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Diatoms from gut contents of museum specimens of an endangered minnow suggest long-term ecological changes in the Rio Grande (USA)

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Abstract Diatoms consumed by Rio Grande silvery minnows (*Hybognathus amarus*) collected 104 years apart were used to deduce ecological requirements of this endangered species and to infer a possible cause of its decline based on environmental conditions in the Rio Grande. In 1874, foraged diatoms were largely motile, silt tolerant generalist and epipelic species (e.g. *Navicula capitatoradiata*, *Navicula cryptotenella*, *Nitzschia palea*, *Sellaphora pupula*) somewhat tolerant to pollution and indicative of eutrophic conditions, low dissolved oxygen, and high biological oxygen demand (BOD). In contrast, diatoms foraged in 1978 were mainly nonmotile epipsammic species (Fragilariaceae) sensitive to pollution and characteristic of low nutrient, oligotrophic conditions with high dissolved oxygen and low BOD. The large-scale difference in composition of the foraged diatom assemblages is consistent with a decline in nutrients and a shift in trophic state commonly associated with river regulation by dams. The results suggest that facilitating allochthonous input of detritus and nutrients into the Rio Grande ecosystem to meet foraging requirements for algivorous and detritivorous fish species such as *H. amarus* would be a good river restoration strategy.

Keywords *Hybognathus amarus* · Rio Grande silvery minnow · River limnology · Diatoms · Conservation · Oligotrophication

Introduction

The Wheeler Surveys west of the 100th Meridian were an important reconnaissance of the natural resources available for population expansion across the western United States. They also provided some of the earliest museum specimens of many plant, wildlife, and fish species of the region. We report here comparisons of two samples of the endangered Rio Grande silvery minnow (*Hybognathus amarus*) taken from a 25 km reach at approximately the same time of year: Wheeler Survey specimens from August 1874 (Cope and Yarrow 1875) and fish collected 26 July 1978—the only *H. amarus* collections made above Cochiti Reservoir after its completion. The purpose of these comparisons is to elucidate

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foraging ecology of *H. amarus* and habitat changes in the Rio Grande. We have used these Wheeler Survey specimens to infer significant features of the life history of *H. amarus* (Cowley et al. 2006). Here we use the historical perspective provided by preserved museum specimens to further study the natural history of the endangered *H. amarus* and infer a possible cause for its decline.

The ecological conditions of aquatic ecosystems worldwide have been altered by flow regulation, habitat destruction, and exotic introductions (Sallenave and Cowley 2004; Cowley 2006). Unfortunately for many river systems, specific ecological conditions prior to major modifications are not well known. One traditional way to understand past conditions of aquatic systems is by identifying the remnant diatom frustules preserved in sediments (Clarke et al. 2005; Ekdahl et al. 2007). Diatoms, which are excellent indicators of environmental conditions (Dixit et al. 1992), can also be extracted from the gut contents of preserved minnow specimens (Rosati et al. 2003). While the examination of gut contents from museum specimens is an undeveloped area of limnology, previous studies show that gut content can be examined after a few decades of specimen preservation (Rachlin and Warkentine 1987; Kido et al. 1993; Rosati et al. 2003). Because members of *Hybognathus* are known to ingest diatoms (Raney 1942; Whitaker 1977; Hlohowskyj et al. 1989; Shirey 2004), we used museum specimens preserved since 1874 to infer forage habitat conditions for the endangered *H. amarus*.

