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ARTICLE

Key Morphological Features Favor the Success of Nonnative Fish Species under Reduced Turbidity Conditions in the Lower Colorado River Basin

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Abstract

As a result of anthropomorphic alterations to the lower Colorado River basin and other southwestern rivers, water turbidity has been greatly reduced and introduced, nonnative fishes thrive in these waterways. To quantify key morphological features that may allow nonnative fishes to displace native fishes, we compared eye diameter (a proxy for visual acuity) and maximum anatomical gape (a proxy for maximum prey size) in native and nonnative fishes of the lower Colorado River basin. In general, nonnative fishes have larger eyes and larger gapes relative to native fishes. Native invertivorous and piscivorous fishes may be at a particular disadvantage when compared with nonnative species from the same trophic guild because native midwater predators have proportionally smaller eyes and mouths. In the historically turbid conditions of the Colorado River, native fish likely had a limited ability to use vision to locate prey and avoid predators. Similarly, native fishes could not identify potential food items from a distance in turbid waters so suction-based prey capture (where the predator is in close proximity to the prey) may have been favored over ram-based prey capture (where fish swim from a distance to overtake prey). Many nonnative fish species have a large eye diameter and maximum anatomical gape; these features likely facilitate their ability to visually identify and capture large, elusive prey. These results suggest that the large eyes and large gapes of nonnative fishes make them superior predators and competitors in the clear, anthropomorphically altered southwestern rivers of the USA.

Fishes endemic to the lower Colorado River evolved under conditions where river flow fluctuated dramatically between wet and dry seasons. During winter and summer wet seasons, flooding occurred in response to snowmelt runoff and monsoonal rains (Christensen et al. 2004). These flooding events brought massive sediment loads, which increased turbidity to values exceeding 10,000 formazin nephelometric units, or FNU (Voichick and Topping 2014). The predam Grand Canyon stretch of the Colorado River had an average turbidity greater than 907 FNU approximately 50% of the time and almost always exceeded 250 FNU (Voichick and Topping 2014). Colorado River postdam turbidity at the same location is now less than 24 FNU approximately 50% of the time (Voichick and Topping 2014). The construction of four large hydroelectric dams on the lower Colorado River from

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1936 to 1966 allows water to collect in reservoirs, significantly reducing the seasonal variability of river flow. Hence, much of the Colorado River basin has been altered away from a periodic system, with drastic—but seasonally predictable—variability in flooding and turbidity, towards an equilibrium system, with little variability in these abiotic parameters (Schuster 1987; Olden et al. 2006).

The completion of dams and filling of reservoirs was accompanied by the introduction of a myriad of nonnative fish species. Since the early 1900s, the number of nonnative fish species in the lower Colorado River basin has tripled and many of these introduced species prey on native fish species (Minckley 1979; Bonar et al. 2004; Cucherousset and Olden 2011).

Two problematic groups of nonnative predators are members of the Centrarchidae (Largemouth Bass *Micropterus salmoides*, Smallmouth Bass *Micropterus dolomieu*, Green Sunfish *Lepomis cyanellus*, and Bluegill *Lepomis macrochirus*) and Salmonidae (Rainbow Trout *Oncorhynchus mykiss* and Brown Trout *Salmo trutta*) families, which have been introduced as sport fish. These fishes feed on aquatic invertebrates and the eggs and young of native fish species (Minckley 1979; Marsh and Douglas 1997). Because native fishes did not evolve sympatrically with members of these families, they are not recognized as predators making native fishes more likely to succumb to predation (Marsh and Douglas 1997). In fact, endemic fishes evolved with only one native piscivore, the Colorado Pikeminnow *Ptychocheilus lucius*. However, this fish has a relatively small mouth (Bestgen et al. 2006). As a result, the Colorado Pikeminnow can only capture and consume small-bodied fishes, such as the Redside Shiner *Richardsonius balteatus*, juvenile Common Carp *Cyprinus carpio*, and young Roundtail Chub *Gila robusta* (Vanicek and Kramer 1969).

A reduction of the concentration of suspended sediments in the Colorado River has created ecological consequences for fishes as they rely upon vision as their primary sensory modality (Lythgoe 1980; Guthrie 1986; Rowe and Dean 1998). Fish use vision to detect prey, find shelter, identify predators and other threats, locate mates, and recognize environmental or geographic cues. Visual capabilities, however, vary among different lineages of fishes (Guthrie 1986). Further, the ability to utilize vision varies with environment. As light availability and/or water clarity are reduced, visual cues become less reliable, therefore, relaxing selection on vision (for a recent review, see Caves et al. 2017). Because transmitted light and visual clarity are reduced, suspended sediments decrease visual reactive distances—potentially reducing foraging success (Barrett et al. 1992; Benfield and Minello 1996; Abrahams and Kattenfeld 1997; Granqvist and Mattila 2004). In situations where transmitted light in the environment is permanently reduced, fishes may rely on alternative sensory modalities. For example, the Blind Cavefish *Astyanax jordani* has greater lateral line, olfactory, and taste capabilities when compared with a sighted relative (Teyke 1990; Boudriot and Reutter 2001). With an altered turbidity regime, fishes native to the lower Colorado River may be less able to capture prey and become more vulnerable to predation.

