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Integrating Studies of Anatomy, Physiology, and Behavior into Conservation Strategies for the Imperiled Cyprinid Fishes of the Southwestern United States

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Synopsis Over the last 100 years, fishes native to the Southwestern United States have faced a myriad of biotic and abiotic pressures which has resulted in most being federally listed as endangered or threatened. Most notably, water diversions and the introduction of non-native fishes have been the primary culprits in causing the downfall of native fish populations. We describe how recent studies of morphology, physiology, and behavior yield insights into the failed (occasionally successful) management of this vanishing biota. We describe how understanding locomotor morphologies, physiologies, and behaviors unique to Southwestern native fishes can be used to create habitats that favor native fishes. Additionally, through realizing differences in morphologies and behaviors between native and non-native fishes, we describe how understanding predator–prey interactions might render greater survivorship of native fishes when stocked into the wild from repatriation programs. Understanding fundamental form–function relationships is imperative for managers to make educated decisions on how to best recover species of concern in the Southwestern United States and worldwide.

Threats to Southwestern native fishes

Riverine habitat modifications have impacted native fishes from the Southwestern United States for the last 1500 years. Known, in part, for their large-scale irrigation techniques, the Hohokam people created miles of sophisticated flood irrigation channels that diverted water from mainstem rivers and streams across the Southwest (Woodbury 1961). Waterway diversions continued to expand and become more sophisticated. Southwestern river diversions culminated in the first hydroelectric dam; The Theodore Roosevelt Dam which was completed in 1911. Over the last approximately 100 years, hydroelectric dams have significantly impacted native fishes across the Southwest (Minckley 1991).

Hydroelectric dams and other river diversions block spawning routes and alter hydrology, thermodynamics, and sediment load in rivers (Reid et al. 2019). Unlike some of the dams in the Northwestern United States, most of the dams and diversions in the Southwest were built without fish passageways (alternate waterways that allow fish to bypass the physical barrier presented by the dam). Consequently, dams are barriers to spawning routes and prevent gene flow. For example, in Colorado in 1993, the Taylor Draw Dam blocked the spawning route of the endangered Colorado pikeminnow causing population densities to drop dramatically (Irving and Modde 1994). Constant controlled release from hydroelectric dams creates homogenized habitats—both downstream and upstream, in reservoirs (Morris et al. 1968; Rahel 2002, 2007). Habitat homogenization in combination with the reduction of natural barriers to movement (ex. narrow sections of

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year round high flow) reduces aquatic biodiversity (Havel et al. 2005). In the Southwest, rivers are characterized as periodic environments, where seasonal flooding maintains variable river hydrology. During high terrestrial input events, flow changes the shape and connectivity of Southwestern waterways which, historically, allowed for population mixing (Gido et al. 2013). Throughout the year, water released from hydroelectric dams is hypolimnetic, which comes from deep within the upstream reservoir. The release of hypolimnetic water creates cold, clear habitats downstream from dams and other diversions, which can impact fish reproduction, physiology, and behavior (Olden and Naiman 2010). The combination of increased clarity and reduced temperature is especially impactful in the Southwest, as natural river conditions were generally warm and highly turbid. Furthermore, this cold clear water creates an environment that favors visually-acute predators.

In the late 1800s, around the same time the earliest hydroelectric dams were being constructed, a variety of non-native fishes were introduced to Southwestern waterways. Since then, over 90 non-native fish species have been introduced, and over half of them have established populations in the Southwest (Rinne and Janisch, 1995; Minckley, 1999). Some of the most prolific introduced fish species include black basses and sunfishes (Centrarchidae), temperate basses (Moronidae), carps (Cyprinidae), shad (Clupeidae), and catfishes (Ictaluridae). In most waterways across the Southwest, native fish populations have declined concomitantly with the presence of non-native fish populations (Minckley and Marsh, 2009).

In habitats where non-native fishes are present, they almost always outnumber native fish species (Minckley 1991). The two most prominent factors leading to greater non-native density and diversity are predation and competition. In most instances, where non-native fishes have taken over the primary causal factor, it appears to be direct predation on young native fishes. Young native fishes are easily consumed and digested by non-native predators as they do not recognize introduced novel predators as threats. In fact, O'Neill and Stewart (2014) noted bonytail using bass as cover in their predator–prey training trials. Furthermore, the Santa Cruz pupfish (*Cyprinodon arcuatus*) was eliminated from its natural habitat by direct predation from largemouth bass (*Micropterus salmoides*) (Minckley and Marsh, 2009). Marsh and Douglas (1997) have also attributed the significant decline in humpback chub (*Gila cypha*) to predation by five introduced predatory fish species.

