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Extinction Rates in North American Freshwater Fishes, 1900–2010

NOEL M. BURKHEAD

Widespread evidence shows that the modern rates of extinction in many plants and animals exceed background rates in the fossil record. In the present article, I investigate this issue with regard to North American freshwater fishes. From 1898 to 2006, 57 taxa became extinct, and three distinct populations were extirpated from the continent. Since 1989, the numbers of extinct North American fishes have increased by 25%. From the end of the nineteenth century to the present, modern extinctions varied by decade but significantly increased after 1950 (post-1950s mean = 7.5 extinct taxa per decade). In the twentieth century, freshwater fishes had the highest extinction rate worldwide among vertebrates. The modern extinction rate for North American freshwater fishes is conservatively estimated to be 877 times greater than the background extinction rate for freshwater fishes (one extinction every 3 million years). Reasonable estimates project that future increases in extinctions will range from 53 to 86 species by 2050.

Keywords: North America, freshwater fishes, extinction rates, E/MSY, aquatic biodiversity

Understanding the underlying causes of the extinction of modern organisms is, in most cases, relatively simple. Extinction is the antithesis of speciation and a natural outcome of evolutionary change (Darwin 1859). Under natural conditions, including catastrophic events, extinction is one of nature's best ideas: It enables life to adapt to ever-changing environments. A fundamental concern among biologists is that contemporary rates of extinction due to human activities are orders of magnitude greater than background rates evidenced in the fossil record, and these rates appear to be increasing (May et al. 1995, Pimm et al. 1995, 2006). Catastrophic events that caused the five well-known mass extinctions, including the cataclysmic extermination of the dinosaurs, are not responsible for the majority of extinctions in geological history. Rather, 90%–96% of all extinct species variably disappeared during the normal give and take of speciation and extinction over geological time scales (May et al. 1995). In phylogenetic theory, ancestral species may become extinct in the evolutionary transition to new species, or conversely, derived taxa may split from the ancestral taxa and remain extant. Both modes are theoretically plausible under allopatric speciation scenarios (Wiley and Mayden 1985). In the present study, I am not concerned with methodological intricacies; rather, I focus on the human-caused extinction of North American freshwater fishes from the close of the nineteenth century to the present. In the context of human life spans, observations of extinction should be extraordinarily rare. Nonetheless, since 1900, at least 57 species and subspecies of North American freshwater fishes have become extinct, and three unique populations have been extirpated (Miller et al. 1989, Jelks et al. 2008).

> *"Do not tell fish stories where the people know you; but particularly, don't tell them where they know the fish." —Mark Twain.*

Declining biodiversity and increasing rates of extinction are fundamentally important metrics of natural resource status and are the subjects of intensive investigation. In particular, the mitigation and prevention of biodiversity loss are among the overarching goals of conservation biology (Helfman 2007, Pereira et al. 2010). The threat of extinction may be greatest in freshwater ecosystems, where the proportion of threatened and endangered species is generally greater than that in terrestrial ecosystems (Pimm et al. 1995, Strayer and Dudgeon 2010) and where imperilment levels are similar to those of tropical rain forests (Ricciardi and Rasmussen 1999). Inferences that the rates of contemporary extinction will increase are based on large numbers of organisms considered to be critically endangered worldwide (IUCN 2011), the increasing negative effects of human activities on the Earth's biosphere (Vitousek et al. 1997, Naiman and Turner 2000, McKee et al. 2004, Davies et al. 2006), and the conclusion that such activities will result in higher near-future extinction rates (Pereira et al. 2010, Barnosky et al. 2011).

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North American freshwater fishes: A brief synopsis

North America is geographically defined as Canada, the United States, and Mexico, including the coastal islands off Canada and Alaska but excluding Hawaii and the southern Mexican states of Quintana Roo and Campeche (Jelks et al. 2008). The diversity of fishes is equivalent to that of all other vertebrate groups combined (Nelson 2006); therefore, the number of descriptions of fishes new to science exceeds that of descriptions of new tetrapods each year. At the close of 2010, the cutoff point for this study, 31,769 valid fish species had been described worldwide (William N. Eschmeyer, California Academy of Sciences [retired], personal communication, 28 August 2011). About 43% of the world's fishes are freshwater or diadromous species (Nelson 2006). Comparatively, the freshwater fish diversity of North America is less than those of Africa (about 2945 species), Asia (3533), and South America (4035), but higher than those of Europe (330), Russia (206), and Oceania (260) (Lévêque et al. 2008). North America has the most diverse nontropical freshwater fish fauna in the world (Lundberg et al. 2000). At the end of 2010, the freshwater fish fauna of North America consisted of 53 families, 214 genera, and 1213 species, or about 8.9% of the Earth's freshwater fish diversity (Nelson et al. 2004). Continental fishes primarily consist of obligate freshwater species, *diadromous* fishes (species in which part of their life cycle occurs in the marine realm), and marine fishes that occasionally or regularly enter freshwater during their lives. The tally through 2010 is based on independent counts of species described after 2004, aided by comments from Larry Page (University of Florida Museum of Natural History, personal communication, 14 October 2010).

Patterns of species richness

Until recently, most species of the modern North American fish fauna were considered derived from the mid-Miocene to the late Pleistocene, or about 15–1.5 million years ago (mya) or less (Mayden 1988, Strange and Burr 1997, Smith GR et al. 2002). However, cross-calibration of molecular-clock and fossil data (chronograms) has significantly revised the concepts of lineage ages in fishes. For example, half of the sunfish family's (Centrarchidae) lineages significantly predate the Pleistocene, and the least-derived taxon—the mud sunfish (*Acantharchus pomotis*)—emerged by the early Oligocene, 33.7 mya (Near et al. 2005). The mean age estimates for species lineages in the diverse family Percidae have been pushed back to the Oligocene, from 30.7 to 34.8 mya (Near et al. 2011). These studies suggest that many North American fishes are likely to be far older than was previously recognized.