Piscivorous fishes typically have large mouths and conical teeth to facilitate the capture and consumption of large prey species (Mittelbach and Persson 1998; Collar et al. 2009). Having a large mouth is a key component of piscivory because predation events are anatomically limited by the ability of the predator to fit prey in the oral cavity (Hoyle and Keast 1987, 1988; Januszkiewicz and Robinson 2007). In addition, functional gape (the gape the predator produces during prey capture) is fundamentally limited by anatomical gape (the gape allowed by morphology; see Arena et al. 2012; Burnette and Gibb 2013). As anatomical gape becomes larger, a fish gains the ability to consume larger items because it is physically able to fit those items between the anterior jaws and then bring them into the oral cavity to be processed. In this manner, a larger gape allows a fish to consume food items of greater body depth, which potentially expands the size range of available prey (Arena et al. 2012).

In this study, we ask what key anatomical features of invasive species enable them to thrive in contemporary, clear-water environments of the lower Colorado River? We suggest that nonnative species are morphologically better equipped to capture prey, survive, and reproduce in the clear-water conditions created by dams present on many southwestern rivers. Specifically, we hypothesize that native fishes have a smaller eye diameter and smaller anatomical gape when compared with nonnative fishes, which will place native species at disadvantage in the current Colorado River conditions.

METHODS

Using a combination of trapping methods (trammel net, hoop net, electrofishing, seine), fish were captured in the field from Lake Havasu, Lake Mohave, Lake Mead, Green River, Little Colorado River, Fossil Creek, Verde River, Virgin River, and the Colorado River by the U.S. Geological Survey, U.S. Fish and Wildlife Service, and Arizona Department of Game and Fish between December 2012 and December 2013 (Table 1); we recorded morphological measurements from these fish in collaboration with agency personnel. Morphological data were also taken from preserved specimens from collections curated by Arizona State University and Northern Arizona University. Nine species of large-bodied (grow to > 150 mm standard length) nonnative fishes were chosen based on their documented negative impacts on large-

TABLE 1. Fish body sizes, sample sizes, trophic designations, and associated citations for the species used in the study. An asterisk indicates nonnative species of fish. Lowercase letters in parentheses are as follows: a = Wydoski and Whitney (2003); b = Fox (1994); c = Elrod (1974) and Munger et al. (1994); d = Davis and Lock (1997); e = Bajer and Sorensen (2010); f = Sullivan (1993); g = Davidson et al. (2014); h = Kaeding and Zimmerman (1983); i = Page and Burr (1991); j = Modde et al. (1996); k = Rinne (1995); l = Bestgen et al. (2006); m = Griffith and Tiersch (1989); n = Cobble (1995); o = García-Berthou and Moreno-Amich (2000); p = Ellison (1984); q = Pine et al. (2005); r = Olson (1996); s = García-Berthou (2001); t = Walter and Austin (2003); u = Marsh and Douglas (1997); v = Paukert and Petersen (2007); w = Marsh and Langhorst (1988); x = Petersen and Ward (1999); y = Reilly and Lochmann (2000).

Species	Size cutoff (mm)	*n* (eye)	*n* (gape)	Trophic guild
Black Crappie *Pomoxis nigromaculatus**	>170 (a)	20	20	Invertivore (o)
Sunfishes*	>60 (b)	24	14	Invertivores (p)
Bluegill Sunfish *Lepomis macrochirus*				
Green Sunfish *Lepomis cyanellus*				
Catfishes*	>400 (c)	17	0	Benthic predators (q)
Flathead Catfish *Pylodictis olivaris*				
Channel Catfish *Ictalurus punctatus*				
Basses*	>250 (d)	30	14	Piscivore (r)
Largemouth Bass *Micropterus salmoides*				
Smallmouth Bass *Micropterus dolomieu*				
Common Carp *Cyprinus carpio**	>270 (e)	12	0	Browser (s)
Striped Bass *Morone saxatilis**	>250 (f)	18	15	Piscivore (t)
Rainbow Trout *Oncorhynchus mykiss*	>170 (g)	15	15	Invertivore (u)
Humpback Chub *Gila cypha*	>250 (h)	8	22	Invertivore (v)
Bonytail *Gila elegans*	>200 (i)	50	0	Invertivore (v)
Razorback Sucker *Xyrauchen texanus*	>300 (j)	20	0	Browser (w)
Suckers	>100 (k)	41	0	Browsers (w)
Sonora Sucker *Catostomus insignis*				
Flannelmouth Sucker *Catostomus latipinnis*				
Utah Sucker *Catostomus ardens*				
Colorado Pikeminnow *Ptychocheilus lucius*	>300 (l)	25	14	Piscivore (x)
Chubs	>120 (m)	50	38	Invertivore (v)
Roundtail Chub *Gila robusta*				
Gila Chub *Gila intermedia*				
Headwater Chub *Gila nigra*				
Yaqui Catfish *Ictalurus pricei*	>200 (n)	11	0	Benthic predator (y)

bodied native fishes (Marsh and Douglas 1997). Eleven species of large-bodied native fishes were chosen as they represent most of the native fishes of the lower Colorado River basin (Table 1). To collect morphological data, both live and preserved individuals were placed on a flat surface with a ruler placed within the field of view for scale and the lateral surface of the fish was digitally photographed. The digital images were subsequently analyzed using ImageJ (Abràmoff et al. 2004) to calculate linear dimensions of key anatomical structures.

