The extinction of the Catarina pupfish *Megupsilon aporus* and the implications for the conservation of freshwater fish in Mexico

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Abstract Extinctions are occurring at an unprecedented rate as a consequence of human activities. Vertebrates constitute the best-known group of animals, and thus the group for which there are more accurate estimates of extinctions. Among them, freshwater fishes are particularly threatened and many species are declining. Here we report the extinction of an endemic freshwater fish of Mexico, the Catarina pupfish *Megupsilon aporus*, the sole species of the genus *Megupsilon*. We present a synopsis of the discovery and description of the species, the threats to, and degradation of, its habitat, and the efforts to maintain the species in captivity before it became extinct in 2014. The loss of the Catarina pupfish has evolutionary and ecological implications, and highlights the crisis of freshwater fish extinctions. It is a warning of the likely fate of more than 200 freshwater fish species threatened with extinction in Mexico. To save these species, the country urgently needs a national strategy to articulate a bold conservation effort, with better policies on ecosystem management and water use.

Keywords Catarina pupfish, conservation, Cyprinodontidae, extinction, fish, *Megupsilon aporus*, Mexico

Introduction

Biodiversity loss is one of the most severe environmental problems, with thousands of species having gone extinct since the start of the 20th century and hundreds of thousands of populations being lost as a result of human activities (Ceballos et al., 2017a). The rate of extinction of vertebrate species in this period has been up to 100 times faster than in the last 2 million years (Ceballos et al., 2015). Extinctions of birds and mammals have been documented more thoroughly than extinctions of fishes and invertebrates, which have often been overlooked (e.g. Dirzo et al., 2014; Régnier et al., 2015). Since the start of the 21st century it has become clear that population depletion and extinction of both freshwater and marine fishes is a severe and widespread problem (e.g. Ricciardi & Rasmussen, 1999; Myers & Worm, 2005; Olden et al., 2007; Burkhead, 2012).

Extinction of freshwater fishes has been relatively well documented in North America (e.g. Miller et al., 1989; Burkhead, 2012). A compilation of the conservation status of freshwater fishes in Mexico has revealed that 10 species have become extinct in the wild or have been extirpated from the country, and > 200 (40% of all species in Mexico) are facing extinction (IUCN, 2016; Ceballos et al., 2017b; Table 1).

While compiling these data we found that the Catarina pupfish *Megupsilon aporus* is the most recently extinct endemic freshwater fish in Mexico. This species, which belongs to the Cyprinodontidae and is one of the smallest fishes in North America, was lost as a result of desiccation of the only freshwater spring it inhabited, in El Potosi, Galeana, Nuevo León (Miller et al., 2005; Bennett & Conway, 2010). Unfortunately, this is not an isolated case. Major threats to freshwater fishes in particular and freshwater biodiversity in general have been grouped into five categories: overexploitation of water resources, water pollution, flow modification, destruction or degradation of habitat, and invasive species (Silk & Ciruna, 2005; Dudgeon et al., 2006). Inland waters in Mexico have experienced these threats, and currently 70% of main rivers are polluted, > 5,000 dams have modified their flow and > 100 invasive species inhabit inland waters (Carabias & Landa, 2005; Domínguez-Domínguez et al., 2007; CONAGUA, 2011).

The effect of these threats on freshwater fishes depends on the particular environmental conditions, the type and amount of pressure exerted by human activities, and the distribution range of species. For instance, species with restricted distributions, such as the Cuatro Cienegas platyfish *Xiphophorus gordoni*, which inhabits desert springs, and the Yucatan tetra *Astyanax altior*, endemic to cenotes in the Yucatan Peninsula, are more imperilled than those with a wide distribution (Jelks et al., 2008; Contreras-MacBeath et al., 2014). Meanwhile, habitats in northern Mexico with major water supply problems as a result of semi-arid and arid conditions are at higher risk of desiccation than aquatic systems in south-east Mexico (Contreras-Balderas & Lozano-Vilano, 1993; Carabias & Landa, 2005; Ceballos

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TABLE 1 Freshwater fish species that are extinct in the wild or extirpated in Mexico (Ceballos et al., 2017b).