There is, however, clear evidence for the derivation of species from the late Pleistocene (Near and Benard 2004, Near et al. 2005) to the last 10,000 years for species that evolved after the glaciers retreated (e.g., Hatfield 2001, Taylor et al. 2006). The end of the Pleistocene was demarked by dramatic changes: subsidence of glaciers, rising sea levels, severing of lateral connections between some coastal drainages, and the filling of numerous basins gouged by the giant ice sheets (e.g., the Great Lakes; Hocutt and Wiley 1986). The evolution and biogeography of the North American fish fauna is intimately linked to transitional changes to landforms and their influences on continental watercourses over time (Mayden 1988, Smith GR et al. 2002). Generally, species richness per drainage (or ecoregion) increases from Canada southward, but over two-thirds of species richness occurs east of the Great Continental Divide, especially in the Interior and Appalachian Highlands (Hocutt and Wiley 1986, Mayden 1992). Fishes in the western United States and Mexico exhibit relatively lower species richness per drainage unit but generally have higher endemism and disproportionate numbers of extinct species (Minckley and Douglas 1991, Burr and Mayden 1992).

Rates of faunal documentation and evidence of extinction

Our knowledge of North American fishes is facilitated by a long tradition of faunal study and public access to most river and lake systems. From 1758 to 2010, the average rate of fish descriptions for North America was 4.8 species described per year, but as is evident in figure 1a, the rates varied over time and logically increased as more biologists studied the fauna. From 1970 through 2010, species documentation averaged 6.7 species described per year, which is considered the modern rate of faunal discovery and documentation (figure 1a). The discovery and description of North American freshwater fishes continues unabated, and unlike birds (see Pimm and colleagues' [2006] figure 1), there is no evidence of an asymptote in the rates of species descriptions.

Modern extinctions of North American fishes were first observed at the dawn of the twentieth century, and the trend continues (figure 1b). The exact year of extinction can be difficult to document (Harrison and Stiassny 1999) because of the inherent difficulty of observing an organism when the probability of its detection approaches zero. Among the first fishes observed to be declining (and later to become extinct) were commercially important Great Lakes fishes for which harvest data were kept (McCrimmon 2002). Included in that group is the first fish population to disappear from North America, the Lake Ontario population of the highly valued Atlantic salmon (*Salmo salar*). The year of expiration for six narrow endemics is exactly known because the desiccation of their habitats (four springs and one caldera) was observed. These species included five desert pupfishes (*Cyprinodon* spp.; Contreras-Balderas and Lozano-Vilano 1996) and the last known fish to go extinct in North America, the Alberca silverside (*Chirostoma bartoni*), which vanished when the Alberca caldera temporarily dried in August 2006 (Edmundo Díaz Pardo, Universidad Autonoma de Queretaro, personal communication, 13 September 2007). In many cases, extinction was recognized only in hindsight, and the last year of observation was used to estimate the extinction year (Miller et al. 1989).

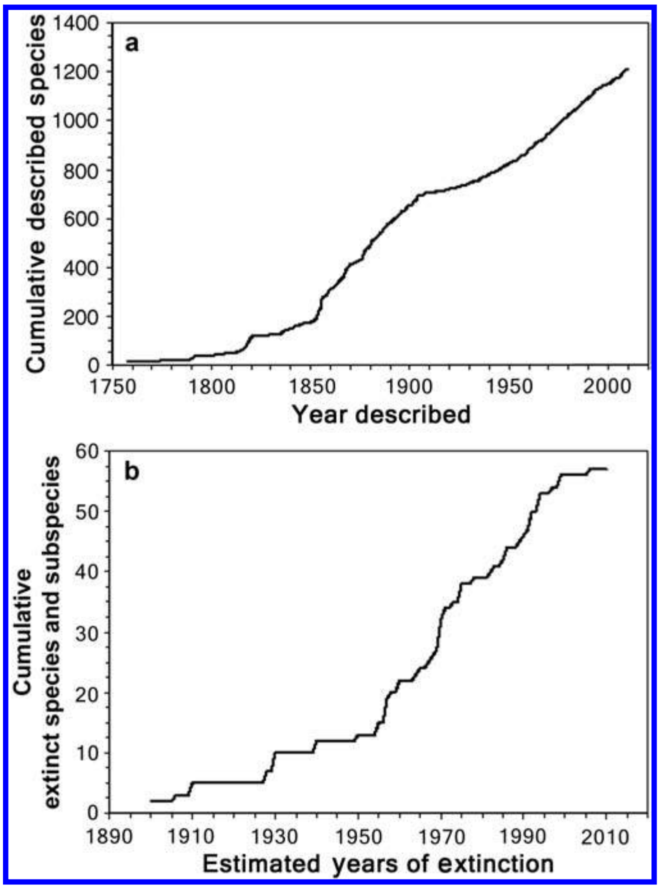

*Figure 1. (a) Cumulative rate of North American fish descriptions from 1758 to 2010 (*n *= 1213 species). (b) Cumulative rate of North American fish extinctions from 1900 to 2010 (*n *= 57 [39 species and 18 subspecies]).*

Data sources, definitions, corrections

The data for this study were derived from the foundational study by Miller and colleagues (1989), which provided the first list of 40 extinct fishes and included the causes and estimated years of their extinction. The conservation assessment by Jelks and colleagues (2008) reduced the number of extinct fishes listed by Miller and colleagues (1989) from 40 to 35 taxa (four fishes were determined to be extant, and one was a synonym), and added 26 new taxa to the list. During data compilation for this report, one fish listed as *possibly extinct* (Jelks et al. 2008), an undescribed species of *Gila*, "carpa gorda de Parras," an endemic known only from desert springs near Parras, Coahuila, Mexico (Contreras-Balderas et al. 2003), was rediscovered from a nearby spring after a 42-year hiatus in observation (Dean Hendrickson, University of Texas at Austin, personal communication, 10 June 2010). Additional data on fish extinction from other continents were downloaded from the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species (IUCN 2011).