With the introduction of food and sport fishes, which prey on native fishes, came the introduction of fast-growing forage fishes for those species. Shiners, shads, and sunfishes were introduced as forage and to consume young native fishes or compete for overlapping resources. In a study comparing the native spikedace (*Meda fulgida*) to the non-native red shiner (*Cyprinella lutensis*), Douglas et al. (1994) found that red shiner overlaps with spikedace in their niche requirements. They concluded that red shiner were outcompeting spikedace, causing a reduction in the spikedace population. Additional examples of competitive exclusions are provided by Meffe et al. (1983) and Marsh and Pacey (2003). Thus, competition among native and non-native species is a large factor in the decline of Southwestern native species.

As a result of the abiotic changes and biotic pressures mentioned above, of the 31 native fishes in the Lower Colorado River Basin, 25 are either extinct, endangered (according to the Endangered Species Act), or threatened. Additionally, recovery efforts by numerous state and federal agencies have been minimally successful (Minckley 1991).

Current management

Given the current status of Southwestern native fishes, managers are faced with the daunting challenges of maintaining genetic diversity for a given species, increasing the numbers of individuals in the wild, and protecting/restoring habitats with the hopes of eventually establishing self-sustaining populations (MSCP LCR 2019). State and federal management plans focus primarily on repatriation of fish populations by stocking hatchery raised fishes into the wild. Stocking programs are not a long term solution so long as non-native predators and competitors remain in high volumes in habitats that favor their anatomical and physiological traits. For instance, the survival of stocked native bonytail rarely reaches 10% after 1 year in the wild. Other stocking programs have demonstrated, similarly, limited successes (Bestgen et al. 2008; MSCP LCR 2019). It is likely that stocked fishes face the same problems that cause extirpations of original native fish populations. However, it is also important to note that these management practices only serve as an interim solution with hopes of eventually increasing the success of native fishes in the wild. Within this context, the goal of this article is to review how studies of the anatomy, physiology, and behavior of native fish can yield insights as to how native fish populations thrive