Species	Distribution	Status
Cyprinodon alvarezi	Mexico, endemic	Extinct in the wild
Cyprinodon longidorsalis	Mexico, endemic	Extinct in the wild
Cyprinodon veronicae	Mexico, endemic	Extinct in the wild
Skiffia francesae	Mexico, endemic	Extinct in the wild
Xyrauchen texanus	North America	Extirpated
Gila elegans	North America	Extirpated
Hybognathus amarus	North America	Extirpated
Notropis simus	North America	Extirpated
Ptychocheilus lucius	North America	Extirpated
Rhinichthys osculus	North America	Extirpated

et al., 2017a,b). Watershed management in Mexico therefore requires addressing local conservation issues with a regional perspective, to ensure the maintenance of these habitats and their fish populations in the long term (Stiassny & Bianco, 1998; Ceballos et al., 2017b).

The Catarina pupfish (Plate 1) was discovered in 1961. It was described in 1972 as the only species of the genus *Megupsilon*, and only 22 years after its scientific discovery it became extinct in the wild. We present a historical synopsis of the species and the causes of its decline, and discuss the implications of the extinction process for the conservation of freshwater fish diversity in Mexico.

The discovery and description of a new species

Available information on the biology and ecology of the Catarina pupfish is scarce but examination of peer-reviewed and grey literature provided us with sufficient details to document the sequence of events and factors that led to the species' decline (Miller & Walters, 1972; Contreras-Balderas & Lozano-Vilano, 1996a,b; Contreras-Balderas et al., 2003; Echelle et al., 2005; Jelks, et al., 2008; Bennett & Conway, 2010; Burkhead, 2012; Liu & Echelle, 2013).

The first recorded individual of the Catarina pupfish was collected from the wild by R.R. Miller and H.L. Huddle in 1961, but the species was not described until 1972 (Miller & Walters, 1972). *Megupsilon aporus* is an endemic Mexican species (Miller, 1956). The generic name and species were assigned based on two particular characters: *Megupsilon* in reference to the huge Y chromosome in males, and *aporus* in reference to the lack of pores in the cephalic sensory system (Miller & Walters, 1972). Although the species is related to *Cyprinodon*, the characters that classified it as a separate species, along with those previously mentioned, were a different number of chromosomes between males (47) and females (48), the presence of side scales between the dorsal and anal fins, the lack of a black terminal border in the anal fin of nuptial males, the presence of an anal fin as large as the dorsal fin in females, and particular behavioural traits (see below; Uyeno & Miller, 1971; Miller & Walters, 1972).

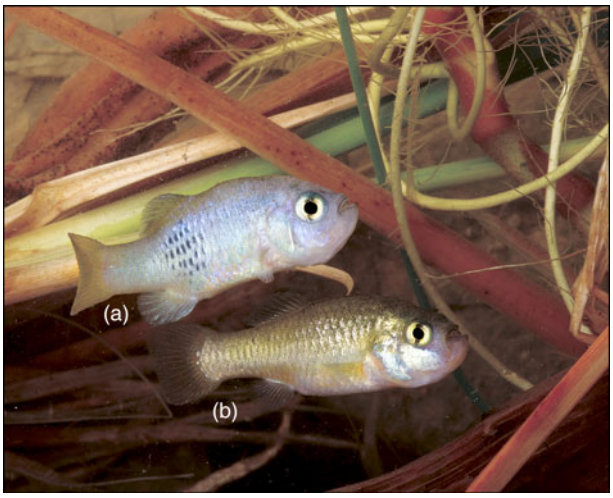

PLATE 1 The Catarina pupfish *Megupsilon aporus* was a freshwater fish endemic to Mexico; it is now extinct: (a) male, (b) female. Photograph by Daniel Garza Tobón.

The small Catarina pupfish exhibited sexual dimorphism. Males were smaller (26 mm in length) than females (36 mm; Miller & Walters, 1972). Adult males were steel blue on the back and sides of the body, with a golden sheen in the caudal peduncle, the caudal fin was orange, and a there was a vertical black bar above and below the pupil on the eyes. Adult females had a golden olivaceous colouration over the body (Miller & Walters, 1972).

Habitat

The Catarina pupfish was endemic to a freshwater spring at El Potosi, on the west side of Sierra Madre Oriental, and within the Sandia basin, Galeana, Nuevo León, Mexico (24°51′N 100°19′W; Fig. 1). This location, at 1,880 m, was also home to the Potosi pupfish *Cyprinodon alvarezi* and the freshwater crayfish *Cambarellus alvarezi* (Rodríguez-Almaraz & Campos, 1994), both also endemic to this small spring. The spring was a remnant of a larger water body in an endorheic basin known as La Hediondilla (Miller & Walters, 1972). It is believed that during the Pleistocene the larger lake was connected with the Rio Conchos basin and Rio Bravo tributaries in the north.