The total richness of freshwater fishes listed here does not include all species characterized as *freshwater fishes* by Nelson and colleagues (2004). Excluded are 77 marine fishes that are tolerant of variable salinities, because these species do not appear to be dependent on freshwater to complete their life cycles throughout their ranges. A well-known example is the bull shark (*Carcharhinus leucas*). Examples of euryhaline species with populations dependent on freshwater and included as part of the freshwater fauna tallied herein are the Atlantic needlefish (*Strongylura marina*), the opossum pipefish (*Microphis brachyurus*), and the California killifish (*Fundulus parvipinnis*).

The term *extirpated* (meaning that all individuals in a population have been lost) is distinguished from *extinct* (all individuals of a species have been permanently lost). The three categories of *extinct* defined in the conservation assessment of North American freshwater fishes—*extinct in nature*, *possibly extinct*, and *extinct* (Jelks et al. 2008)—are combined herein to simplify the analyses. Three taxa listed as *extinct* by Jelks and colleagues (2008) are actually extirpated populations, but they are retained on the list (table 1) because their ranges and years of extirpation are known and because they are analogous to regionally extinct taxa tracked by the IUCN (Snoeks et al. 2011). The last year of observation and the estimated year of extinction listed by Miller and colleagues (1989) for three species of the minnow genus *Evarra* are corrected to be 1957 and 1970, respectively (Edmundo Díaz Pardo, Universidad Autonoma de Queretaro, personal communication, 13 August 2011). Because the AFS definitions of *possibly extinct* and *extinct* incorporate hiatuses of 20 or 50 years since the last observation of a species, respectively (Jelks et al. 2008), it is possible, even though 12 years have passed, that the tally of twentieth century fish extinctions remains incomplete. I reviewed literature cited by Miller and colleagues (1989) and data compiled by Jelks and colleagues (2008) to determine the last year of observation to estimate the difference in years between the last observation and the estimated year of extinction for the 60 fish taxa.

The Highland splitfin (*Girardinichthys turneri*), a species listed as *extinct* by Jelks and colleagues (2008), was reported to be extant in Lake Zacapu but as *Hubbsinna turneri* (Ramírez-Herrejón et al. 2010). The Lake Zacapu population in Michoacán, Mexico, is recognized as a distinct sister taxon, the Zacapu splitfin (*Girardinichthys ireneae*; Radda and Meyer 2003). Therefore, of the 60 extinct taxa (table 1), 35 are from Miller and colleagues (1989) and 25 are from Jelks and colleagues (2008), including three extirpated populations.

This assessment of North American fish extinctions is a spin-off study of the AFS Endangered Species Committee (ESC) that was active from 2004 to 2008 (i.e., after Jelks et al. 2008). This report is the first of three articles on the extinction patterns in North American fishes that are built on the data developed by Miller and colleagues (1989) and Jelks and colleagues (2008). A summary of data on extinct North American freshwater fishes is at the USGS Web site, as are relevant definitions and other information sources. In the present article, I focus on the current, background, and

Table 1. Extinct North American freshwater fishes as of December 2010.

Family	Scientific name	Common name	Estimated year of extinction
Cyprinidae (minnows)	*Cyprinella lutrensis blairi*[a]	Maravillas red shiner	1960
	Evarra bustamantei[a]	Mexican chub	1983
	Evarra eigenmanni[a]	Plateau chub	1983
	Evarra tlahuacensis[a]	Endorheic chub	1983
	Gila bicolor sp.[b,c]	"High Rock Springs Tui chub"	1989
	Gila crassicauda[a,c]	Thicktail chub	1957
	Gila sp.[b,c]	"Carpa delgada de Parras"	1968
	Lepidomeda altivelis[a]	Pahranagat spinedace	1940
	Notropis aulidion[a]	Durango shiner	1965
	Notropis orca[a,c]	Phantom shiner	1975
	Notropis saladonis[b]	Salado shiner	1992
	Notropis simus simus[a,c]	Rio Grande bluntnose shiner	1964
	Pogonichthys ciscoides[a,c]	Clear Lake splittail	1970
	Rhinichthys cataractae smithi[a]	Banff longnose dace	1982
	Rhinichthys deaconi[a]	Las Vegas dace	1955
	Rhinichthys osculus reliquus[a]	Grass Valley speckled dace	1950
	Stypodon signifer[a]	Stumptooth minnow	1930
Catostomidae (suckers)	*Chasmistes liorus liorus*[a,c]	June sucker	1935
	Chasmistes muriei[a]	Snake River sucker	1928
	Moxostoma lacerum[a]	Harelip sucker	1910
Ictaluridae (North American catfishes)	*Noturus trautmani*[b,c]	Scioto madtom	1957
Salmonidae (trouts and salmons)	*Coregonus johannae*[a]	Deepwater cisco	1955
	Coregonus kiyi orientalis[a]	Lake Ontario kiyi	1967
	Coregonus nigripinnis nigripinnis[a,c]	Blackfin cisco	1969
	Coregonus reighardi reighardi[b,c]	Shortnose cisco	1985
	Oncorhynchus clarkii alvordensis[a]	Alvord cutthroat trout	1940
	Oncorhynchus clarkii macdonaldi[a,c]	Yellowfin cutthroat trout	1910
	Salmo salar[b,c]	Atlantic salmon, Lake Ontario pop	1898
	Salvelinus fontinalis agassizii[a,c]	Silver trout	1930
	Thymallus arcticus[b,c]	Arctic grayling, Great Lakes pop	1935
Atherinopsidae (New World silversides)	*Atherinella callida*[b,c]	Cunning silverside	1957
	Chirostoma bartoni[b,c]	Alberca silverside	2006
	Chirostoma charari[b,c]	Least silverside	1957
	Characodon garmani[a]	Parras characodon	1900
Goodeidae (goodeids)	*Empetrichthys latos concavus*[a]	Raycraft Ranch poolfish	1960
	Empetrichthys latos pahrump[a,c]	Pahrump Ranch poolfish	1958
	Empetrichthys merriami[a]	Ash Meadows poolfish	1953
	Girardinichthys turneri[b]	Highland splitfin	1990
	Skiffia francesae[b]	Golden skiffia	1978
Fundulidae (topminnows)	*Fundulus albolineatus*[a]	Whiteline topminnow	1900
Cyprinodontidae (pupfishes)	*Cyprinodon alvarezi*[b,c]	Potosí pupfish	1994
	Cyprinodon arcuatus[a]	Santa Cruz pupfish	1971
	Cyprinodon ceciliae[b,c]	Villa Lopez pupfish	1991