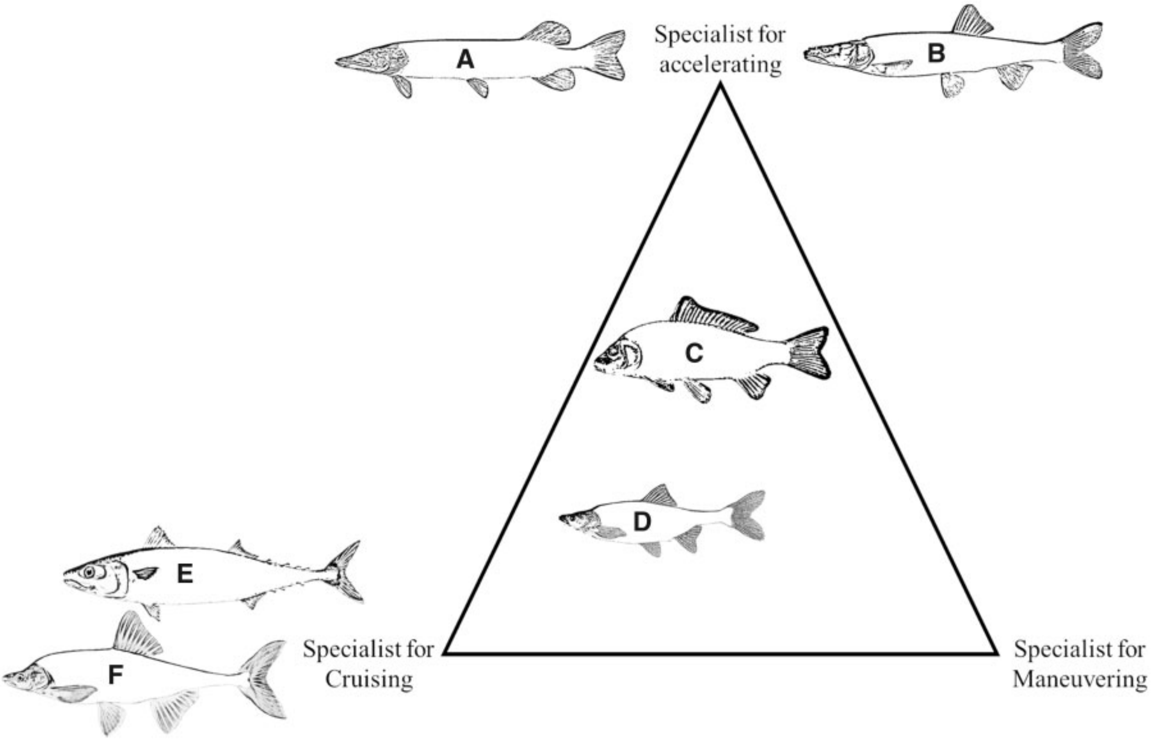

Fig. 1 A recreation of the "Functional-Morphology Plane" from Webb (1984) proposing three axes of variation in the locomotor morphology of fishes. Included here are hypothetical positions of some of the fishes used in the studies summarized here. (**A**) pike (*Esox lucius*), (**B**). Colorado pikeminnow (*Ptychocheilus lucius*), (**C**). common carp (*Cyprinus carpio*), (**D**) roundtail (*Gila robusta*), (**E**) chub mackerel (*Scomber japonicus*), (**F**) bonytail (*Gila elegans*). Pike and Colorado pikeminnow have morphologies that confer a locomotor advantage during acceleration. Common carp and roundtail are in the middle of the morphospace, as their swimming morphologies and performance would be considered intermediate. Conversely, the mackerel and bonytail have morphologies that suggest they are fishes that can sustain high-swimming speeds for long periods of time.

or fail under historic and modern conditions in the waterways of the southwest.

Organism–environment interactions, Part I: swimming morphology, physiology, and behavior

Locomotor morphologies of fishes are adapted for particular habitats and swimming modes. Webb (1984) provided a comprehensive framework for understanding swimming specializations and their associated morphological adaptations. For instance, fishes that have specializations for swimming at high-speeds for long periods of time typically have a streamlined body shape, lunate tail, and shallow caudal peduncle, whereas fishes adapted for accelerating have narrow bodies with fins located toward the posterior region of the body. Webb (1984), and others, have emphasized that the extraordinary diversity in fish shape and fin placement suggests that fishes can be cruising specialists, maneuvering specialists, accelerating specialists, or some intermediate morphology (Fig. 1). Until recently, little work had considered the locomotor morphologies of Southwestern native fishes in this form–function context.

Some fish species native to the high flow environment of the Colorado River have morphological adaptations similar to high-performance swimmers from marine systems (Moran et al. 2016). Specifically, bonytail (*Gila elegans*) has a streamlined body, narrow caudal peduncle, high aspect ratio lunate tail, and skeletal specializations in the axial skeleton. When compared to the roundtail chub (*Gila robusta*), a closely related species from the less torrential Colorado River tributaries, a suite of morphological variables indicates that bonytail are specialized for swimming at high-speeds for extended periods of time. This conclusion was further supported when comparing bonytail to invasive common carp (*Cyprinus carpio*), which has a more generalized body shape. Furthermore, bonytail demonstrate morphological characteristics more similar to that of the chub mackerel (*Scomber japonicus*, high-performance swimmer from the marine environment) than its close-relative the roundtail chub and invasive common carp (Fig. 1).

Following morphological analyses, flow tank experiments were conducted to examine the

