1	57	67	67	1.3	0.80	3	1	up	1	N
Tiaroga cobitis[k]	69	17	3	22	32	25	15.0	0.56	3	4	down	2	1
Other native species													
Agosia chrysogaster	386	77	7	32	24	0	65.9	0.45	5			5	2
Catostomus latipinnis	31	10	3	64	68	57	12.2	0.76	5			5	5
Gila cypha	7	3	2	61	57	33	6.5	0.85	3			1	N
Gila elegans	3	1	1	93	95	83	4.5	0.90	2			1	1
Gila robusta	120	38	6	42	43	33	28.4	0.60	5			5	3
Pantosteus discobolus	85	23	4	38	30	20	14.3	0.52	5			5	N
Poeciliopsis occidentalis	27	6	2	53	70	67	2.4	0.63	5			1	2
Ptychocheilus lucius	0	0	0	100	100	100	0	na	3			1	1
Rhinichthys osculus	417	93	11	30	21	8	51.6	0.51	5			5	1
Xyrauchen texanus	22	6	2	70	80	71	33	0.85	2			1	1

[a] Decline from historical distribution at the 5-, 100-, and 2500-km scales, based on a comparison of species from 1840–1980 versus 1981–1998 (Fagan et al. 2002, 2005).

[b] Calculated 5 km (reach length) * the widths of occupied reaches. Each 5-km reach was assigned a width of 10, 30, 100, or 300 m.

[c] Calculated as the scale-area slope from occurrence data cumulated over the period 1981–1998 (Fagan et al. 2002).

[d] IUCN ranking from the Hilton-Taylor (2000): 1, critically endangered; 2, endangered; 3, vulnerable; 4, lower risk; 5, not threatened or not evaluated. Assessments for these IUCN rankings were last conducted in 1996.

[e] Status according to USFWS (1999): 1, endangered; 2, threatened; 5, unlisted; 5(C), unlisted but candidate for federal listing since 1973; 5(X), unlisted but extinct.

[f] Status according to SMARN (2002): 1, critically endangered; 2, endangered; 3, subject to special protection; 5, unlisted; N, no occurrences in Mexico.

[g] Taxa endemic to the lower Colorado Basin within the larger SONFISHES database region. Occurrence and occupancy data for other native species pertain only to that portion of those species' ranges occurring inside the lower Colorado Basin.

[h] A morphologically differentiated but as-yet-unnamed species Catostomus "Little Colorado R." is designated following Minckley (1973).

[i] Data collected recently suggest that the number of occurrences of this species has declined even further, and it would now warrant an IUCN ranking of 1.

[j] Would move from vulnerable to critically endangered following the loss of a single occurrence at the 100-km scale or a slight increase in its fragmentation score.

[k] Routinely present in low abundance (Minckley 1973), a factor we did not take into consideration in this analysis. Consequently, it may be more appropriate to maintain a vulnerable ranking rather than down ranking as suggested by the spatial data.
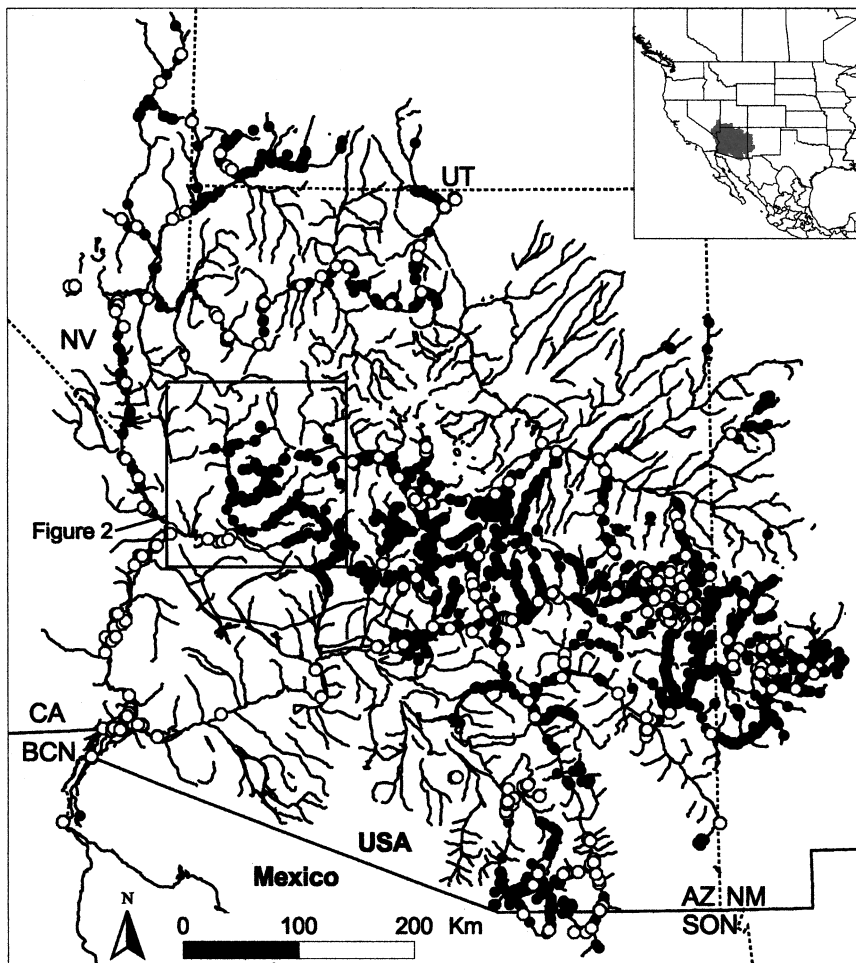
Figure 1. Map of the lower Colorado River Basin showing all collection records for native fishes. Open circles represent sites with historical records only (1980 or before), and closed circles represent sites with both historical and modern records (post-1980). Many of the stream reaches lack occurrence records due to an absence of perennial water (see text). Inset is the region appearing in Fig. 2. Abbreviations: NV, Nevada; UT, Utah; CA, California; BCN, Baja California; AZ, Arizona; NM, New Mexico; SON, Sonora.