Habitat descriptions by Miller & Walters (1972) mentioned the presence of a main pond (c. 1 ha) with an inner stream and some secondary ponds. Clear water was present year-round, with depths of 0.4–4 m (Miller & Walters, 1972). These conditions remained until the early 1980s (Plate 2; Rodriguez-Almaraz & Campos, 1994). The vegetation in the area included pennywort *Hydrocotyle* sp., herbaceous flowering plants *Nasturtium* sp., water primrose *Lugwigia* sp., hornwort *Ceratophyllum demersum*,

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FIG. 1 Location of El Potosi spring in Nuevo León, Mexico, which is the only known habitat of the Catarina pupfish *Megupsilon aporus*.

pondweed *Potamogeton* sp., duckweed *Lemna* sp., green algae, and grasses restricted to shallow areas (Miller & Walters, 1972; Guzmán-Cedillo, 1981).

Natural history and ecology

Megupsilon aporus was considered to be part of a relict fauna isolated from the Rio Grande system more than 5 million years ago (Echelle et al., 2005). It diverged from the common *Cyprinodon* ancestor to constitute a monotypic genus in the late Miocene (Echelle et al., 2005). Following its discovery, several expeditions were made to gather information on the species and its habitat (Table 2). On an expedition in 1968 Contreras-Balderas and Lozano-Vilano found that the flow in the pond was constant year-round and that aquatic vegetation was abundant. They also described the abundance of *M. aporus*; c. 6,000 individuals were found in pockets of the aquatic vegetation mat, which was mainly composed of *Ceratophyllum* sp. (Contreras-Balderas & Lozano-Vilano, 1996a). By 1974, individuals of largemouth bass *Micropterus salmoides* were collected in El Potosi and the abundance of *Megupsilon* was significantly lower. There is no information regarding the introduction of this exotic fish but its presence was one of the causes of the decline of the Catarina pupfish, although not the most pervasive (Contreras-Balderas & Lozano-Vilano, 1996a; see below).

The Catarina pupfish was oviparous, with no breeding territoriality. The species presented two characteristic behaviours: opercular rotation and jaw-nudging during courtship (Liu & Echelle, 2013). Courtship and mating took a unique form, with no aggressive behaviour; instead attractive movements were performed to bring about successful spawning. Mating was usually carried out at dawn or dusk

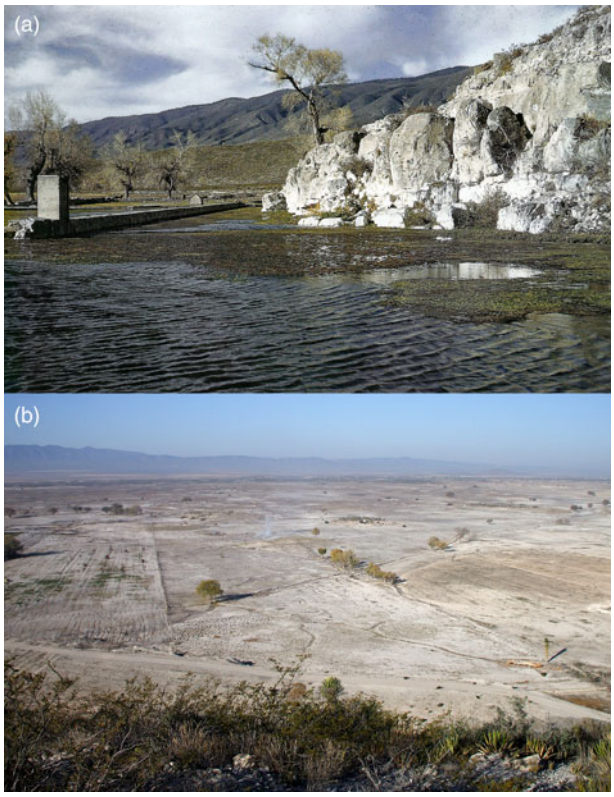

PLATE 2 Habitat degradation and desiccation of the El Potosi spring in Nuevo León, Mexico (Fig. 1). (a) The spring in 1961 (photograph from Miller et al., 2005), and (b) in 2009 (photograph by María Elena Ángeles Villeda).

and there was no cannibalistic egg consumption nor aggression of any kind among males and females (V. González, pers. comm.).