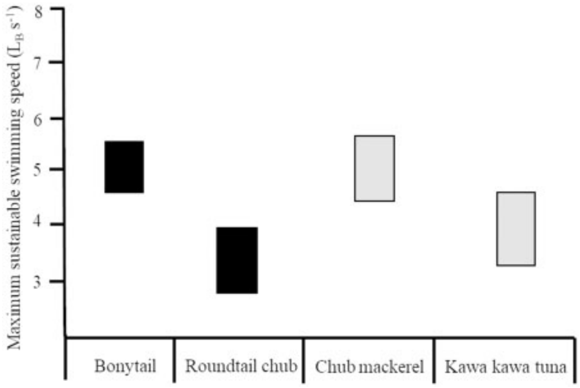

Fig. 2 Bonytail, a cyprinid fish native to the Colorado River, have similar maximum swimming speeds (BL per second) to pelagic scombrids. Maximum sustainable swimming speeds for size matched native fishes as reported in Moran et al. (2018a) and scombrid fishes as reported by Sepulveda and Dickson (2000). Box size was determined by the range of maximum sustainable swimming speeds for size matched individuals. Bonytail (*n* = 5) and roundtail chub (*n* = 5) are native to the Southwestern United States, while Kawa kawa tuna (*n* = 7) and chub mackerel (*n* = 8) are high-performance swimmers from the marine environment.

form–function relationships between different swimming morphologies. Moran et al. (2018a) found bonytail performance to match predictions based on morphological specializations. Bonytail were able to sustain higher maximum sustainable swimming speeds than roundtail chub, introduced rainbow trout (*Oncorhynchus mykiss*) and smallmouth bass (*Micropterus dolomieu*). High sustainable swimming speeds may help prevent displacement/dislocation during periodic, massive flooding-events (Moran et al. 2018a). Bonytail swimming performance, in fact, was not very different from some of the aforementioned high-performance swimmers from the marine environment. Sepulveda and Dickson (2000) examined swimming performance of chub mackerel and kawa kawa tuna (*Euthynnus affinis*) using the same swim tunnel and similar methods to those in Moran et al. (2018a). The range of speeds that bonytail were able to maintain was similar to that maintained by size matched kawa kawa tuna and chub mackerel (Fig. 2). Thus, somewhat surprisingly, bonytail can be deemed high-performance swimmers because they can maintain comparable maximum swimming speeds compared to scombrids under similar experimental conditions.

While bonytail were able to maintain their position in high flow speeds by actively swimming during flow tunnel experiments, roundtail chub employed a different behavior. At speeds ≥3.5 body lengths (BLs)/second, roundtail chubs used their pelvic and pectoral fins to adhere to the bottom of the tank. The ventral anterior half of their bodies contacted the swim tunnel while the posterior portion of their body, including their caudal fin, remained in the flow (~30–45° angle). This paired-fin-based attachment behavior was associated with a reduction in metabolic rate as the fish “rested” on the bottom of the swim tunnel. In addition, flow speeds could be increased to >5 BLs/second, while roundtail were able to remain attached to the bottom, resisting displacement by the flow (Moran et al. 2018a). As is characteristic of members of the family Cyprinidae, the pectoral and pelvic fins of the roundtail chub are oriented toward the ventral surface of the animal, which assists them in maintaining this orientation in the face of swift moving water. Ward et al. (2003) noted a similar behavior in the speckled dace (*Rhinichthys osculus*) during flooding event simulations (short periods of very high-water flow); this behavior allowed speckled dace to resist displacement, while similarly-sized, non-native species were displaced downstream. Thus, a paired-fin-based attachment behavior may have evolved in native fishes to maintain their position during periods of high flow.

Taken together, these studies suggest that Southwestern native fishes have evolved morphological, physiological, and behavioral strategies to maintain position during high-flow events. By returning flow to Southwestern waterways, managers might exclude non-native species that evolved in low-flow (e.g., carp) or consistent, intermediate-flow habitats (e.g., centrarchids), while allowing native species to flourish. Furthermore, returning to a natural flow regime will aid in recovering other abiotic and biotic factors key to restoring a more natural ecosystem in downstream habitats (reviewed in Bednarek (2001)). Marks et al. (2010) published an example of the impact of dam removal on native fishes in a tributary of the Colorado River. Years of monitoring before and after restoration of the waterway reveals that Fossil Creek (Arizona, USA) experienced a proliferation in native fish populations following dam removal. Marks et al. (2010) noted, however, that non-native fish removal was a key component of restoration. When the areas affected by water restoration were compared, it was clear that if non-natives were not removed concomitantly with flow restoration, it effectively neutralized the impacts of dam removal—and native fish population densities remained low despite the return of natural flow regimes. Thus, a multipronged management approach must be considered to increase the success of wild native fishes.