Evaluating Extinction Risks for Lower Colorado Basin Endemics

To determine whether distributional losses and/or spatial fragmentation correspond to the perceived risk of extinction for a species, we considered how well those spatial factors correspond to extinction risk according to the IUCN Red List (Hilton-Taylor 2000). Under the IUCN's ranking scheme critically endangered species are at greater risk of extinction than endangered species, which are more at risk than vulnerable species. Each of these categories of risk is associated with a particular quantitative threshold for loss or threat (IUCN 2001). The red-list system, however, is flexible in that it allows a wide diversity of data types to inform the ranking process.

To determine how well IUCN rankings mirror the current distributions of species or their declines from historical distributions, we restricted our analyses to the 15 species endemic to the lower Colorado Basin because for nonendemic species the status of the species outside the study area would influence ranking decisions. Because our database details species spatial distributions rather than abundances, we addressed criterion B2 of the IUCN's ranking system (IUCN 2001), in which a species may be assigned to a particular risk category on the basis of its geographic "area of occupancy." To be considered critically endangered under this criterion a species must occupy < 10 km^2 of habitat, whereas the corresponding thresholds for endangered and vulnerable are 500 km^2 and 2000 km^2, respectively. In addition to having a reduced area of occupancy, a ranked species must meet two of three additional subcriteria pertaining to (1) severe fragmentation or reduced number of occurrences (specifically, 1 occurrence for critically endangered, ≤ 5 occurrences for endangered, and ≤ 10 occurrences for vulnerable), (2) continuing decline in geographic distribution, or (3) extreme fluctuations in population status (IUCN 2001). Because the area-occupancy tallies for all 15 endemic species have been shrinking for the last several decades, we assumed that subcriterion 2 has been met for all endemics. Consequently, to evaluate the current status of a species under IUCN criteria, we addressed subcriterion 1 by evaluating area of occupancy, extent of fragmentation, and number of occurrences for each species.
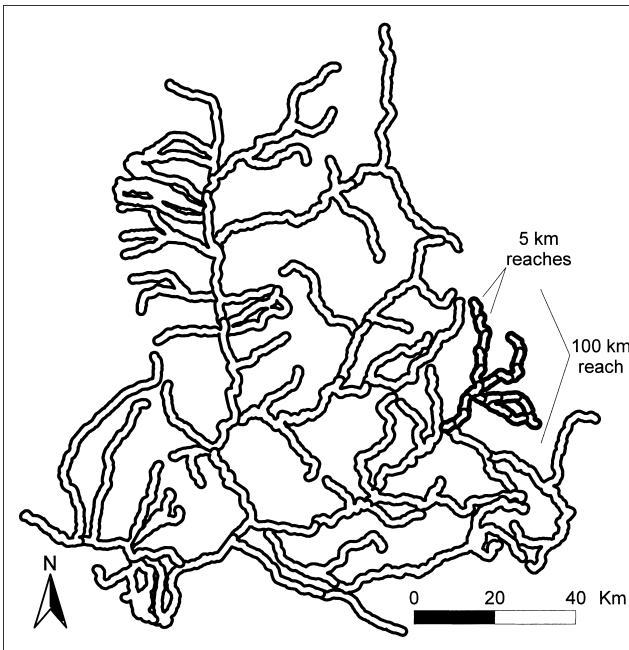
Figure 2. An exemplary 2500-km reach (the location of which is indicated by the inset box in Fig. 1), with all nested 100-km reaches marked and within one 100-km reach all 5-km reach boundaries marked.