To test the prediction that nonnative fishes have a larger eye (diameter) relative to native species, measurements of standard length and eye diameter were taken from photos of each individual. During ontogeny, eyes do not scale proportionally (or isometrically) with body length; instead, juvenile fish eyes are larger relative to body length than those of adults (thus eyes show negative allometry; see Caves et al. 2017). Because of this, only adult individuals were used for eye analysis. Published literature for all 20 species that reported minimum size at reproduction allowed us to define the adult size ranges of the fish considered here (Table 1). Scaling equations were determined by plotting the log of the variable of interest (eye diameter or gape) against the log of standard length, which yielded a linear equation from which scaling factors could be determined. To determine if there were differences in the scaling of natives versus nonnatives, we used a mixed-model ANOVA with species as a random factor. We also calculated the ratio of eye diameter (D_e) to standard length (L_s) to enable us to visualize differences among taxa without the confounding effects of body size.

To assess the prediction that nonnative fishes have a larger maximum anatomical gape than native fishes, maximum anatomical gape was expressed in each fish by manually prizing the jaws open until the upper and lower jaws could no longer be distended in the dorsal–ventral direction. Photographs of the fish were taken with the jaws in this position, and from these images we measured standard length and the distance between the tips of the upper and lower jaws (gape depth or D_g). Size and sample numbers for some species were lower for the gape portion of the study because we excluded fixed specimens for which the jaws could not be manipulated. In contrast with eye measurements, no size cutoffs were imposed for maximum anatomical gape, as gape typically scales in direct proportion (isometrically) with body length (Wainwright and Richard 1995; Hernandez 2000). Scaling equations were determined by plotting the log of the variable of interest (eye diameter or gape) against the log of standard length, which yielded a linear equation from which scaling factors could be determined. We also calculated the ratio of gape depth (D_g) to standard length (L_s) to enable us to visualize differences among taxa without the confounding effects of body size. To determine if there were differences between natives and nonnatives, we used a mixed-model ANOVA with species as a random factor.

In a post hoc analysis, native and nonnative species were assigned to four trophic guilds (browser, benthic predator, invertivore, or piscivore) based on common prey items found in the guts of each respective species, based on trophic descriptions (Table 1). Descriptions included diet data and prey commonly encountered in their respective habitats (not necessarily in the Colorado River). Suckers, which search for diet items along the bottom and consume both plant and animal material, were classified as browsers. Catfishes, which spend most of the time hunting on or near the benthos, were considered benthic predators. Fishes that actively seek and consume other fishes as a part of their diet were classified as piscivores. Fishes that primarily feed in the water column on invertebrate species were considered invertivores. Intratrophic guild comparisons were used to make inferences about competition between native and nonnative fishes within a given trophic guild. Within a trophic guild, statistical comparisons were made among and between species using the eye/body and gape/body ratios and a one-tailed Student's *t*-test with an alpha of 0.05 or an ANOVA with an accompanying least-significant-difference post hoc test with an alpha of 0.05.

RESULTS

Nonnative fishes generally had larger eyes per unit standard length relative to native fishes (Figure 1A; $P < 0.01$). When all nonnatives were considered together, it became apparent that the difference in eye size between native and nonnative fishes was greater in larger individuals (Figure 1A). The scaling coefficient for eye diameter was always less than one (that is, eye growth does not keep pace with body growth, showing negative allometry), but the scaling exponent varied among species: eye diameter scaling ranged from $L_s^{0.52}$ to $L_s^{0.79}$ for nonnative fishes (catfishes were excluded from this analysis because the sample size was too small) and from $L_s^{0.29}$ to $L_s^{0.50}$ for native fishes (Table 2).