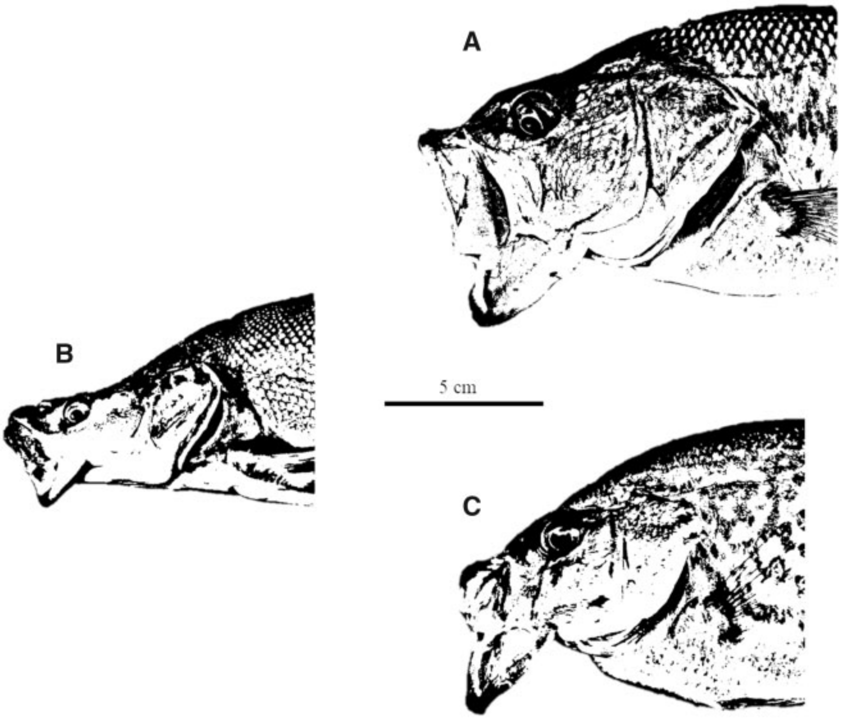

Fig. 3 Non-native fish introduced to the Colorado River and other Southwestern waterways have much larger eyes and mouths, relative to native species. Line drawings illustrate the differences in eye size between sample individuals from both native and non-native fishes (a 5 cm scale bar is included for scale.). (**A**) non-native largemouth bass (37 cm TL), (**B**) native bonytail (41 cm TL), (**C**) non-native black crappie (21 cm TL).

Organism–environment interactions, Part II: predator anatomy and prey behavior

A relatively understudied abiotic condition of freshwater systems is turbidity or the opacity of water due to the presence of suspended particles. Pre-dam Colorado River turbidity levels were commonly around 1000 Nephelometric Turbidity Units (NTUs) (Voichick and Topping 2014). Hence, Southwestern native fishes evolved in naturally turbid environments. Today, after the installation of hydroelectric dams, turbidity downstream of the dams rarely exceeds 10 NTUs (Voichick and Topping 2014). This has created large stretches of clear-water habitat, advantageous for visually-oriented predators (Gido et al. 2013), which are characterized by having proportionally large eyes. Larger eyes confer better visual capabilities simply by allowing more physical space for light receptive cells (Caves et al. 2017). To quantify the visual capacity of native and non-native fish species from the Southwest, Moran et al. (2018b) sampled individuals representing 10 native and 10 non-native species across large body-size ranges. When taking body size into consideration, non-native species have consistently larger eyes, relative to native species (Fig. 3). Furthermore, non-native fishes, on average, have a greater scaling coefficient when comparing eye diameter to size; that is, the eyes of non-native fish remain relatively larger as they grow. This implies that, for sized-matched individuals, non-native fishes will always have a greater eye diameter, endowing them with greater visual acuity.

Many predatory fishes rely on visual cues to locate their prey. The ability to use vision, however, is limited by the "visual reactive distance," which decreases as turbidity increases. This has been well documented in a variety of fish species such as: Gulf killifish (*Fundulus grandis*)(Benfield and Minello 1996), rainbow trout (Barrett et al. 1992), smallmouth bass (Sweka and Hartman 2003), bluegill sunfish (*Lepomis macrochirus*)(Vinyard and O'brien 1976), Atlantic cod (*Gadus morhua*)(Meager et al. 2005), three-spined stickleback (*Gasterosteus aculeatus*)(Sohel et al. 2017). Ward et al. (2016) recently investigated the effect of turbidity on the ability of two non-native trout species to identify, capture, and consume endangered humpback chub. For rainbow and brown trout (*Salmo trutta*), turbidity levels above 50 NTUs were sufficient to reduce their ability to locate, capture, and consume juvenile humpback chub.