Area of Occupancy

Under the IUCN criteria, area of occupancy is measured in two spatial dimensions (e.g., a 5 × 5 km block of habitat) and occupancy thresholds separating the different IUCN risk levels are in terms of square kilometers. These two-dimensional thresholds are somewhat difficult to apply to freshwater fishes or other lotic species (e.g., unionid mussels) for which spatial distribution patterns are frequently quantified in terms of stream reach length occupied. One option for circumventing a two-dimensional measure is to calculate area of occupancy in terms of the size of the watersheds that a fish species inhabits. This results, however, in hugely overestimating the inhabited area for any aquatic species (Keith & Marion 2002). Furthermore, for desert regions in general, substantial mismatches exist between watershed size and the amount of stream reach suitable for fishes (Brown et al. 1981) because vast portions of a desert landscape may feed into only a tiny reach of perennial water. Consequently, we opted to quantify area of occupancy for fishes in terms of reach length occupied multiplied by the average width of aquatic habitats along the stream (e.g., main stream course, side channels, backwaters). This approach reflects the procedure provisionally recommended by the IUCN for quantifying occurrence patterns in riverine systems (C. Hilton-Taylor, personal communication).

We assigned each 5-km reach to one of four average stream width categories: 10, 30, 100, or 300 m. Stream widths generally increased from headwaters to downstream but reflected the vagaries of local topography, including contributions of co-occurring main and side channels where present. We then estimated area of occupancy for each fish species as the sum of the widths of the individual 5-km reaches occupied by that species multiplied by 5 km.

Extent of Fragmentation and Number of Occurrences

We considered that species with scale-area slopes > 0.65 satisfied the IUCN's definition of severely fragmented because all native fish species of the lower Colorado Basin whose historical (i.e., before 1980) scale-area slopes exceeded 0.65 suffered at least 50% loss of local occurrences by 1980 (Fagan et al. 2002). Many of our 5-km-reach "localities" were far from independent of one another because of their small size and proximity within connected stream networks. On the other hand, our 2500-km reach would greatly overestimate occupancy for some species (e.g., at this large scale, significant portions of some reaches would be dry and hence not occupied by fish). Thus we designated the number of 100-km reaches occupied as the "number of occurrences" for each species for comparison with the IUCN subcriteria.

In summary, we considered a species critically endangered if it was estimated to occupy < 10 km^2 of habitat and either had a severely fragmented population (i.e., fragmentation score > 0.65) or had only one current occurrence (at the 100-km scale). A species was considered endangered if it occupied < 500 km^2 and had either a severely fragmented population or ≤ 5 occurrences (at the 100-km scale). A species was considered vulnerable if it occupied < 2000 km^2 and had either a severely fragmented population or ≤ 10 occurrences (at the 100-km scale). If a species had either a relatively unfragmented distribution (fragmentation score less than 0.65) or > 10 occurrences (at the 100-km scale), then it was considered lower risk.

Results

Evaluating Assumptions

Before proceeding to a complete description of our findings, we report the consequences of key assumptions underlying our analyses. First, we considered that situations in which a species was absent from a reach during the historical period but present during the modern period constituted cases of historical undersampling. If incorrect, this assumption would artifactually inflate the historical distribution for that species. Our analyses revealed that such situations were rare, however, and hence unlikely to exert a major influence on the observed patterns. For

example, cases of assumed historical undersampling occurred in only 58 of the 1107 species × reach combinations at the 100-km scale (5.2%). The fact that three relatively common species (*Agosia chrysogaster*, *Catostomus insignis*, and *Rhinichthys osculus*) were responsible for 28 of these 58 occurrences further supports our assumption that these cases represent historical undersampling. Given increasing fragmentation (i.e., desiccation) of aquatic systems through human water use, the alternative explanation of fish dispersal and colonization of a new site seems less likely, especially at the larger scales where it would have the most substantial implications for interpreting long-term declines in species distributions. Nevertheless, one alternative to treating these few cases as artifacts of historical undersampling is to exclude them from consideration when evaluating changes in species distributions. Fagan et al. (2002) adopted this approach and found that ignoring these historically undersampled occurrences did not qualitatively change any of the strong, assemblage-wide patterns evident in the database, such as the link between a highly fragmented regional distribution and an enhanced risk of local extinction.