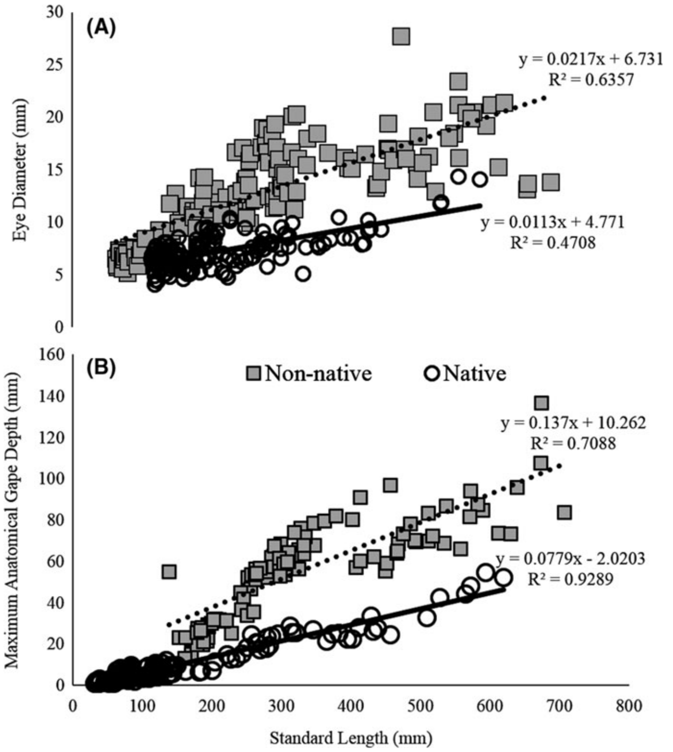

FIGURE 1. In general, nonnative fishes have larger **(A)** eye diameters and **(B)** maximum anatomical gapes per unit standard length relative to native fishes from the lower Colorado River. Both native and nonnative fishes demonstrate a positive linear relationship between length and eye diameter and maximum anatomical gape. The dashed line represents the trend line for all nonnative species considered together, while the bold line represents the trend line for all native species.

Relative to body size, the sunfishes and the Black Crappie *Pomoxis nigromaculatus* had the largest eyes of all fishes in this study (Figure 2; Table 2). Relative to body size, the catfishes had the smallest eyes of all of the nonnative fishes in this study (Table 2). The chubs in the Roundtail Chub complex (Roundtail Chub, Headwater Chub *Gila nigra*, Gila Chub *Gila intermedia*) had the largest size-specific eye diameter of the native fishes considered here, and the so-called "big-river chubs" (Humpback Chub *Gila cypha* and Bonytail *Gila elegans*), two species that are found in the main stem of the Colorado River, had the smallest size-specific eye diameter of the native fishes considered here (Figure 2; Table 2).

TABLE 2. Eye ratio (D_e/L_s), gape ratio (D_g/L_s), and scaling relationship data for native and nonnative fish species from the Colorado River basin.

Origin	Species	Average ± SE eye ratio	Scaling[a]	Average ± SE gape ratio (n)	Scaling[b]
Nonnative	Black Crappie	0.060 ± 0.001	$-0.70L_s^{0.79}$	0.208 ± 0.010 (20)	$-0.71L_s^{1.00}$
Nonnative	Sunfishes	0.075 ± 0.002	$-0.44L_s^{0.66}$	0.160 ± 0.006 (14)	$-1.00L_s^{1.03}$
Nonnative	Catfishes	0.027 ± 0.002	$1.17L_s^{0.0001}$		
Nonnative	Basses	0.049 ± 0.002	$-0.44L_s^{0.63}$	0.205 ± 0.005 (18)	$-1.19L_s^{1.20}$
Nonnative	Common Carp	0.035 ± 0.002	$-0.15L_s^{0.52}$		
Nonnative	Striped Bass	0.037 ± 0.001	$-0.65L_s^{0.71}$	0.144 ± 0.003 (12)	$-0.67L_s^{0.93}$
Nonnative	Rainbow Trout	0.0516 ± 0.001	$0.84L_s^{0.8}$	0.146 ± 0.002 (15)	$-0.61L_s^{0.9}$
Native	Humpback Chub	0.024 ± 0.001	$-0.01L_s^{0.39}$	0.082 ± 0.006 (10)	$-0.62L_s^{0.75}$
Native	Bonytail Chub	0.0223 ± 0.0004	$-0.03L_s^{0.36}$		
Native	Razorback Sucker	0.037 ± 0.002	$-0.26L_s^{0.50}$		
Native	Suckers	0.039 ± 0.001	$-0.13L_s^{0.41}$		
Native	Colorado Pikeminnow	0.028 ± 0.001	$0.08L_s^{0.33}$	0.080 ± 0.004 (20)	$-0.78L_s^{0.87}$
Native	Chubs	0.052 ± 0.001	$0.05L_s^{0.36}$	0.058 ± 0.004 (23)	$-1.54L_s^{1.12}$
Native	Yaqui Catfish	0.038 ± 0.003	$0.19L_s^{0.29}$		

[a] Scaling equation for all fishes used in eye diameter analysis: $-0.32L_s^{0.57}$, nonnatives: $-0.11L_s^{0.59}$, natives: $0.52L_s^{0.14}$.

[b] Scaling equation for all fishes used in gape analysis: $-1.82L_s^{1.31}$, nonnatives: $-1.01L_s^{1.08}$, natives: $-1.62L_s^{1.17}$.