The seven *Hybognathus* species of North America have been threatened with river flow regulation and habitat destruction over the past century. Although *H. amarus* was once an abundant (Bestgen and Platania 1991) and widely distributed species in the Rio Grande (Sublette et al. 1990; Cowley 2006), it is presently the most geographically restricted species of *Hybognathus*, occupying only a small fraction of its historic range (Bestgen and Platania 1991). In a broader context, *H. amarus* is the last remaining pelagic spawning minnow species native to the Rio Grande in New Mexico; the other three species were extirpated prior to 1980 (Sublette et al. 1990). Extensive river and floodplain modifications within the Rio Grande (reviewed by Cowley 2006) have limited our potential for understanding ecological requirements for *H. amarus* because the remaining occupied habitats are highly altered from the historical conditions (Bestgen and Platania 1991; Bestgen and Propst 1996). Continuous water depletion from the Rio Grande and extended climatic drought conditions have necessitated discovery of the specific habitat conditions that will promote recovery of the endangered *H. amarus*. Despite the destruction of its former habitats, the once prolific *H. amarus* might be restored if river managers were provided with more detailed knowledge of favorable habitat conditions.

Description of sites studied

The oldest museum specimens of *H. amarus* from the Rio Grande of New Mexico were collected in August 1874 at San Ildefonso (Fig. 1) by Edward Cope and Henry Yarrow, naturalists assigned to the Wheeler Survey (Cope and Yarrow 1875; Rio Grande at San Ildefonso, $N = 20$, USNM 15801). This collection of *H. amarus* specimens predated major dam construction and therefore provided a reference for comparison to specimens collected after major river manipulations that led to highly regulated flows. The contemporary specimens of *H. amarus* were collected from the Rio Grande on July 26th, 1978 approximately 25 km downstream from San Ildefonso at the Rio Grande's confluence with Cochiti Reservoir (NM-SA-78-170-03, $N = 26$, Eastern New Mexico University). Collection dates from August and late July allowed for a comparison that is assumed to be unaffected by seasonal variation.

The San Ildefonso area has a long history dating to Native American pueblo culture and it is likely that fish habitats in the Rio Grande had been affected by the long period of human settlement when Cope and Yarrow collected their sample in 1874. By the time Spanish explorers made first contact with the Pueblo Indians in 1540, more than 12,000 hectares of land along the Rio Grande in northern New Mexico were under cultivation (Scurlock 1998). In addition to San Ildefonso Pueblo, the pueblos of Santa Clara and San Juan were a short distance upstream. Hispanic colonization of New Mexico began in 1598 with an expedition led by Juan de Oñate that established a settlement at the confluence of the Rio Chama and the Rio Grande (Baxter 1997), at San Juan Pueblo.

Fig. 1 The Rio Grande and its tributaries

By 1874, numerous Spanish land grant settlements were interspersed among the continuously occupied pueblos. Many small-scale irrigation networks were supplied by primitive rock, brush and sod diversion dams, which were frequently destroyed by high flows (Baxter 1997).

The San Ildefonso reach of the Rio Grande was isolated from downstream reaches by the completion of Cochiti Dam in 1975. The contemporary sample of *H. amarus* collected in 1978 was the last record of the species from the San Ildefonso reach upstream of Cochiti Reservoir (Cowley 2006). The major differences in conditions of the Rio Grande at San Ildefonso in 1978, compared to 1874, included river flow regulation, three upstream reservoirs, and an annual large volume interbasin transfer of water into the Rio Grande basin (San Juan-Chama Diversion, reviewed by Cowley 2006). As a result, contemporary samples may be influenced by diminished peak flows, elevated base flows, and reduced nutrient availability.

Materials and methods

The Smithsonian Institution granted us permission to dissect digestive tracts from three of the 20 specimens in the 1874 sample. We used the same number of specimens from the 1978 sample to provide gut contents. Methods on gut content removal and diatom slide preparation are described by Rosati et al. (2003). For each slide, diatom valves were counted at 1,000× magnification to the lowest taxa possible until 10 valves were observed for any 10 species and until no new species were observed over the last 100 valves (Barbour et al. 1999). Diatom species were identified using keys and descriptions by Van Heurck (1885), Wolle (1890), Hustedt (1930), Patrick and Reimer (1966), Weber (1971), and Round et al. (1990).