A second major assumption was that 1980 represented a meaningful breakpoint between the historical and modern periods. To evaluate whether this assumption affected the generality of our findings, we conducted a series of analyses in which we replaced the 1980 break point with a range of alternative breakpoint years. As expected, the number of occurrences in the database deemed extant changed as the breakpoint was moved (declining as the breakpoint approached the most recent records in the database). The interspecific relationships linking rarity, range fragmentation, and extinction risk, however, remained insensitive to the use of alternative breakpoints ranging from 1965 to 1985 (Fig. 3). In contrast, earlier dates yielded no relationships between metrics of spatial distribution and extinction risk because until 1960 few extirpations had occurred.

We also addressed a third concern that is associated frequently with analyses involving biodiversity databases, namely vagrant or misplaced records. We did this by restricting historical occurrences to those localities that had three or more records per species per reach (rather than the one record per species per reach that we used in the remainder of our analyses). If we were to substitute this far more restrictive definition of species ranges, our estimates of the numbers of occurrences, percentage declines, and other quantitative metrics that we report below would obviously change. We found, however, that substituting the altered definition of species historical distributions had no qualitative effects on the assemblage-wide link between spatial distribution and extinction risk. This result, together with the evaluations of our other database assumptions reported above, suggests that we can be confident in the broad-scale patterns and results
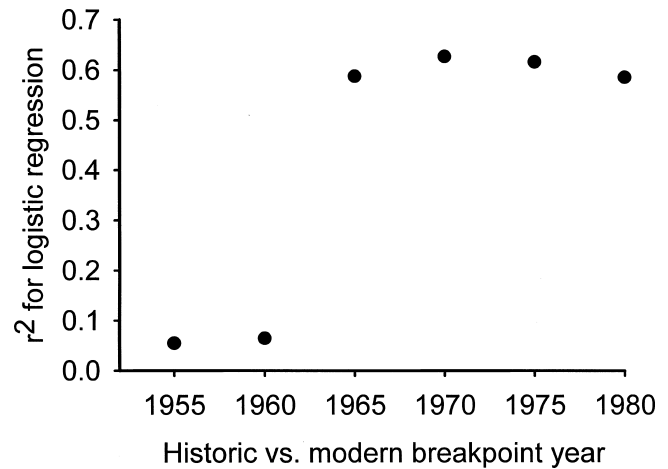

Figure 3. Goodness-of-fit measures (McFadden's r^2 for logistic regression) summarizing the among-species relationship between range fragmentation (quantified by the scale-area slope statistic) and local extinction risk (calculated as the proportion of historical occurrences at the 5-km scale that were absent during the modern period) for fishes native to the lower Colorado River basin. Fit was consistently good when the breakpoint defining historic and modern periods for these calculations was 1965 or later. Prior to 1965, no among-species relationship was evident between range fragmentation and the likelihood of local extinction.

emerging from our analyses, even if there are particular concerns about specific data points or interpretations of occurrence records from the SONFISHES database.