Table 1. Continued

Family	Scientific name	Common name	Estimated year of extinction
	Cyprinodon inmemoriam[b,c]	Charco Azul pupfish	1986
	Cyprinodon latifasciatus[a]	Parras pupfish	1930
	Cyprinodon longidorsalis[b,c]	La Palma pupfish	1994
	Cyprinodon nevadensis calidae[a]	Tecopa pupfish	1971
	Cyprinodon veronicae[b,c]	Charco Palma pupfish	1997
	Megupsilon aporus[b,c]	Catarina pupfish	1994
Poeciliidae (livebearers)	*Gambusia amistadensis*[a,c]	Amistad gambusia	1973
	Gambusia georgei[a]	San Marcos gambusia	1983
	Priapella bonita[b]	Graceful priapella	1906
Gasterosteidae (sticklebacks)	*Gasterosteus* sp. cf. *aculeatus*[b,c]	"Benthic Hadley Lake stickleback"	1999
	Gasterosteus sp. cf. *aculeatus*[b,c]	"Limnetic Hadley Lake stickleback"	1999
Cottidae (sculpins)	*Cottus echinatus*[a,c]	Utah Lake sculpin	1928
Moronidae (temperate basses)	*Morone saxatilis*[b,c]	Striped bass, St. Lawrence Estuary pop	1968
Percidae (perches)	*Etheostoma sellare*[b,c]	Maryland darter	1988
	Sander vitreus glaucus[a]	Blue pike	1970
Cichlidae (cichlids)	*Cichlasoma urophthalmus conchitae*[b,c]	Mojarra del cenote Conchita	1975
	Cichlasoma urophthalmus ericymba[b,c]	Mojarra de Sambulá	1975

Note: The common names of undescribed taxa are in quotation marks. Abbreviations: sp., species; ssp., subspecies; pop, extirpated population.
[a]35 extinct fishes (Miller et al. 1989).
[b]25 taxa added to the list by Jelks and colleagues (2008).
[c]32 taxa for which the last year of observation is the same as the estimated year of extinction.

near-future extinction rates out to 2050 in the continent's freshwater fish fauna.

Current rates of extinction

Rates of extinction can be estimated indirectly using species–area relationships (May et al. 1995), from models (Ricciardi and Rasmussen 1999), or directly when extinct taxa and associated data are known. All extinct or extirpated fishes treated herein represent modern losses as opposed to extinctions in the geological past (table 1). The rates of extinction fluctuated by decade, with a significant increase in the mean number of extinctions per decade after 1950 (figure 2). The post-1950s increases in extinction probably resulted from indirect effects of the post–World War II baby boom, including demographic shifts from rural to urban areas, increased construction of large and small dams, increased alteration of natural water bodies (e.g., channelization, pollution), and other consequences of economic growth and industrial expansion (CEC 2001, McKinney 2002, De Souza et al. 2003). The recent decline in extinction rates is the fourth decadal decline since 1900, but three of the extinction declines were followed by episodes of increasing or stable extinction rates (figure 2).

The patterns of decadal extinctions in North America roughly paralleled those on other continents, but the number of extinctions across decades was significantly higher in North America than those in all other continents combined (figure 3). Of the estimated 83 extinct fish species and subspecies worldwide (IUCN 2011), North America accounts for 57, Eurasia 19, Africa and Madagascar 5, South America 1, and Oceania 1. Some of these discrepancies clearly relate to the numbers of ichthyologists and the history of faunal investigation in different regions of the world. Other regions with long (or longer) traditions of faunal study exhibit similar overall extinction rates to that of North America—for example, in Europe, 3.4% of 531 species are extinct or possibly extinct (Freyhof and Brooks 2011), and in the Mediterranean basin, 3.2% of 253 species are extinct (Smith KG and Darwall 2006). Around 43% of the 31,769 fish species on Earth are freshwater fishes (Nelson 2006), which equals about 13,661 species, 3% of which would be approximately 410 extinct freshwater species worldwide. This elementary extrapolation based on the North American proportion of extinct fishes suggests that worldwide tallies of extinct freshwater fishes significantly underestimate the actual number suggested by current databases (IUCN 2011)—perhaps by several times.