Habitat preferences were listed for each diatom species based on reports in the literature. Diatoms were classified as epipelic (growing on fine sediment), epilithic (attached to rock), epipsammic (growing on sand grains), epiphytic (attached to plant material), or planktonic (growing unattached) (Round et al. 1990; Winter and Duthie 2000; Vilbaste 2001; Vilbaste and Truu 2003). Relative abundances of different diatom species within the six classifications above were used to infer the type of habitat where the *H. amarus* specimens had foraged.

We inferred water quality of the foraged habitat by using the Trophic Diatom Index (Kelly and Whitton 1995), the Lange-Bertalot Index (Lange-Bertalot 1979), and known ecological preferences of each diatom species (Lowe 1974; Beaver 1981; Van Dam et al. 1994). The value of the Trophic Diatom Index can range from 1 (very low nutrient concentrations) to 5 (very high nutrient concentrations). The interpretation of the Trophic Diatom Index is supplemented by determining the percent of diatoms in the sample tolerant to organic pollution (Tolerant Species Index) (Kelly and Whitton 1995). Taxa included in the percent tolerant species calculation are small *Navicula* species, *Sellaphora* species, *Navicula lanceolata*, *Nitzschia palea*, and other *Nitzschia* species (Kelly and Whitton 1995). The values of the Lange-Bertalot Index are 1 (species that are most tolerant to pollution, indicating eutrophic conditions), 2 (species less tolerant or indifferent to pollution, indicating mesoeutrophic conditions), and 3 (species sensitive to pollution, indicating oligotrophic conditions).

We calculated Shannon–Weiner diversity index (Magurran 1988) values for both years. We calculated a similarity matrix using Ružička's similarity index (Ružička 1958; Pielou 1984; Rosati et al. 2003). From this matrix, we produced a hierarchical cluster dendrogram (unweighted pair-group method with arithmetic means) using StatistiXL, a software package for Microsoft Excel, to determine similarity of diatom communities from the gut contents of individual fish within a sample and between the two years sampled. All summary measures of the foraged diatom assemblages were obtained by calculating values for each fish in a sample and then averaging those values across the three specimens. Standard errors were calculated to represent the variation between individuals in a sample.

Results

A total of 89 diatom taxa, comprising 38 genera, nine families, and 5,054 specimen valves were identified from the 1874 ($n = 3$ fish, 2,277 diatom valves) and 1978 ($n = 3$ fish, 2,777 diatom valves) samples (Table 1). The diatom assemblage from 1874 (70 total taxa) was richer in species composition than the assemblage from 1978 (48 total taxa) (Table 2). Twenty-four diatom species and 19 genera were common to both dates. Diatom diversity (Shannon diversity index, natural logarithms) was significantly higher for the 1874 collection compared to the 1978 collection (Table 2). The cluster dendrogram shows the samples fall into two clusters: 1874 and 1978 (Fig. 2).

The diatoms present in the 1874 and 1978 samples indicated little change over time in salinity. The diatoms indicate that pH had likely increased, nitrogen had likely decreased, saprobity had decreased (β-mesosaprobous to α-mesosaprobous in 1874 to oligosaprobous to β-mesosaprobous in 1978), and mesotraphentic species had increased. Oxygen requirements of the diatoms were strikingly different, with 98% of taxa requiring 30–75% O_2 saturation in 1874, while 87% of the taxa required near 100% O_2 saturation in 1978. A change in diatom habitat was suggested by replacement of epipelic species (80% in 1874) by epipsammic species (88% in 1978). Sand and silt particles within the gut content were also noticeably larger in 1978 compared to 1874.

The Lange-Bertalot Index values show the diatoms in 1978 were sensitive to pollution while the 1874 diatoms had a significantly higher level of pollution tolerance (Table 2). The Trophic Diatom Index values show that the diatoms from 1874 indicate substantially higher concentrations of nutrients present than the diatoms from 1978 (Table 2). An average of 31.5% of the 1874 diatoms were tolerant to organic pollution (indicating some evidence of organic pollution) while only 2.4% of the 1978 diatoms were tolerant to organic pollution (suggesting the site was free of organic pollution) (Table 2).