Current Distributions and Losses

The lower Colorado Basin fish fauna suffered major distributional losses over the 155-year period, including extinction of one species (*Cyprinodon arcuatus*) and regional extirpation of another (*Ptychocheilus lucius*). Averaged across extant species, distributional losses exceeded 40% of historical ranges, regardless of the scale of analysis. Eight of the 23 regionally extant species (35%) suffered distributional losses exceeding 50% on both fine and coarse scales. One additional species had > 50% loss on at least one spatial scale (Table 1). Eleven species suffered the greatest losses at 5-km scale, and an equal number of species suffered their greatest losses at the 100-km scale. On average, extant species suffered a 33% decline from historical distributions at the 2500-km scale. Such extensive losses translate into region-wide changes in patterns of biodiversity. For example, species richness in the four lowest 100-km reaches of the Colorado River effectively was reduced from seven native species to one (*Cyprinodon macularius*), which is currently restricted to a few spring-fed areas.
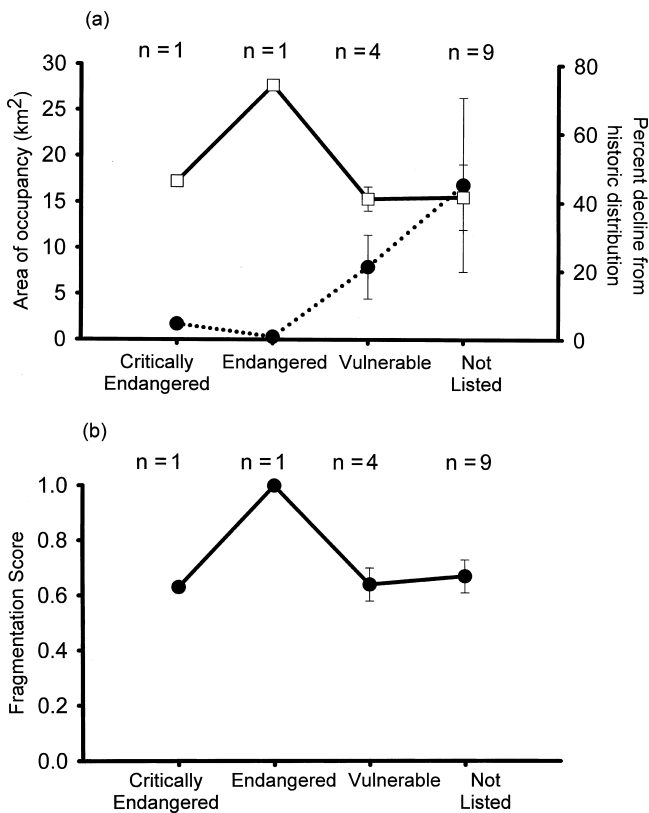
Figure 4. (a) Area of occupancy (solid circles) and percent decline from historical distributions at the 5-km scale (squares) for the 15 lower Colorado River endemic fishes, grouped by their current IUCN Red List status. (b) Current fragmentation score for the same species as in (a). Sample sizes shown as n = *for each category. In both panels, means (±SE) are plotted when* n > 1. *When* n = 1 *it is not possible to calculate an SE.*

The average fragmentation score of extant species was 0.67, with five species having fragmentation scores of 0.85 or greater. Seven species now restricted to 40 or fewer 5-km reaches are widely distributed (i.e., the few 5-km reaches they occupy are scattered across two, three, or four 2500-km reaches). Five formerly more widespread species have declined such that each species now occurs in only one 2500-km reach, and all but one of these species are limited to fewer than 10 5-km reaches within the larger networks.

Extinction Risks for Lower Colorado Basin Endemics

According to the current IUCN listings (IUCN 2001), one of the lower Colorado basin species is critically endangered, three are endangered, and six are vulnerable. By restricting our analysis to the 15 endemic species, only one or only a few species fell within some risk categories. Although these sample-size constraints led us to not in-

clude *p* values, the apparent relationship between spatial distribution and risk categories could be examined (Fig. 4a). Under the current IUCN ranking system, species with a greater area of occupancy tend to rank lower than others in terms of extinction risk. *Oncorhynchus apache* is an exception to this pattern. This species has a higher area of occupancy and is ranked highly in terms of extinction risk. Likewise, with the same exception, species that suffered the most substantial losses relative to their historical distributions tend to be ranked higher with regard to extinction risk. Results were similar for all three spatial scales, but, for brevity, are not shown for 100- and 2500-km scales. Relationships between species distributions, losses, and risk status, however, remain unclear. Similarly, we found no significant association between risk status and fragmentation score for IUCN rankings (Fig. 4b).

Based on our analyses of the current distributions of fishes endemic to the lower Colorado Basin, we propose revisions to IUCN listings to include six updated rankings and nine new rankings (Table 1). In the updated rankings, we suggest that 3 species should be categorized at a higher risk level, 2 should be downgraded, and 1 should remain unchanged. Based on our new rankings, 7 of the 15 lower Colorado Basin endemics are critically endangered, 1 is endangered, 2 are vulnerable, and 1 is already extinct. We categorized the remaining 4 endemics as lower risk.