According to Miller & Walters (1972), *M. aporus* coexisted with the Potosi pupfish via niche partitioning. The Catarina pupfish preferred shallow areas close to the surface, whereas the Potosi pupfish occurred predominantly in the deep waters of the spring. The two species had different dietary preferences; the Catarina pupfish was carnivorous, feeding mainly on insect larvae and chironomids, whereas the Potosi pupfish fed mainly on algae.

Habitat degradation

The habitat, described by Miller & Walters (1972), remained in good condition for more than 15 years (Rodríguez-Almaraz & Campos, 1994). During 1968–1983 the area covered by the spring contracted and expanded as a result of water extraction for agriculture and subsequent recovery during the wet season. However, in 1985 the spring was reduced to 10% of its former size as a result of intensified groundwater pumping. By 1986 only a shallow irrigation ditch and small tributaries

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TABLE 2 Details of expeditions to the El Potosi spring in Nuevo León, Mexico (Fig. 1), the only known habitat of the Catarina pupfish *Megupsilon aporus* (Contreras-Balderas, 1991; Rodríguez-Almaraz & Campos, 1994; Contreras-Balderas & Lozano-Vilano, 1996a).

Date	Lead scientists	Comments
Feb. 1961	R.R. Miller & H.L. Huddle	Specimen of *Megupsilon aporus* found
Feb. 1968	V. Walters & J. Bleck	510 individuals of *M. aporus* collected
Mar. 1968	R.R. Miller & H.L. Huddle	Holotypes of *M. aporus* collected
June 1968	V. Walters & B.J. Turner	151 individuals of *M. aporus* collected
1968	S. Contreras-Balderas & M.L. Lozano-Vilano	Circa 6,000 individuals of *M. aporus* reported
July 1972	V. Walters, R.E. Brown Jr., R. Haas, R.K. Liu & S.H. Walters	High abundance of *M. aporus* reported
1974	S. Contreras-Balderas	Collection of largemouth bass *Micropterus salmoides*, reported as common species
1974	S. Contreras-Balderas	Translocation of individuals of *M. aporus* to adjacent springs without largemouth bass
Late 1970s & early 1980s	G.A. Rodriguez-Almaraz & E. Campos	Contraction of the spring as a result of intensified groundwater pumping
Early 1990s	S. Contreras-Balderas	Overexploitation of water for crop irrigation
1994	S. Contreras-Balderas	*M. aporus* considered extinct in the wild
1995	S. Contreras-Balderas	Desiccation of El Potosi spring

remained (Contreras-Balderas & Lozano-Vilano, 1996a; Plate 2).

Overexploitation of water was the main cause of the decline of *M. aporus* (Contreras-Balderas & Lozano-Vilano, 1996a). By 1990 more than 80 wells of > 100 m depth had been dug for irrigation of corn and potato fields in El Potosi and Sandia Valleys, causing the desiccation of springs and creeks in the region. As a result, aquatic species, including the fishes *Cyprinodon veronicae*, *Cyprinodon longidorsalis*, *Cyprinodon ceciliae* and *Cyprinodon inmemoriam* became locally extinct (Contreras-Balderas, 1991). The Catarina pupfish was considered to be extinct in the wild by 1994, and in 1995 El Potosi spring was completely dry (Tveteraas, 1993; Contreras-Balderas & Lozano-Vilano, 1996b).

Given the grave situation, a strategic plan to protect the area was presented by the first Mexican fish recovery team, which comprised researchers from Universidad Autonoma de Nuevo León. However, the proposal was not adopted or enforced (Contreras-Balderas, 1991).

In the early 2000s natural coal deposits in the area started burning as a result of the collapse and subsidence of sediments, causing the ground to sink in both the El Potosi and La Sandia valleys. Burning episodes have been intermittent, with wet and dry periods (Valdés González, 1997; Amezcua Torres, 2009).

Captivity and extinction

One of the first attempts to protect the Catarina pupfish was made by Salvador Contreras-Balderas, who in 1974 moved numerous individuals to other springs in the area to reduce the pressure exerted by the largemouth bass (Contreras-Balderas & Lozano-Vilano, 1996a). One year later, a small population of *M. aporus* was identified in a small spring in the area. In 1976 Armando J. Contreras-Balderas and his team eradicated the largemouth bass, removing > 280 individuals from the spring (Contreras-Balderas & Lozano-Vilano, 1996a). In the following years, the rapid degradation of the habitat as a result of water extraction increased the need to maintain the species in captivity to avoid extinction. Since 1984 the Catarina pupfish remained in captivity in a management unit specifically for the conservation of the species.