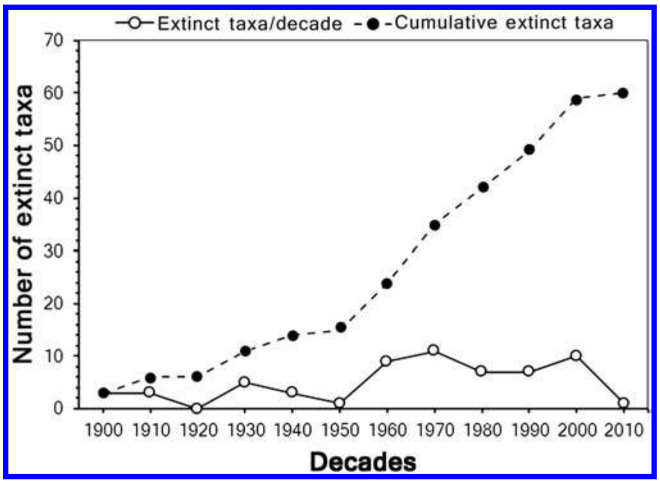

Figure 2. Extinction rates of North American freshwater fishes by decade (*n *= 60). The solid black circles and dashed line represent cumulative extinctions and extirpations from 1898 to 2006. The open circles and solid line represent extinctions by decade (range = 0–11 extinctions per decade; pre-1950s mean = 2.5; post-1950s mean = 7.5;* t*-test for unequal variances,* t*(7) = –6.16, two-tailed,* p *= .0004).

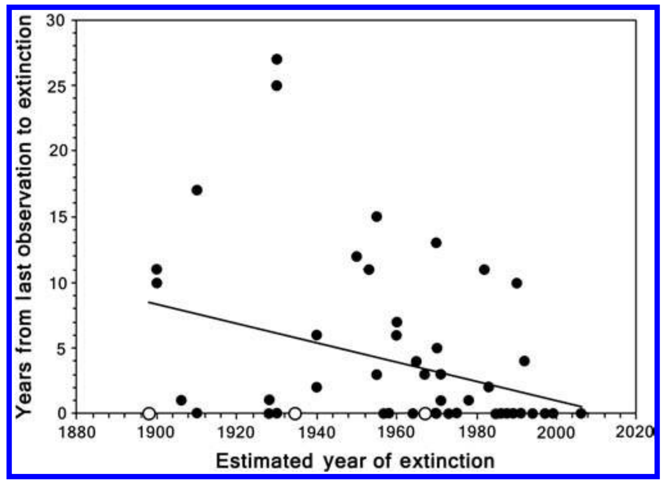

Figure 4. Lag time in years between the last observation of a species and its estimated year of extinction for North American freshwater fishes. Mean lag time = 3.8 years. The closed circles represent extinct species and subspecies, including undescribed taxa. The open circles represent extirpated populations (32 taxa had lag times of 0 years). The fitted black trend line is that described by a simple linear regression (*R² *= .0994,* p *< .0001).

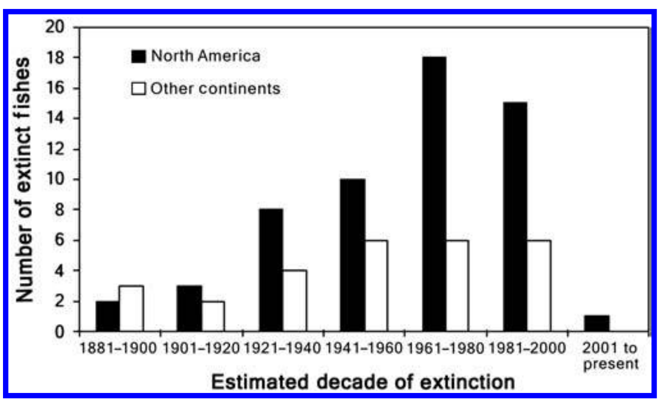

Figure 3. Comparison of extinction rates for freshwater fishes of North America (black bars) and those from other continents (white bars). The other continents and islands include Africa and Madagascar, Eurasia, South America, and Oceania. The data are from the International Union for Conservation of Nature (2011). The categorical differences in decadal proportions between North America and the other continents are significantly different (Fisher's exact test,* p *< .0001).

It has been argued that extinction dates should be classified relative to the strength of evidence supporting their validity, known as *effective extinction dates* (Harrison and Stiassny 1999). Harrison and Stiassny (1999) recommended listing a range of dates when the year of disappearance is not precisely known, and they suggested nine categories of extinction. The AFS definitions of *extinction* explicitly require that searches for missing species be performed by experienced biologists and provides classifications based on different hiatuses in years since the last observation. I elected to compare the last year of observation with the estimated year of extinction for North American fishes. The data indicated that the differences were greatest prior to 1940 and decreased thereafter (figure 4). Some fishes may have been extinct when they were described, although their fate was unknown at that time. For example, a silverside species that was known only from a single site (a narrow endemic), the cunning silverside (*Atherinella callida*), was captured only once, in 1962, and its common name was ironically coined for its ability to avoid detection (Chernoff 1986)—when it was described, it may have already been extinct. Unexpectedly, the last year of observation was the same as the estimated year of extinction for 29 fishes and was the same as the year of extirpation for the three populations (table 1, figure 4). Examples of these fishes include commercially important Great Lakes fishes for which annual catches were tracked (McCrimmon 2002). Also included in this number are fishes that were narrow endemics, for which the years of habitat destruction or introductions of a nonindigenous species were known (Contreras-Balderas and Lozano-Vilano 1996, Hatfield 2001). The largest differences in lag times occurred in the first half of the twentieth century, and the differences generally declined toward the close of the twentieth century (figure 4). The taxa with the three highest lag times were the Parras pupfish (*Cyprinodon latifasciatus*, 27 years), the stumptooth minnow (*Stypodon signifer*, 25 years), and the harelip sucker (*Moxostoma lacerum*, 17 years). The loss of 57 species and subspecies and three unique populations since 1898 is intuitively significant, but only a comparison of modern with background extinction rates (BERs) will enable a robust evaluation of these losses.