Discussion

An important element for recovery of an endangered species is deducing ecological requirements (Cowley 2006). The task of learning how best to conserve an endangered species is especially difficult when occupied habitats are altered from their historic conditions. Preserved museum specimens provide a window of opportunity to learn important aspects of natural history that might improve recovery efforts. The Wheeler Survey specimens examined in this study were collected prior to dam construction on the Rio Grande and therefore were sampled from habitat conditions that existed before major flow regulation by dams.

Our results suggest large differences in ecosystem conditions between 1874 and 1978. The motile, epipelic diatom species and fine silt in the gut contents from 1874 indicate that *H. amarus* foraged in a shallow silted habitat with elevated nutrient levels and flow less than 20 cm sec^{-1} (Hickman and Round 1970; Vilbaste and Truu 2003). The dominance of non-motile, chain forming, epipsammic Fragilariaceae (*Fragilaria*, *Staurosira*, *Staurosirella*) in the 1978 sample suggest that *H. amarus* foraged in a shallow sandy habitat with confined flow and lower nutrient concentrations than in 1874 (Hickman and Round 1970; Round 1984; Miller et al. 1987; Vilbaste and Truu 2003). Results indicate a large reduction in nutrient availability and ecosystem trophic state in the contemporary Rio Grande (Table 2).

The change observed in the composition of the diatom communities foraged by *H. amarus* in 1874 and 1978 gives support to river regulation as a

Table 1 Diatom species found in the digestive tracts of Rio Grande silvery minnows collected in August 1874 and July 26, 1978 are given with percentages for each fish (1874 *A*, *B*, and *C* and 1978 *D*, *E*, and *F*). Both samples were collected upstream of present-day Cochiti Reservoir

Taxon	Year					
	1874			1978		
	A	*B*	*C*	*D*	*E*	*F*
Achnanthidium exiguum Hustedt					0.11	
Achnanthidium minutissimum (Carter) Lange-Bertalot		0.52		0.11	0.11	0.11
Amphora ovalis Kützing	0.43	0.39	0.25			
Amphora sp.			0.25			
Anomoeneis sphaerophora (Kützing) Pfitzer		0.13	0.37			
Aulacoseira granulata var. angustissima (Müller) Simonsen					0.11	
Bacillaria paradoxa Gmelin	0.29					
Caloneis amphisbaena (Bory) Cleve			0.37			
Caloneis bacillum (Grunow) Cleve	2.43	1.17	2.35			
Caloneis ventricosa (Ehrenberg) Meister	0.86	1.04	2.72			
Cocconeis pediculus Ehrenberg				0.56	0.96	0.32
Cocconeis placentula Ehrenberg			0.25	1.80	1.17	1.26
Craticula ambigua (Ehrenberg) Mann	2.00	1.43	4.08			
Cyclotella sp.	0.43	0.13		0.45	0.53	0.63
Cymatopleura solea (Brébisson) Smith	0.29	0.52	0.99			
Cymbella sp.			0.25			0.11
Denticula elegans Kützing			0.50			
Diatoma vulgare Bory					0.53	
Encyonema minutum (Hilse in Rabenhorst) Mann				0.45	0.32	
Encyonema triangulum (Ehrenberg) Kützing		0.26	1.11			
Epithemia sorex Kützing	0.14	0.52	0.62		0.11	0.42
Epithemia turgida (Ehrenberg) Kützing			0.25			
Eunotia sp.				0.11		
Fallacia pygmaea (Kützing) Stickle and Mann						0.53
Fragilaria pinnata var. subrotunda Mayer				18.24	16.72	14.84
Fragilaria vaucherae (Kützing) Petersen			0.25		0.11	
Gomphoneis olivacea (Hornemann) Dawson ex Ross and Sims		0.39		0.11	0.43	0.21
Gomphonema sp.	0.29		0.25			
Gyrosigma sp. 1	1.43	0.78	1.24			
Gyrosigma sp. 2	0.43					
Hannaea arcus (Ehrenberg) Patrick			0.25			
Hantzschia amphioxys (Ehrenberg) Grunow		0.39				
Navicula capitatoradiata Germain	11.84	13.41	10.89	1.01	1.17	4.63
Navicula cryptocephala Kützing	3.57	2.47	2.85			
Navicula cryptotenella Lange-Bertalot	8.99	13.02	11.14	0.34	0.32	0.21
Navicula lanceolata (Agardh) Ehrenberg	2.57	2.08	0.87	0.23	0.11	
Navicula sp. 1	0.43	0.78	0.62			
Navicula sp. 2	0.14					
Navicula sp. 3				0.11	0.32	
Navicula symmetrica Patrick	5.99	10.42	6.19	0.11		0.11
Navicula tripunctata (Müller) Bory		1.56	1.73	0.23	0.32	0.21