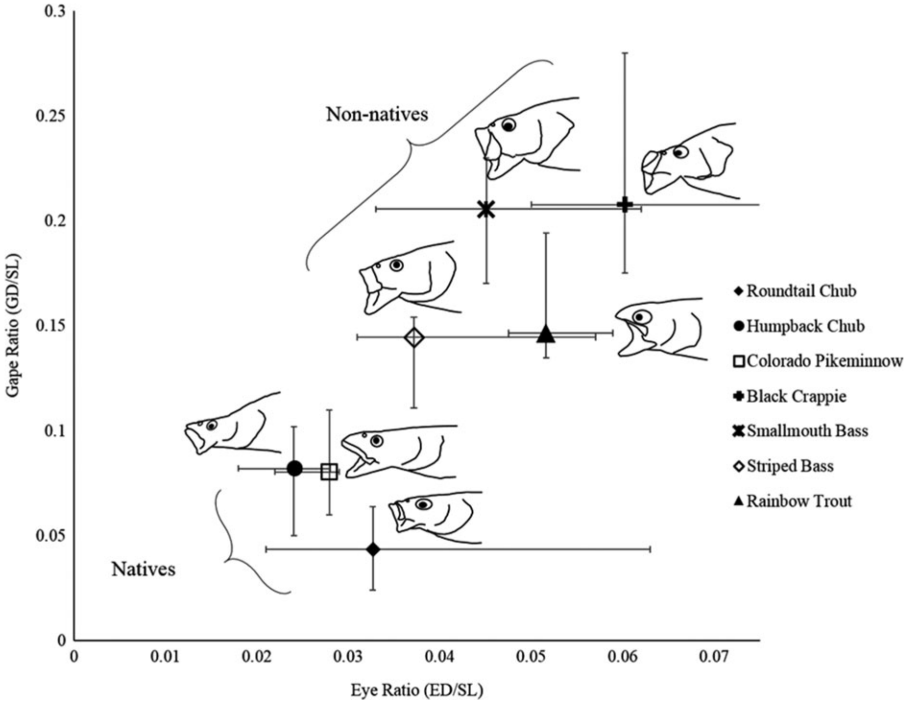

FIGURE 2. Nonnative and native fishes from the lower Colorado River occupy different morphospace when the ratios of eye size : body length and anatomical gape : body length are considered. As a group, nonnative fishes have proportionally larger eyes ($P < 0.01$) and maximum anatomical gapes ($P < 0.001$) relative to native fishes from the lower Colorado River (only individuals from which both measurements were taken are illustrated here; see text for details). For clarity, Roundtail Chub was chosen as an illustration of the representative species for the small-river chubs. Filled symbols represent invertivorous fishes and open symbols represent piscivorous fishes. Symbols represent averages for each species, and capped bars represent maximum and minimum measurements for each species. Abbreviations are as follows: SL = standard length, ED = eye diameter, and GD = gape depth.

For browsers, the native Sonora Sucker *Catostomus insignis* had the largest size-specific eye diameter (Figure 3A; $P < 0.01$), while eye diameter of the invasive Common Carp did not differ from the rest of the native sucker species considered here. Similarly, for the benthic predators (catfishes), the native Yaqui Catfish *Ictalurus pricei* had the largest relative eye diameter when compared with two nonnative catfishes (Figure 3B; $P < 0.01$).

However, nonnatives had larger size-specific eyes than natives in both midwater piscivores and invertivores. Within the piscivores, the Striped Bass *Morone saxatilis* and Largemouth and Smallmouth basses had larger ($P < 0.001$) size-specific eye diameters when compared with the only native piscivore (Colorado Pikeminnow) (Figure 3C). Among the invertivores, the nonnative sunfishes had the largest relative eyes ($P < 0.01$). The species within the Roundtail Chub complex (Roundtail Chub, Headwater Chub, Gila Chub; Gerber et al. 2001) did not significantly differ in relative eye diameter from Black Crappie and Rainbow Trout. All nonnative species, however, had larger eyes than the big-river chubs (Humpback Chub and Bonytail) ($P < 0.001$; Figure 3D).

Nonnative fishes generally had larger maximum anatomical gapes per unit standard length relative to native fishes (Figure 1B; $P < 0.001$). When all nonnatives were considered together, it was apparent that the