Background rates of extinction

In their seminal studies, Pimm and colleagues (1995, 2006) demonstrated the utility of comparing modern extinctions with BERs in birds by estimating the number of extinctions per million species years (E/MSY). This logical approach facilitates comparing modern bird extinction rates with those of other biotas, and the examination of changes in bird extinction rates in the past 500 years. To estimate the E/MSY, the following must be known: the mean species duration interval from origination to extinction (from the fossil record) in millions of years, the total number of extant taxa, the number of modern extinct taxa, and the interval in years in which modern extinctions occurred. Pimm and colleagues (1995, 2006) lacked data for the mean species duration interval for birds, so they substituted data from terrestrial vertebrates (mammals; Pimm et al. 1995, May et al. 1995). They also considered 1 million years as the benchmark interval prior to human impacts.

Pimm and colleagues (2006) specifically posited that around 1.3% of the roughly 10,000 known bird species have become extinct since 1500, which equals a modern to BER of approximately 26 E/MSY (calculated by multiplying the quotient of the mean species duration interval for birds and total bird diversity [$10^6/10^4 = 100$] by the mean annual bird extinction rate [130 extinctions/500 years = 0.26]). When shorter intervals over which extinction occurred (e.g., since 1900) were examined, global extinction rates were as high as 65 E/MSY (Pimm et al. 2006).

For North American freshwater fishes, the mean species duration interval from the fossil record is 3 million years (Stanley 1990), the total number of species is 1213, the time interval over which modern extinctions were examined is 110 years (1900 to 2010), and the number of extinct fish species is 39 (3 of which are undescribed). The modern to BER estimate is 877 E/MSY for North American freshwater fishes—the highest estimate reported for contemporary vertebrates (Pimm et al. 2006, Pereira et al. 2010 [and its supplemental material], Barnosky et al. 2011).

Several issues merit a brief discussion relative to the comparison of modern extinction rates with BERs. First, the actual species richness of North America freshwater fish fauna is not yet known, as is indicated by the lack of an asymptote in the rate of fish descriptions (figure 1a), and it is possible that not all recent fish extinctions are known. In addition, fishes are not equal entities evolutionarily or with respect to species duration intervals. The latter spans several orders of magnitude, from about 10,000 years ago to the present for fishes that diverged after the last glaciation (Smith GR et al. 2002, Taylor et al. 2006) to over 160 mya for extant archaic fishes, such as the longnose gar (*Lepisosteus osseus*; Grande 2010). The loss of species such as sturgeon or gar would significantly increase the mean duration intervals for freshwater fishes because of the tremendous species durations of these archaic fishes. At least two sturgeon species of *Pseudoscaphirhynchus* are considered critically endangered in Eurasia (IUCN 2011); if one of these sturgeons disappeared, the mean species duration interval for fishes would significantly increase, causing estimates of E/MSY to increase likewise. If evolutionarily old taxa such as sturgeons, paddlefishes, or gars became extinct, it might be appropriate to divide extinct fishes into two groups—archaic and modern bony fishes. The species duration interval estimated for freshwater fishes (Stanley 1985, 1990) is based on Lyellian percentages—proportions of living species within fossil faunas (Stanley et al. 1980). As was noted in Near and colleagues' (2005, 2011) discussions of recent chronogram estimates for centrarchids and percids, the lineage derivation estimates are far older than was previously known, and it is possible that the mean duration interval of one extinction every 3 million years (Stanley 1985, 1990) underestimates, perhaps significantly, the species age for freshwater fishes. If that were true, it would make the E/MSY estimates low, possibly by an order of magnitude. For example, if the mean species duration for freshwater fishes is actually closer to one extinction each 11 million years, the modern to BER estimate for North American fishes would be 3215 E/MSY.

The ability to compare modern extinction rates with BERs facilitates meaningful comparisons of contemporary extinction rates among different biotas (Pereira et al. 2010 [and its supplemental material], Barnosky et al. 2011). Most of the bird extinctions investigated by Pimm and colleagues (2006) were of island species, which are inherently susceptible to extinction because of high endemism; habitat destruction; and the introduction of nonnative organisms, including humans. BERs are compared among world vertebrate groups for the twentieth century in table 2. The E/MSY estimate for freshwater fishes in the twentieth century was nearly twice that of other vertebrate groups. The BER estimated for birds (table 2) is higher than that estimated by Pimm and colleagues (2006) because I used different species duration data for birds (i.e., 2.5 million years; Stanley 1990). As was noted in the "Current rates of extinction" section, the reported extinction rates for freshwater fishes from other continents appear grossly underestimated. If, for example, the continental extinction rate for North America (3.2%) mirrors the extinction rates of freshwater fishes in other continents, the number of extinct fishes for the twentieth century would be around 384 species (instead of 81 in table 2) and the twentieth century BER would be 960 E/MSY.

The continental list of extinct fishes from Africa and Madagascar differs from the data given in the worldwide assessment of extinct fishes by Harrison and Stiassny (1999), in which about 50 haplochromine cichlids from Africa and Madagascar were considered *possibly extinct*. In a recent assessment, Snoeks and colleagues (2011) determined that these species are critically endangered or that their status is data deficient and in need of further study.