Table 1 continued

Taxon	Year					
	1874			1978		
	A	*B*	*C*	*D*	*E*	*F*
Navicula veneta Kützing	1.71	3.26	2.72	0.11	0.11	
Navicula viridula var. rostellata (Kützing) Kützing emend. Van Heurck	1.14	2.21	1.36		0.11	
Neidium affine (Ehrenberg) Pfitzer	0.29		0.25			
Neidium sp.	0.57	0.13	0.99			
Nitzschia acicularis (Kützing) Smith	0.29	0.26	0.87			
Nitzschia amphibia Grunow			0.12		0.32	0.21
Nitzschia angustata (W. Smith) Grunow			0.25			
Nitzschia dissipata (Kützing) Grunow		0.26				
Nitzschia dissipata var. media (Hantzsch) Grunow	5.71	9.90	5.45	0.23		
Nitzschia filiformis (W. Smith) Van Heurck	2.28	0.78	0.99			
Nitzschia fonticola Grunow				0.23	0.21	0.42
Nitzschia frustulum (Kützing) Grunow				0.68	0.43	
Nitzschia inconspicua Grunow				1.13	0.32	0.11
Nitzschia palea (Kützing) W. Smith	10.84	9.11	5.20	0.11		0.11
Nitzschia paleacea Grunow in Van Heurck	8.56	6.12	6.06	0.11		0.84
Nitzschia recta Hantzsch ex Rabenhorst	2.57	2.86	0.62			
Nitzschia sigmoidea (Nitzsch) W. Smith		0.65				
Nitzschia sp. 1	2.57					
Nitzschia sp. 2	1.71					
Nitzschia sp. 3	0.29	0.78	1.24			
Pinnularia brebissonii (Kützing) Rabenhorst	0.57	0.26	0.12			
Pinnularia sp. 1			0.50			
Pinnularia sp. 2						0.11
Placoneis elginensis (Gregory) Cox	0.14		0.62	0.11	0.21	0.32
Pseudostaurosira brevistriata (Grunow in Van Huerck) Williams and Round				0.34	0.11	
Reimeria sinuata (Gregory) Kociolek and Stoermer	0.29		0.62	1.24	0.32	0.11
Rhoicosphenia abbreviata (Agardh) Lange-Bertalot					0.11	
Rhopalodia gibba (Ehrenberg) Müller		0.26	1.11			
Rhopalodia gibberula (Ehrenberg) Müller		0.26	0.37		0.21	0.63
Sellaphora pupula (Kützing) Meresckowsky		0.13	0.25			
Sellaphora rectangularis (Gregory) Lange-Bertalot and Metzeltin	10.41	6.25	11.14	0.23	0.32	1.26
Staurosira construens Ehrenberg			0.50	11.37	10.33	16.74
Staurosira construens var. binodis (Ehrenberg) Grunow	0.86			35.25	35.89	31.79
Staurosira construens var. cf. pumila (Grunow) Williams and Round				6.08	2.02	5.05
Staurosira construens var. venter (Grunow) Williams and Round				8.90	15.02	11.68
Staurosirella leptostauron (Ehrenberg) Williams and Round				0.23		
Staurosirella pinnata (Ehrenberg) Williams and Round	0.57			3.49	3.51	2.00
Staurosirella pinnata var. lancettula (Schumann) Siver and Hamilton		0.13	0.25	5.63	4.69	4.00
Stephanocyclus meneghiniana (Kützing) Skabitschevsky			0.12	0.45	1.81	0.84
Stephanodiscus sp.					0.32	0.11
Surirella angustata Kützing	1.85	1.56	2.23	0.11	0.21	0.11
Surirella sp.	0.29	0.13	0.74			