In the early 1990s the New York Aquarium and Universidad Autonoma de Nuevo León established a programme (Emerging rescue of Mexican fish species in imminent danger of extinction) to protect the most representative and threatened freshwater fishes of Mexico. The effort was also joined by the Children's Aquarium at Fair Park, Dallas, Texas. The aims of the programme were to sustain stocks of species over the long term, to maintain sufficient individuals to repopulate native habitats, and to exchange specimens to ensure the diversity of the genetic pools, all by recruiting museums and public aquariums with sufficient space and technical and economic resources.

Individuals of the Catarina pupfish were maintained in various places, including San Luis Potosi in Mexico, Denver and Arkansas in the USA, Zaragoza in Spain, and Germany. However, the species was particularly sensitive to environmental conditions and prone to infections. In 2011 most individuals of the captive populations succumbed to *Mycobacteria* infections and those that remained were too weak or sterile.

In 2012 the Children's Aquarium at Fair Park, Dallas, Texas, held the last surviving population, with only 20 individuals (Liu & Echelle, 2013). The last two males were used in an attempt to save the species through hybridization and

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TABLE 3 Freshwater fish species endemic to Mexico or Mexico and the USA that are now extinct, with former geographical location, and causes of extinction (Burkhead, 2012; Ceballos et al., 2017b).

Species	Distribution	Geographical location	Cause of extinction (estimated year)
Atherinella callida	Mexico	Rio Tonto drainage, Veracruz	Pollution (1957)
Chirostoma bartoni	Mexico	Crater lake at Valle de Santiago, Guanajuato	Desiccation (2006)
Chirostoma charari	Mexico	La Mintzita spring, Morelia	Habitat degradation (1957)
Evarra bustamantei	Mexico	Xochimilco, Mexico City	Habitat degradation; pollution (1983)
Evarra eigenmanni	Mexico	Chalco/Xochimilco, Mexico City	Habitat degradation; pollution (1983)
Evarra tlahuacensis	Mexico	Chalco, Mexico City	Habitat degradation; pollution (1983)
Notropis aulidion	Mexico	Tunal River, Durango	Invasive species (1965)
Notropis orca	North America	Rio Grande, USA/Mexico	Invasive species (1975)
Notropis saladonis	Mexico	Salado River, Nuevo León, Coahuila	Unresolved (1992)
Stypodon signifer	Mexico	Spring, Parras Coahuila	Desiccation (1930)
Cyprinodon ceciliae	Mexico	La Presa Spring, Nuevo León	Desiccation (1991)
Cyprinodon inmemoriam	Mexico	Ojo la Trinidad, Nuevo León	Desiccation (1986)
Cyprinodon latifasciatus	Mexico	Parras, Coahuila	Pollution (1930)
Megupsilon aporus	Mexico	Spring, El Potosi, Nuevo León	Desiccation/invasive species (2014)
Characodon garmani	Mexico	Spring, Parras Coahuila	Desiccation/pollution (1900)
Priapella bonita	Mexico	El Refugio, Veracruz	Pollution (1906)

backcross with a female of *C. alvarezi*. The reproduction was successful, yielding more than 30 newborn individuals; however, all of them were females with mycobacteriosis, and all eventually died.

Lessons learned

The extinction of the Catarina pupfish has implications at various scales. *Megupsilon aporus* was a monotypic genus that diverged from *Cyprinodon* c. 7 million years ago according to molecular analyses (Echelle et al., 2005). The loss of this species precludes any opportunity to study its unique evolutionary history and to understand the adaptive processes by which it was able to survive as a relic for thousands of years. Its extinction, as suggested by Burkhead (2012) for freshwater fishes in general, is evidence of a much larger problem: the current loss of freshwater biodiversity.

Freshwater fishes are being lost at a faster rate than terrestrial species. Jelks et al. (2008) reported 700 imperilled freshwater fishes in North America; of the 280 species categorized as Endangered, 65 are endemic to Mexico (Jelks et al. 2008; Burkhead, 2012). In the 20th century Mexico has lost 16 species, 15 of them endemic (IUCN, 2016; Ceballos et al., 2017a,b; Table 3). The extinction of these species is attributed to two main causes: habitat degradation and pollution. Habitat degradation by desiccation of water bodies affected species that inhabited springs in arid and semi-arid environments, which are under water stress as a result of low precipitation and a high demand for water for human activities (De la Vega, 2003). Species that were affected by pollution lived in environments close to large cities or to industries that discharge pollutants to the water without regulation or previous treatment (Alcocer, 2007). The species that became extinct were vulnerable, microendemic species whose life histories were adapted to isolated environments and particular conditions. However, the increasing pressure on freshwater resources may cause a generalized extinction trend, affecting even widely distributed species.