Table 2. Comparison of current to background extinction rates for world vertebrates in the twentieth century.

Vertebrate group	Total number of species	Total number of extinct species	Mean species duration	E/MSY
Freshwater fishes	11,997	81[a]	3.0[b]	203
Amphibians	5743[c]	25[a]	1.0	44
Reptiles	8860[d]	11[a]	~2.2[e]	27
Birds	9917[c]	45[c]	2.5[b]	113
Mammals	4853[c]	31[c]	1.7[b]	109

Note: The number of freshwater fishes in 2000 was 43% of about 27,901 total species (Eschmeyer and Fong 2012). Mean species duration is the species life span in millions of years from origination to extinction; when it was not known, it was estimated to be 1.0 E/MSY, which is also considered the benchmark extinction rate prior to human impacts (Pimm et al. 1995). The correct twentieth century background extinction rate for fishes may be over 900 E/MSY (see the "Background rates of extinction" section).
Abbreviations: E/MSY, extinctions per million species years.
[a]IUCN 2011. [b]Stanley 1990. [c]Pereira et al. 2010. [d]Uetz 2000. [e]Stanley 1985.

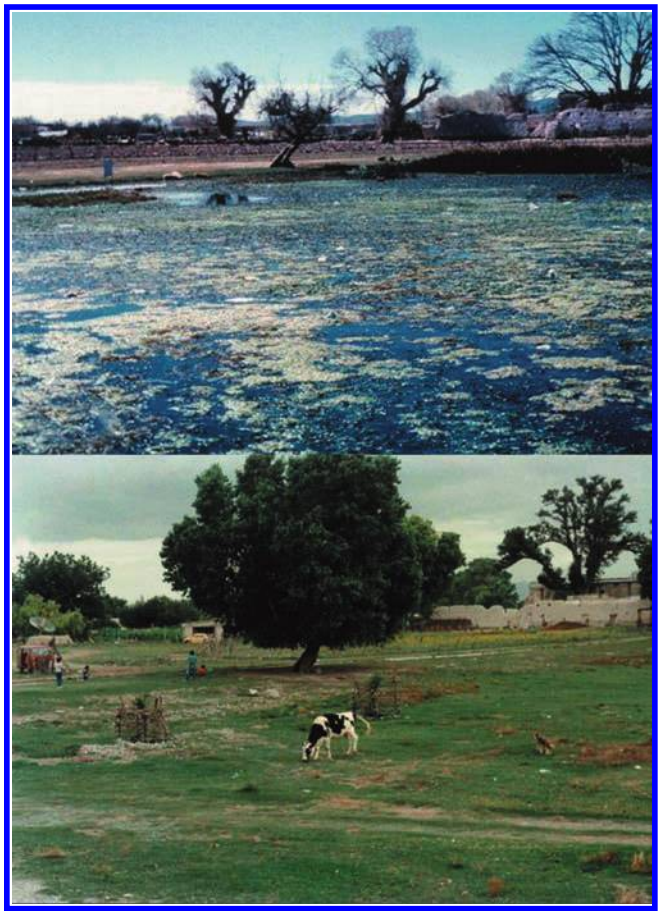

*Figure 5. Potosí Spring, northwest of Galeana, Nuevo León, Mexico, was the only known locality for two narrow endemic fishes, the Potosí pupfish (*Cyprinodon alvarezi*) and Catarina pupfish (*Megupsilon aporus*). The top image is from 1972, and the bottom is from 1995. Groundwater pumping caused the spring to dry in 1994 and two pupfishes to go extinct. Photographs: Salvador Contreras-Balderas (deceased); images courtesy of his family.*

Predicting extinctions to 2050

Human activities are inexorably linked to fish extinctions, which makes prediction of future extinctions challenging. The primary causes of imperilment and extinction in freshwater fishes are the loss of habitat and the introduction of nonindigenous fishes (Harrison and Stiassny 1999, Jelks et al. 2008). Even with prescient knowledge, it is doubtful that some extinctions resulting from introductions of alien fishes could ever be anticipated. For example, the unlikely introduction of brown bullhead catfish (*Ameiurus nebulosus*) into one of a few lakes on small coastal islands off British Columbia (Hatfield 2001) resulted in the decimation of sympatric populations of distinct sticklebacks (table 1). Likewise, the very remoteness of desert springs seemed to ensure the security of isolated pupfishes, but in hindsight, groundwater pumping was an obvious threat to the persistence of the springs (figure 5; Contreras-Balderas and Lozano-Vilano 1996).

Future extinctions will probably include some of the North American fishes recently classified as *threatened* (190) and *endangered* (280), particularly the 73 endangered species that were identified as *declining* (Jelks and colleagues' [2008] appendix 1). The Southeastern Fishes Council published a list of the 12 most endangered fishes in the southeastern United States (SFC 2008), all of which are vulnerable to extinction in the near future. One of these fishes, the slender chub (*Erimystax cahni*; figure 6), is a minnow that is most recently known only from a few sites in a 13-kilometer section of the Clinch River in northeastern Tennessee. Despite repeated intensive seining and snorkeling surveys focused on the species, it has not been observed since 1996 (SFC 2008). The slender chub is on the knife's edge; we do not know whether it was the last fish to disappear in the twentieth

*Figure 6. The slender chub (*Erimystax cahni*), a narrow endemic in the upper Tennessee River drainage that has not been observed since 1996 despite repeated, intensive searches. The slender chub may be the next fish declared* possibly extinct *in North America (adult male, 81.1 millimeter standard length, Clinch River, Hancock County, Tennessee, 29 June 1985). Photograph: Noel M. Burkhead and Robert E. Jenkins, courtesy of the Virginia Division of Game and Inland Fisheries.*

century or whether it made it to the twenty-first century. If it is not found in 5 years, the slender chub could be the next fish to qualify for *possibly extinct* status in North America.