Discussion

Extent of Losses

Our results provide a comprehensive and quantitative overview of distributional status for 25 fishes native to the lower Colorado Basin. For 15 of the species, these assessments characterize their global status. Our most alarming finding was the overall magnitude of loss. Most extant species suffered the greatest distributional losses at the local scale, a pattern that generally translates into the extirpation of individual populations. Losses at large scales, however, also have important conservation implications because evolutionary differentiation can occur between watersheds in the basin (e.g., Tibbets & Dowling 1996), suggesting that considerable genetic variation may have been lost as fish distributions collapsed from many to few watersheds. Extensive declines at the 2500-km scale (Table 1) represent substantial losses in regional- and landscape-level richness of native species, illustrating the spatial extent over which human activities alter riverine communities in deserts.

Because distributional fragmentation is a strong predictor of the risk of local extirpation for lower Colorado Basin fishes (Fagan et al. 2002), further losses in area of occupancy are likely for most of these species, and species with the most fragmented current distributions have a higher risk of extinction. All 10 lower Colorado Basin

species with historical distributions featuring fragmentation scores of at least 0.65 currently occupy <50% of their historical habitat at the 5-km scale (Fagan et al. 2002). Fourteen of the 23 extant species currently have range fragmentation scores of 0.63 or higher. These high fragmentation scores imply that fishes of the lower Colorado Basin are under considerable risk of further losses. Because these species inhabit progressively smaller fractions of their original ranges, their persistence in this landscape will become increasingly less likely. The challenges involved in preventing extinction of these species are significant. A variety of conservation and restoration techniques will be necessary to facilitate their persistence, including elimination of non-natives (Minckley 1991), translocations (Minckley 1995), enhanced cooperation among resource managers (Deacon & Minckley 1991), the acquisition of habitat and water rights (Williams 1991), and various combinations of these techniques (Minckley et al. 2003).

Implications for Conservation Ranking

Data available to environmental professionals charged with policy and management decision making regarding threatened, endangered, and declining species are often limited to presence and absence information that comes from myriad sources and efforts. Using such data in a meaningful way is a challenge. Because of factors such as differential sampling effort, collector bias for rare species, or geographical bias favoring accessible areas, estimates of extirpation frequencies from presence and absence transitions are often deemed biased or imprecise (e.g., Bock 1987; Fagan & Kareiva 1997; Patton et al. 1998; Funk & Richardson 2002). Evaluating extinction rates at a series of hierarchical scales, however, as presented here (see also Hartley & Kunin 2003), increases the likelihood of successfully identifying meaningful patterns. As spatial scale increases and map units extend across multiple historical sampling sites, it becomes less probable that the absence of modern records for a species in a reach is because of a lack of sampling effort. In a similar vein, dividing a database into few time periods such as our contrasting historical versus modern distributions reduces temporal variation in sampling effort, avoiding problems that emerge when extirpation studies are based on year-to-year transitions (Holmes & Fagan 2002). An additional advantage is that this approach (multiple scales, few time periods) does not require sophisticated adjustments for differential sampling effort or make assumptions about temporal constancy of collecting rates. Thus we were able to make meaningful comparisons between a 137-year historical time frame and an 18-year modern time frame because each subset represents an effectively complete portrait of species distributions, affording time-compressed, before-and-after snapshots.

We demonstrated a strategy that allows presence and absence data to be used readily and reliably to evaluate extinction risk for an assemblage of species. We also showed how conservation listing may be improved by accounting for distributional fragmentation of species at multiple scales. Nevertheless, even though the scale-area curve may prove a useful metric for comparative risk assessment among species, the technique may still underestimate losses. In particular, the approach fails to capture such information as the relative abundance of species, population age structure (Marsh et al. 1990; USFWS 1999; Holden et al. 2005; Marsh et al. 2005), and details about recruitment success (Marsh & Minckley 1989; Minckley et al. 1991; Mueller 1994; Marsh et al. 2005). To account for the myriad processes affecting species' vulnerability to extinction, area-of-occupancy measures ideally should be complemented by details on the biology and demography of the species in question. Unfortunately, for many species—indeed the majority of species of conservation concern—we may have only presence and absence data, and it is important to continue finding reliable ways to use such data.

In spite of the limitations inherent in the approach, matching quantitative spatial metrics such as the scale-area slope statistic to extinction risk criteria can provide a quantitative basis for conservation listing for species whose persistence is strongly influenced by spatial distribution. A benefit of this approach is that it provides a scale-independent measure of range fragmentation, which is a powerful counterpart to the area-sensitive rarity data on which conservation practitioners often rely.

Acknowledgments

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