Concern for Mexican freshwater fishes has led to an increase in knowledge about this group and the habitats on which they depend. For instance, in 2012 a national-level analysis of the gaps in the conservation of aquatic biodiversity in Mexico was published (Aguilar et al., 2012). This effort, which involved more than 250 specialists, resulted in the identification of priority sites and their representativeness in the national system of protected areas. Although the results indicated that only 15.8% of the area covered by priority sites is currently protected, it was a first step to increase action focused on the conservation, management and restoration of aquatic systems in Mexico.

In 2016 Mexico included 17 freshwater fishes as part of the Alliance for Zero Extinction, an international initiative to safeguard places with microendemic species (AZE, 2018). Local efforts to protect the species and their habitats have increased awareness among the population. For instance, the designation of the RAMSAR site Manantiales geotermales de Julimes, in 2014, was supported by the presence of the Julimes pupfish *Cyprinodon julimes*. This killifish was described in 2009 and its distribution is limited to El Pandeño hot spring in Chihuahua, Mexico (De la Maza-Benignos & Vela-Valladares, 2009). The local community, together with non-profit organizations, researchers and the local government have developed a conservation strategy for the area, which includes the establishment of a state park (Blando-Navarrete et al., 2007; De la Maza-Benignos, 2009).

Research conducted by Mexican academic institutions, sometimes in collaboration with international partners,

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has increased the ex situ conservation efforts for imperilled freshwater fishes. Universidad Michoacana de San Nicolas de Hidalgo and Universidad Autonoma de Nuevo León have led the efforts, with more than 40 species kept in captivity (Lascuráin et al., 2009). In particular, the golden skiffia *Skiffia francesae* and tequila splitfin *Zoogoneticus tequila* are examples of species that otherwise would be extinct, as they no longer exist in the wild (Lascuráin et al., 2009).

There is still an urgent need to implement programmes focused on the maintenance of freshwater systems. Lack of regulation and enforcement are threatening both freshwater fishes and water provision. The extinction of the Catarina pupfish is a reminder of the vulnerability of aquatic systems. There is a need to improve ecosystem management strategies and the policies related to freshwater resources, and the development of a national strategy for the conservation of freshwater fishes should be a priority. Such a strategy should include reintroduction of species extinct in the wild, securing populations of the most threatened species both in captivity and in the wild, and reduction of threats. This strategy would bring together scientists and practitioners to identify species and priority sites for conservation, design a monitoring system to assess the current state of the populations, improve watershed management practices, and increase the impact of ex situ and in situ conservation actions to maintain species in the long term. A concurrent citizen science programme in which local communities would play a main role in the protection and monitoring of the habitats could have a positive impact, with relatively low investment costs. There is still time to avert further extinctions of fish species in Mexico, but the window of opportunity is closing. The next 2 decades will be critical for most species at risk.

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Author contributions Conceptualization: GC; compilation of information on the Catarina pupfish: AVG, MEAV, LME; writing: LME, GC.

Conflicts of interest None.

Ethical standards This research complied with the *Oryx* Code of Conduct for authors.

References

Aguilar, V., Alarcón, J., González, L., Kolb, M., Koleff, P. & Urquiza-Haas, T. (2012) *Vacíos y omisiones en conservación de la biodiversidad acuática epicontinental de México ríos, cuerpos de agua y humedales*. CONABIO, CONANP, Ciudad de México, México.

Alcocer, J. (2007) El agua epicontinental de México. *Ciencia*, July–September, 26–35.

Amezcua Torres, N. (2009) Caracterización de materia orgánica sedimentaria lacustre: un ejemplo del paleolago El Potosí, Nuevo León, México. *Revista Geociencia*, 5, 21–32.

AZE (Alliance for Zero Extinction) (2018) Http://www.zeroextinction.org [accessed 27 July 2018].

Bennett, M.G. & Conway, K.W. (2010) An overview of North America's diminutive freshwater fish fauna. *Ichthyological Exploration of Freshwaters*, 21, 63–72.