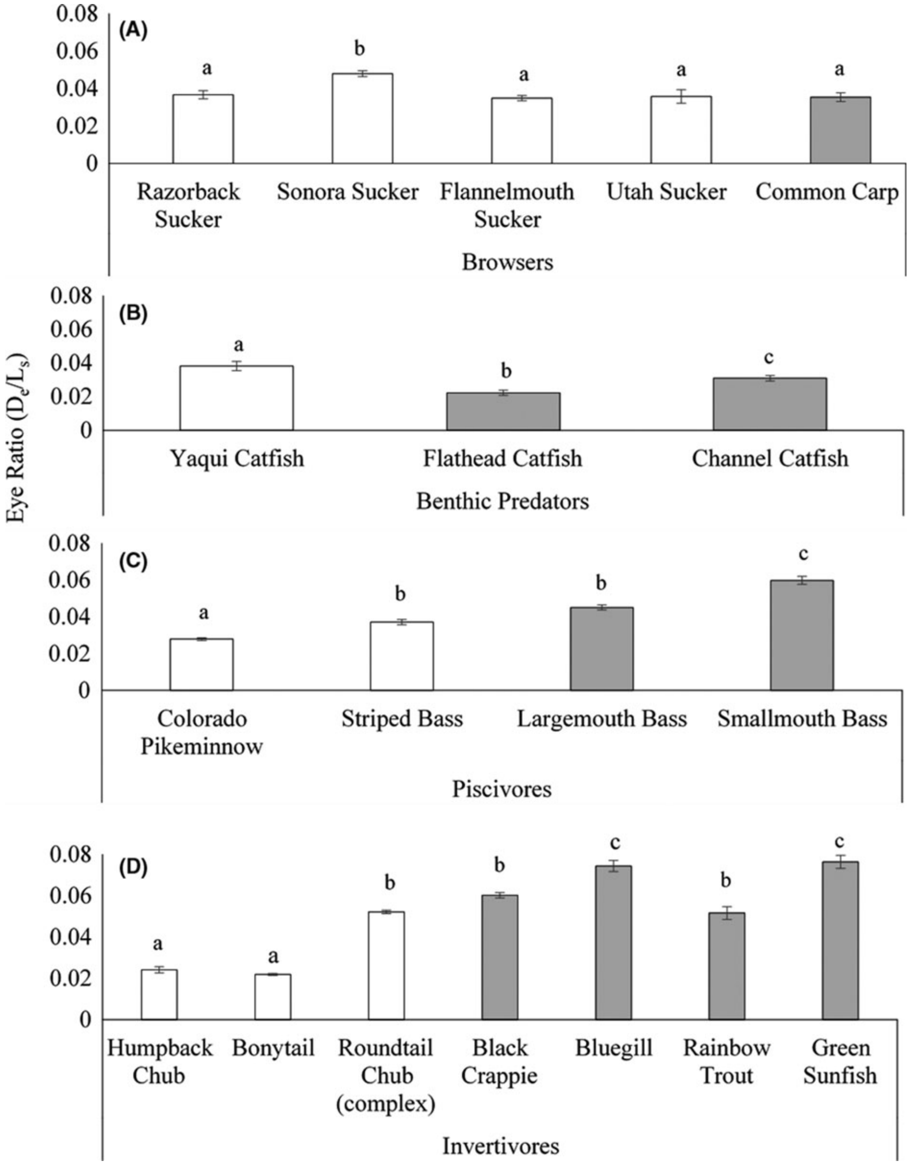

FIGURE 3. Nonnative fishes that feed on midwater elusive prey have larger eyes than native fishes, although native fishes feeding on or near the benthos have relatively larger eyes than nonnatives in the same trophic guilds. The bar graph shows the relative eye diameters of **(A)** native and nonnative browsers (carps and suckers), **(B)** native and nonnative benthic predators (catfishes), **(C)** native and nonnative piscivores, and **(D)** native and nonnative invertivores. White bars represent native fishes, while gray bars represent nonnative fishes. Lowercase letters above the bars indicate statistical significance; bars with the same letter are not significantly different from each other. Variables are defined as follows: L_s = standard length and D_e = eye diameter.

difference in maximum anatomical gape between native and nonnative fishes was greater for larger individuals (Figure 1B). Gape measurements in some species examined in this study demonstrated positive allometry (scaling exponent greater than 1). In others, mouth size scaled isometrically with body size (scaling exponent ~1), and in certain species negative allometry was observed (scaling exponent less than 1). For nonnative fishes, maximum anatomical gape scaling factors ranged from ${L_s}^{0.93}$ to ${L_s}^{1.20}$. For native fishes, maximum anatomical gape scaling factors ranged from ${L_s}^{0.75}$ to ${L_s}^{1.12}$ (Table 2).

Members of the Centrarchidae family (two sunfishes, Black Crappie, and the two basses) had the largest size-specific anatomical gapes of all the fishes in this study (Figure 2; Table 2). The Striped Bass and the Rainbow Trout had the smallest size specific gape of any nonnative fish considered in this study (Figure 2; Table 2). The Humpback Chub and the Colorado Pikeminnow had the largest size-specific gapes for the native fishes in this study. The small-river chubs in the Roundtail Chub complex had the smallest relative anatomical gapes, while scaling with positive allometry, of all the native fishes examined here (Figure 2; Table 2).

The relationship of nonnatives having a larger relative maximum anatomical gape relative to the natives was maintained within trophic guilds. Within the piscivorous fishes, Striped Bass had a larger ($P < 0.001$) gape when compared with the only native piscivore (Colorado Pikeminnow) (Figure 2). Within the invertivorous fishes, the nonnative centrarchids (Largemouth and Smallmouth basses, Black Crappie, and the sunfishes) and Rainbow Trout had larger ($P < 0.001$) size-specific gapes than the native chub species.