Mexico has a large number of fishes vulnerable to extinction in the near future, primarily because of high levels of endemism. Of the 280 North American fishes identified as *endangered*, 65 were exclusively from Mexico, 70 were from the United States, and 21 were from Canada (Jelks et al. 2008). For example, the Ameca River system, noted for its high levels of endemism, has lost 70% of its native fish fauna (López-López and Paulo-Maya 2001, Pérez-Rodríguez et al. 2009). The family Goodeidae has a large number of endangered and extinct species in Mexico. Of the extant Mexican goodeids, 16 were identified as *critically endangered* and 7 as *endangered* (Domínguez-Domínguez et al. 2005); all are small fishes, and most are narrow or localized endemics exposed to multiple threats. Another nine Mexican fishes were recently categorized as *in danger of extinction* (Schmitter-Soto 2006).

A frequently cited exponential-decay model used to estimate future extinction rates required recent data on the numbers of threatened and endangered species in order to model future extinctions (Ricciardi and Rasmussen 1999) and was therefore unable to estimate the number of future fish extinctions by 2050. Assuming no near-future catastrophic events, different elementary approaches were used to estimate the numbers of extinct fish species by 2050. The number of currently declining endangered fishes (see Jelks and colleagues' [2008] appendix 1) plus the number of currently extinct species equals 113 species. Although it is unlikely that all currently declining endangered fishes would become extinct by 2050, 113 species could be considered the upper limit of extinction in a worst-case scenario. Two elementary extrapolations based on the mean annual extinction rate (MAER) and on the mean annual description rate (MADER) yielded the following estimates: The overall MAER is 0.35 extinct fish species per year (which is more conservative than the post-1950s rate of 0.73 species per year; see figure 2). Beginning with 39 extinct species in 2010, the MAER extrapolation approximates 53 extinct species by 2050 (an increase of 14 species). The MADER extrapolation based on 6.7 species described per year yields 1482 species by 2050. Under the assumption that the continental proportion of extinct fishes remains about 3.2% until 2050, the number of extinct fish species approaches 86 (an increase of 47 species). Therefore, by 2050, the number of extinct fishes is estimated to range from 53 to 86 species, representing an increase of 35.9%–120.5%, with an improbable upper limit of 113 species (a 190% increase).

What is more important to resource managers than estimating the number of future extinctions is identifying which fishes are more likely to become extinct in the near future. Of the endangered fishes listed by Jelks and colleagues (2008), those that are narrow or localized endemics and in proximity to major urban areas, transportation corridors, future energy development, or resource extraction sites or whose ranges are truncated by large impoundments are probably more vulnerable to future extinction because of exposure to multiple stressors (McKinney 2002, McKee et al. 2004).

Conclusions

Each continental fish fauna is a unique, globally important resource of immensurable worth. The North American fish fauna has tremendous recreational and commercial value, as well as aesthetic, scientific, and cultural importance (Helfman 2007, NFHB 2010). In particular, fish represent important sources of protein for individuals at lower socioeconomic levels worldwide (Helfman 2007). With respect to scientific and ecological studies, fishes are especially useful for evaluating environmental change, because biologists know much more about their biology than they do those of other aquatic biotas. Actually, declining fishes represent just the tip of the iceberg regarding losses of freshwater biota and their habitats. Comparatively, mussels and snails are exceptionally imperiled, with BERs an order of magnitude greater than that of freshwater fishes.

The exigent issue regarding these extinctions is not so much the number of missing fishes but the fact that these fishes disappeared in only 110 years (figures 1b and 2). Fish extinction rates are currently 877 times greater than BERs, and since 1900, those rates have fluctuated between 556 and 1042 E/MSY. These BER estimates are low because they do not include infraspecific taxa (extinct subspecies or extirpated populations). Future freshwater fish extinctions in North America are estimated to range from 53 to 86 species by 2050.

Current estimates of the number of extinct fishes from all other continents are significantly lower than decadal extinction rates for North America (figure 3). In most cases, these discrepancies represent gross underestimates of true extinction levels on those other continents. However, recent changes in some of the IUCN (2011) data resulted from increased caution about the accuracy of previously reported extinction estimates, particularly in the African rift lakes, where funding and logistics reduces the ability to intensively sample and where the fauna is taxonomically complex (Snoeks et al. 2011). Based on the continental extinction rate of 3.2% for North America, the worldwide loss of freshwater fishes may exceed 400 species.

After 253 years of faunal discovery and documentation (figure 1a), the freshwater fishes remaining to be discovered are more likely to be narrow or localized endemics, cryptic, and imperiled (Burkhead and Jelks 2000). The number of humans recently increased to 7 billion individuals; the totemic effects of our activities on the Earth's systems and processes are quantifiable at global scales, are observable from space, and include ongoing biodiversity decline and loss as well as worldwide changes to geochemical cycles and increasing climatic variability (Rockström et al. 2009, Pereira et al. 2010 [and its supplemental material], Barnosky et al. 2011). The loss of 3.2% of the continental fish diversity is not trivial and demonstrates that some of our resource practices are detrimental to the persistence of freshwater fishes and likely to that of other aquatic faunas.

Online data on extinct North American freshwater fishes, as well as any potential errata from this report may be found at the USGS–AFS Web site (*http://fl.biology.usgs.gov/extinct_fishes/index.html*).

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