Blando-Navarrete, J.L., Jiménez-González, J., Valencia-Castro, C.M., Castañeda-Gaytán, G. & Carrillo-Flores, R. (2007) *Estudio técnico justificativo para declarar Parque Estatal El Pandeño de los Pando, en el Municipio de Julimes Chihuahua*. Biodesert A.C., World Wildlife Fund, Universidad Juárez del estado de Durango, Universidad Autónoma Chapingo, México.

Burkhead, N.M. (2012) Extinction rates in North American freshwater fishes, 1900–2010. *BioScience*, 62, 798–808.

Carabias, J. & Landa, R. (2005) *Agua, medio ambiente y sociedad. Hacia la gestión integral de los recursos hídricos en México*. UNAM, El Colegio de México, Fundación Gonzalo Río Arronte, Ciudad de México, México.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M. & Palmer, T.M. (2015) Accelerated modern human-induced species losses: entering the sixth mass extinction. *Science Advances*, 1, e1400253.

Ceballos, G., Ehrlich, P.R. & Dirzo, R. (2017a) Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences of the United States of America*, 114, E6089–E6096.

Ceballos, G., Díaz-Pardo, E., Martínez-Estévez, L. & Espinosa Pérez, H. (2017b) *Peces dulceacuícolas de México en peligro de extinción*. Fondo de Cultura Económica, Ciudad de México, México.

CONAGUA (Comisíon Nacional del Agua) (2011) *Informe Estadísticas del agua en México*. Http://www.conagua.gob.mx/CONAGUA07/Publicaciones/Publicaciones/SGP-1-11-EAM2011.pdf [accesed 24 March 2017].

Contreras-Balderas, S. (1991) Conservation of Mexican fresh water fishes: some protected sites and species, and recent federal legislation. In *Battle Against Extinction. Native Fish Management in the American West* (eds W.L. Minckley & J.E. Deacon), pp. 191–197. The University of Arizona Press, Arizona, USA.

Contreras-Balderas, S. & Lozano-Vilano, M.L. (1993) Water, endangered fishes, and development perspectives in north-eastern Mexico. *Conservation Biology*, 8, 379–387.

Contreras-Balderas, S. & Lozano-Vilano, M.L. (1996a) Survival status of the Sandia and Potosi Valleys endemic pupfishes and crayfishes from the Mexican plateau in Nuevo León, Mexico, with comments on extinct snails. *Proceedings of the Desert Fishes Council, Volume XXVII, 1995 Annual Symposium, 28*.

Contreras-Balderas, S. & Lozano-Vilano, M.L. (1996b) Extinction of most Sandia and Potosí valleys (Nuevo León, México) endemic pupfishes, crayfishes and snails. *Ichthyological Exploration of Freshwaters*, 7, 33–40.

Contreras-Balderas, S., Almada-Villela, P., Lozano-Vilano, M.L. & García-Ramírez, M.E. (2003) Freshwater fish at risk or extinct in México. A checklist and review. *Reviews in Fish Biology and Fisheries*, 12, 241–251.

Contreras-MacBeath, T., Brito Rodríguez, M., Sorani, V., Goldspink, C. & McGregor Reid, G. (2014) Richness and endemism of the freshwater fishes of Mexico. *Journal of Threatened Taxa*, 6, 5421–5433.

De la Maza-Benignos, M. (ed.) (2009) *Los Peces del Río Conchos*. Alianza WWF – FGRA y Gobierno del Estado de Chihuahua, Chihuahua, México.

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De la Maza-Benignos, M. & Vela-Valladares, L. (2009) *Cyprinodon julimes* sp. nov. In *Los Peces del Río Conchos* (ed. M. De la Maza-Benignos), pp. 185–189. Alianza WWF-FGRA y Gobierno del Estado de Chihuahua, Chihuahua, Mexico.

De la Vega, M.Y. (2003) Situación de los peces dulceacuícolas de México. *Ciencias*, 72, 20–30.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J. & Collen, B. (2014) Defaunation in the Anthropocene. *Science*, 345, 401–406.

Domínguez-Domínguez, O., Boto, L., Alda, F., Pérez-Ponce de León, G. & Doadrio, I. (2007) Human impacts on drainages of the Mesa Central, Mexico, and its genetic effects on an endangered fish, *Zoogoneticus quitzeoensis*. *Conservation Biology*, 21, 168–180.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C. et al. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, 81, 163–182.