DISCUSSION

The nonnative fish species considered here generally had larger eye diameters when compared with native fishes; this was particularly true for piscivores and invertivores, fishes that actively forage for prey in the water column. In vertebrates, larger eyes are associated with greater visual capabilities because larger lenses reduce light diffraction as the light passes though the eye (Fernald and Wright 1985). In addition, the greater the distance between the lens and the retina, the larger the image displayed on the retina. Increased image size can have a profound effect on acuity because the image that is projected onto the retina is sampled by more sensory cells (rods for light reception and cones for acuity; see Easter et al. 1977). However, improved acuity can only be realized if the increase in retinal area is not accompanied by a corresponding *decrease* in cone density. Studies quantifying the relationship between eye size and cone density across vertebrate groups suggest that, although the increase in size of the retina during growth can be associated with a decrease in cone density, additional cones are often added to the retinal mosaic during growth—resulting in an increased acuity in animals with larger eyes (Yamanouchi 1956; Lyall 1957; Tamura 1957; Blaxter and Jones 1967; Neave 1984). Thus, generally, as lens size increases, chromatic and spherical aberration decreases, enabling a clearer image to be projected onto the retina (Otten 1980).

The effect of eye size and vision on predation capabilities has been measured for some of the species considered here. Hairston et al. (1982) found that planktivorous Bluegills with larger eyes could detect smaller prey items than conspecifics with smaller eyes; thus, larger eyes were associated with increased visual capabilities, which increased predation success. In addition, experiments conducted with salmonids (Gregory 1993; Gregory and Levings 1996; Vogel and Beauchamp 1999; Sweka and Hartman 2001), centrarchids (Vinyard and O'brien 1976; Sweka and Hartman 2003; Shoup and Wahl 2009), cyprinodontids (Benfield and Minello 1996) and moronids (Abrahams and Kattenfeld 1997) demonstrate that predation success decreases as turbidity increases. Across these four fish lineages, when turbidity levels exceed 100 FNU, capture success drops to close to 0% (Ward et al. 2016). The likely mechanism for reduced predation success with increased turbidity is reduced predator–prey interactions because visual-based hunting cannot occur if the prey cannot be visually identified by the predator.

The ability to identify prey from a distance is particularly important for midwater feeding piscivores and invertivores. Many of the larger nonnative species introduced into the Colorado River drainage evolved in clear-water streams, lakes, and deep pools (Olden et al. 2006), where vision is key for identifying potential food resources and potential predatory threats. Centrarchids and salmonids that are now present in southwestern waterways originally evolved in habitats that are characterized by clear water (rarely exceeding turbidity levels of 50 FNU; Trebitz et al. 2007). In clear-water habitats, it is likely that there has been selection for larger eyes that could detect predators and prey from a greater distance. Unfortunately, the construction of dams and diversions has increased the prevalence of low-turbidity waterways in the American Southwest (Olden and Poff 2005; Olden et al. 2006; Johnson et al. 2008; Cucherousset and Olden 2011), potentially giving fish with larger eyes an advantage and likely assisting in the expansion of the ranges of nonnative fish species that can impact native fish populations.

However, we note that native benthic predators (catfishes) and browsers (suckers and carp) did *not* have significantly smaller eyes relative to introduced, nonnative competitors. We suggest that browsing and sit-and-wait predation rely on alternative sensory modalities (i.e., barbels in catfishes and carp), which might relax selection on visual capabilities (Atema 1971). Indeed, the relative size of a fish's eyes provides information about the importance of vision to the animal. In many fish species, including the less visually oriented fishes in the family Cyprinidae, the eyes become proportionally smaller as the fish grow larger (negative allometry; see Fernald 1990). In this study, all 20 species showed negative allometry, but nonnative fishes tended to have larger scaling factors than native fishes (except for the catfishes). This suggests that, in general, nonnatives direct more resources into maintaining eye size as they grow relative to native fish species.

With turbidity levels around 1,000 FNU under historic hydrologic conditions in the Colorado River, it is likely that native fishes could not rely on vision to detect potential predators or prey in the water column. As a result, selection pressure for other sensory systems may have occurred concomitantly with a decrease in eye size in southwestern invertivorous and piscivorous fish species. Although there has been little work examining sensory systems of native fishes, we suggest that anatomical features provide "clues" about sensory capacity. Native fishes may have evolved a heightened sense of smell to compensate for the lack of visual capabilities, as many of the native fishes used in this study have large nasal pores, with flesh that extends up to 3 mm from the body (C. J. Moran, personal observation). These fleshy extensions may increase olfaction capabilities by concentrating the water and dissolved chemicals into a narrow tube. In addition, many of the native fishes in the southwestern USA are ostariophysan fishes that produce an alarm pheromone when threatened (Von Frisch 1938; Smith 1982). Taken together, nasal morphology and alarm pheromones suggest that native fishes (in the family Cyprinidae) may use a heightened sense of smell to increase the likelihood of finding food and avoiding predators in turbid environments.