Table 1 continued

Taxon	Year					
	1874			1978		
	A	*B*	*C*	*D*	*E*	*F*
Suririella brightwellii W. Smith	0.29					
Synedra arcus Kützing		0.13				
Synedra sp.		0.65	0.87	0.11		
Synedra ulna (Nitzsch) Ehrenberg	0.86					
Tryblionella apiculata Gregory			0.62			
Tryblionella sp.	2.85	2.47	3.22			
Total Diatoms	701	768	808	888	939	950
			2277			2777

Table 2 Differences in diatom indices (LBI, TDI, and TSI), species richness, and Shannon diversity from gut contents of Rio Grande silvery minnows collected in August 1874 and July 26, 1978

Index	1874	1978	*t*	*P*
Species richness	46.30 ± 10.70	35.00 ± 4.81	2.68	0.055
Shannon diversity	3.07 ± 0.29	2.16 ± 0.03	8.69	<0.001
Lange-Bertalot Index (LBI)	2.08 ± 0.06	2.93 ± 0.04	31.80	<0.001
Trophic Diatom Index (TDI)	4.11 ± 0.19	2.77 ± 0.12	16.80	<0.001
Tolerant Species Index (TSI) (%)	31.54 ± 8.94	2.43 ± 1.00	8.99	<0.001

The value of the TDI ranges from 1 (very low nutrient concentrations) to 5 (very high). The values used in calculating the LBI are 1 (species that are most tolerant to pollution, indicating eutrophic conditions), 2 (species less tolerant or indifferent to pollution, indicating mesoeutrophic conditions), and 3 (species sensitive to pollution, indicating oligotrophic conditions). Both samples were collected upstream of present-day Cochiti Reservoir

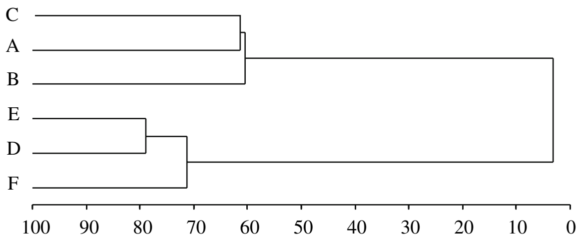

Fig. 2 Cluster dendrogram based on Ružička's similarity index showing similarity of diatom communities from gut contents of Rio Grande silvery minnows collected in August 1874 (*A*, *B*, and *C*) and July 26, 1978 (*D*, *E*, and *F*). Both samples were collected upstream of present-day Cochiti Reservoir

contributing factor in the decline of the species. It is well known that reservoirs trap sediment and nutrients, alter food webs downstream, and limit nutrient exchanges with floodplains due to reduced peak flows (Vörösmarty et al. 2003). The replacement of diatoms tolerant of eutrophy with species characteristic of low nutrient enrichment in 1978—oligotrophication—is consistent with the loss of nutrients to upstream reservoirs and reduced flooding consequent with flow regulation.