Echelle, A.A., Carson, E.W., Echelle, A.F., Van Den Bussche, R.A., Dowling, T.E. & Meyer, A. (2005) Historical biogeography of the New-World pupfish genus *Cyprinodon* (Teleostei: Cyprinodontidae). *Copeia*, 2005, 320–339.

Guzmán-Cedillo, L.M.P. (1981) *Aspectos biológicos de dos peces Cyprinodontidos y un crustáceo Cambaridae de Potosí, N.L.* BSc thesis. Universidad Autónoma de Nuevo León (Facultad de Ciencias Biológicas), Nuevo León, México.

IUCN (2016) *IUCN Red List Categories and Criteria (Version 3.1)*. Http://www.iucnredlist.org/ [accessed 24 March 2017].

Jelks, H., Walsh, S.J., Burkhead, N.M., Contreras-Balderas, S., Díaz-Pardo, E., Hendrickson, D.A. et al. (2008) Conservation status of imperiled North American freshwater and diadromous fishes. *Fisheries*, 33, 372–407.

Lascuráin, M., List, R., Barraza, L., Díaz Pardo, E., Gual Sill, F., Maunder, M. et al. (2009) Conservación de especies ex situ. In *Capital natural de México, vol. II: Estado de conservación y tendencias de cambio*, pp. 517–544. CONABIO, Ciudad de México, Mexico.

Liu, R.K. & Echelle, A.A. (2013) Behavior of the Catarina pupfish (Cyprinodontidae: *Megupsilon aporus*), a severely imperiled species. *The Southwestern Naturalist*, 58, 1–7.

Miller, R.R. (1956) A new genus and species of cyprinodontid fish from San Luis Potosi, Mexico, with remarks on the subfamily Cyprinodontinae. *Occasional Papers of the Museum of Zoology, University of Michigan*, 581, 1–17.

Miller, R.R. & Walters, N. (1972) A new genus of cyprinodontid fish from Nuevo León, Mexico. *Contributions in Science of the Natural History Museum of Los Angeles County*, 233, 1–13.

Miller, R.R., Williams, J.D. & Williams, J.E. (1989) Extinctions of North American fishes during the past century. *Fisheries*, 14, 22–38.

Miller, R.R., Minckley, W.L. & Norris, S.M. (2005) *Freshwater Fishes of Mexico*. The University of Chicago Press, Chicago, USA.

Myers, R.A. & Worm, B. (2005) Extinction, survival or recovery of large predatory fishes. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 360, 13–20.

Olden, J.D., Hogan, Z.S. & Zanden, M. (2007) Small fish, big fish, red fish, blue fish: size-biased extinction risk of the world's freshwater and marine fishes. *Global Ecology and Biogeography*, 16, 694–701.

Régnier, C., Achaz, G., Lambert, A., Cowie, R., Bouchet, P. & Fontaine, B. (2015) Mass extinction in poorly known taxa. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 7761–7766.

Ricciardi, A. & Rasmussen, J.B. (1999) Extinction rates of North American freshwater fauna. *Conservation Biology*, 13, 1220–1222.

Rodríguez-Almaraz, G.A. & Campos, E. (1994) Distribution and status of the crayfishes (Cambaridae) of Nuevo León, Mexico. *Journal of Crustacean Biology*, 14, 729–735.

Silk, N. & Ciruna, K. (eds) (2005) *A Practitioner's Guide to Freshwater Biodiversity Conservation*. Island Press, Washington, DC, USA.

Stiassny, M. & Bianco, P.G. (1998) The medium is the message. Biodiversity freshwater diversity in peril. In *The Living Planet in Crisis: Biodiversity Science and Policy* (eds J. Cracaft & F. Grifo), pp. 53–71. Columbia University Press, New York, USA.

Tveteraas, A. (1993) Mexikanische Killifische am Rande der Ausrottung. *Datz Aquarien Terrarien*, 12, 802–806.

Uyeno, T. & Miller, R.R. (1971) Multiple sex chromosomes in a Mexican cyprinodontid fish. *Nature*, 231, 452–453.

Valdés González, A. (1997) *Influencia de la calidad del hábitat y el alimento sobre la viabilidad y aptitud ecológica de dos especies del género* Cyprinodon, C. veronicae *y* C. longidorsalis *(Lozano y Contreras 1993) del sur de Nuevo León, México*. PhD thesis. Universidad Autónoma de Nuevo León, Nuevo León, Mexico.

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