Because native fishes may have evolved to rely on senses other than vision to detect prey, this may have had direct consequences on feeding mode. Fish that capture prey by ram feeding, or swimming to overtake the prey with an open mouth, may travel up to 60 mm to capture prey (e.g., Largemouth Bass); fish that capture prey by suction feeding typically travel < 10 mm to capture their prey (e.g., Pumpkinseed Sunfish *Lepomis gibbosus*) (Norton and Brainerd 1993). Studies in the lower Colorado River basin of native fish feeding are limited, but Roundtail Chub are known to produce suction while feeding on the benthos (Arena et al. 2012). Enhanced suction feeding occurs with a "narrow" (small) gape because a smaller gape enhances the ability to produce a high-velocity, directed flow of water (Carroll et al. 2004; Collar and Wainwright 2006; Holzman et al. 2012). In contrast, ram feeders are characterized by high burst-swimming speeds that are combined with large mouth gapes to capture prey (Ferry et al. 2015). Because visual reaction distance is low in highly turbid environments, it seems likely that native fishes would be unable to use ram feeding effectively in turbid environments. Thus, high turbidity may have produced a selection pressure against large gapes, and toward smaller gapes, in native fishes from the desert Southwest.

Indeed, the advantages endowed by superior visual capabilities of nonnatives under current Colorado River conditions are further enhanced by their proportionally larger gapes. The only native piscivore, the Colorado Pikeminnow, has the largest maximum anatomical gape of all the native fishes considered here. However, when the native piscivore is compared to the introduced, nonnative piscivores, the Striped Bass and Largemouth Bass (Figure 2), the Colorado Pikeminnow has a smaller gape and smaller eyes, which may make the Colorado Pikeminnow a less effective predator under current Colorado River conditions. Because prey size is proportional to gape size (Hoyle and Keast 1987, 1988), a very large gape could enable fish to consume a large variety of prey. This suggests that nonnative fishes may be able to consume a wider range of prey items when compared with native fishes (but see Arena et al. 2012). If nonnative fishes can capture a wide range of food items more effectively than native fishes, they may continue to outcompete native fishes. Many species of native fishes across the Southwest are thought to be imperiled because of competition from nonnative fishes for food resources (Ross 1991; Marsh and Douglas 1997; Mueller and Marsh 2002; Olden et al. 2006).

In the lower Colorado River, most of the large-bodied native fishes belong to the families Cyprinidae and Catostomidae, while many of the large-bodied nonnative fishes belong to the Centrarchidae family. As a result, most of the fishes sampled here belong to one of those three clades. This yields a potential clade effect, where the species sampled here could reflect the morphology of their common ancestor rather than more recent natural selection for a particular habitat. This raises the following question: do native fish simply have smaller eyes and mouths because their ancestors had smaller eyes and mouths? A large-scale phylogenetic study of gape and eye size in cyprinid, catostomid, and centrarchid families is beyond the scope of this study. However, mouth size and shape can vary within a single species, as is seen in the polymorphic Cuatro Cienegas Cichlid *Herichthys minckleyi* (Swanson et al. 2008)—which can occur in a large-gaped piscivorous "morph" as well as in several nonpiscivorous, benthic-foraging morphotypes. In addition, recent studies of cave-dwelling loaches (genus

Barbatula) show that the evolution of reduced eye size and increased alternative sensory structures can occur in as little as 20,000 years (Behrmann-Godel et al. 2017). The lower Colorado River basin has been isolated from other freshwater lakes or rivers for 2–3 million years (Echelle et al. 2005). Given the rate at which eyes can be reduced and other sensory systems enhanced, it seems probable that small eyes have evolved in endemic Colorado River fishes over several million years in response to consistently turbid river conditions. In addition, even if small eyes are the ancestral condition for these 11 native species, there is a consistent and prevalent association in fishes between eye size and visual acuity (Caves et al. 2017). Thus, even if eye size is simply a relict of ancestral traits, the physiological limits imposed on vision by eye size (Caves et al. 2017) may place native species at a disadvantage in clear waters relative to introduced nonnatives with larger eyes and greater visual capabilities. Our results indicate that predatory nonnative fish species have (1) larger eyes that will provide them with greater visual acuity to identify prey from a distance and (2) larger mouth gapes that enable them to capture and consume other fishes.

This study supports the overarching ecological hypothesis that the installation of dams and diversions has created clear waters that favor large-mouthed, visual predators (Gido et al. 2013; Ruhí et al. 2016). Therefore, management actions designed to benefit native fishes should focus on enhancement of specific habitat features that will reduce predation vulnerability (Matter and Mannan 2005). One way to potentially reduce the predation and competition pressures on native fishes may be to increase the turbidity of southwestern rivers, which would create a visual refuge for vulnerable native fishes. Increased turbidity could be accomplished by deliberately releasing sediment from diversions (Gilvear and Petts 1985). By resuspending sediment in areas directly upstream of dam releases, the turbidity of downstream waterways could be increased (Albrecht et al. 2010). Increasing turbidity could reduce predation vulnerability of native fishes (Ward et al. 2016) and may allow native fishes to forage using alternative sensory mechanisms while remaining undetected by introduced predators.

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