Two important problems must be resolved for our results to be of value to endangered species management. First, how well do the diatom assemblages foraged by *H. amarus* correspond to other observations of the Rio Grande in 1874 and 1978? The high relative abundances of silt tolerant diatoms in 1874 suggest streambed instability and possible lateral flooding (Bahls 1993; Kutka and Richards 1996). This suggestion is supported by the fact that floods of the Rio Grande destroyed buildings in 1874 (Wozniak 1998). Lateral flows within the floodplain would help sustain side channels, wetlands, and pools that are likely to be important for *H. amarus* as they are for other *Hybognathus* species (Scheurer et al. 2003). U.S. Geological

Survey data (Hale 1978) showed that 1978 was a year of reduced flow in the Rio Grande. The same survey also showed that the family Fragilariaceae (Williams and Round 1987) was most abundant in plankton samples taken in July of 1978 (Hale 1978), which coincides with the predominant diatom taxa observed in the 1978 gut contents from fish collected in the same month. The USGS recorded pH of 8.3 from July of 1978 (Hale 1978) also coincides with the alkaliphilous taxa observed from the 1978 gut contents. Therefore, we conclude that the diatom assemblages sampled by *H. amarus* in 1874 and 1978 were consistent with external information about the Rio Grande.

The second important issue is how well does *H. amarus* sample the diatom assemblage? This question is composed of two parts, how consistent is the diatom assemblage sampled by different fish, and how "representative" is the diatom assemblage from the gut of a fish to the assemblage in the ecosystem? Our results show high similarity in the diatom assemblages sampled by different fish in the same year and the result is consistent within the 1874 and 1978 samples. The similarity suggests that diatom communities foraged by *H. amarus* are representative of extensive conditions in the Rio Grande. Sellman et al. (2002) noted that diatoms from the gut contents of stoneroller minnows (*Campostoma anomalum*) did not differ significantly from diatoms collected in a survey of stream substrate. Rosati et al. (2003) confirmed that *C. anomalum*, bluntnose minnows (*Pimephales notatus*) and creek chubs (*Semotilus atromaculatus*) are representative samplers of diatoms when they compared gut contents to human collected diatom samples. It is reasonable to surmise that *H. amarus* is also a representative sampler of diatoms because the *Hybognathus* species forage on diatoms (Whitaker 1977; Hlohowskyj et al. 1989; Rosati et al. 2003). The species richness and diversity metrics for the 1874 and 1978 diatoms support *H. amarus* as a representative sampler of the diatom community.

The resilience of *H. amarus* is underscored by the fact that the 1874 specimens foraged in eutrophic oxygen-stressed habitats with an age distribution from 1 to 5 years (Cowley et al. 2006). It further suggests that irrigation and human settlements are not the direct reason for the species' decline. The species still occurs downstream from the San Ildefonso area in the heavily-irrigated middle Rio Grande valley, where it is found in river and irrigation canal habitats (Cowley et al. 2007). The Rio Grande, even in 1874, could not be considered to be free of human modification because Native American pueblos had been in existence along the San Ildefonso reach for more than 500 years (Stuart and Gauthier 1986) and Spanish settlements for more than 250 years. Given that *H. amarus* was extirpated from the San Ildefonso reach soon after collection of the 1978 sample and within 10 years of completion of Cochiti Dam (Cowley 2006), we recommend that the remaining habitat of *H. amarus*, from Cochiti Dam to Elephant Butte Reservoir, be managed to maximize silted pools and side channels and that flow regulation accommodates periodic inundation of lateral areas in the floodplain.

This study demonstrates the importance of museum specimens for determining the ecological requirements of an endangered minnow, supporting prior studies that suggest museum specimens offer useful ecology and paleolimnology data (Rachlin and Warkentine 1987; Kido et al. 1993; Rosati et al. 2003). Using museum specimens to determine the life history and habitat requirements of an endangered species decreases the need to sample extant populations (Rachlin and Warkentine 1987). We believe that museum specimens will find increasing use in the study of how river flow regulation, habitat alteration, introduced species, and pollution have affected aquatic communities. In the long term, the knowledge that may be gained from natural history collections helps justify the cost of maintaining these museum repositories.

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