In addition to the ability of predators to locate prey, successful predation events are also dependent on the relationship between the size of the predators' mouth and the size of the prey. Predator gape-depth must exceed the maximum body depth of the prey to enable the entire prey item to pass through the oral jaws. For a given fish length, non-native fishes have consistently larger maximum anatomical gapes than native fishes (Moran et al. 2018b). Functionally, this implies that non-native fishes have a greater prey breath, given the wider size-range of items they can fit in their oral jaws. For example, even when comparing size-matched bonytail and largemouth bass, the maximum anatomical gape of the largemouth bass is much larger than that of the bonytail. Furthermore, even when comparing a 41 cm total length (TL) bonytail to a 21 cm TL black crappie (*Pomoxis nigromaculatus*), the physically smaller black crappy (only about 50% as large as the bonytail) has a larger gape-depth than the bonytail (Fig. 3). This problem is further exacerbated by prey depth. Many non-native fishes including the centrarchids and moronids have evolved large gapes to consume deep bodied prey. Conversely, Southwestern native fishes are considered shallow bodied (especially when compared to regular prey items for black basses and striped bass), making them easily consumed by the large gapes of non-native fishes. Furthermore, as with eye diameter, non-native fishes typically have a greater scaling coefficient for gape-depth relative to body size. Thus, the relative advantage of non-native fish to consume large prey becomes even more pronounced as individuals of native and non-native species grow larger.

Because large eyes and large mouth-gapes make non-native fishes better predators and competitors, it is likely that these two factors have significantly contributed to the decline in native fish populations. An example of this problem can be seen in a comparison between the only native piscivorous fish, the Colorado pikeminnow (*Ptychocheilus lucius*) and the piscivorous non-native striped bass (*Morone saxatilis*). The Colorado pikeminnow is a cyprinid and, as is with all cyprinids, individuals of this species lack teeth on the oral jaws. Thus, even more than for some species, Colorado pikeminnow are limited by what they can fit into their mouths because they cannot employ teeth to pin a prey item between the upper and lower jaws (Burnette and Gibb 2013). After adjusting for body size, the eye diameter of striped bass is greater than the eye diameter of Colorado pikeminnow (Fig. 4A). Similarly, if a striped bass and Colorado pikeminnow are size-matched, the striped bass will have a larger gape (Fig. 4B). Thus, the evolutionary history of the striped bass has endowed it with functional "tools"—large eyes for identifying prey from a distance in clear water, teeth (albeit small) to process prey, and a large gape for consuming other fishes ("the better to see you with, the better to eat you with")—that are not possessed by the native Colorado pikeminnow, thereby rendering it at a disadvantage in current Colorado River conditions. In fact, many of the piscivorous fishes introduced to the Southwest have larger maximum anatomical gapes, relative to the native Colorado pikeminnow (David Ward, pers. comm. 2020).

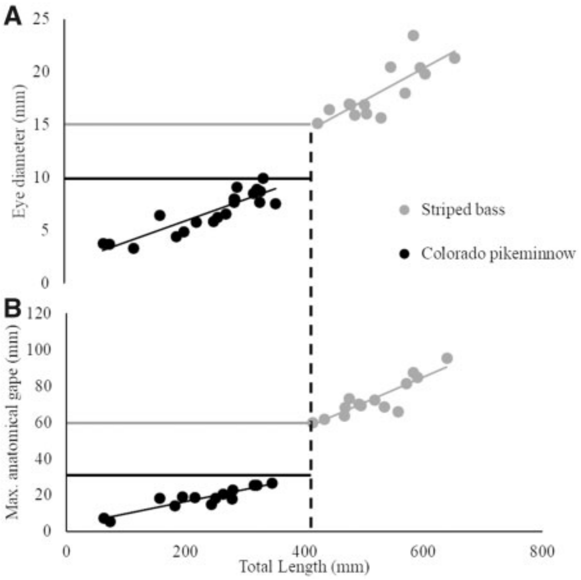

Fig. 4 Non-native striped bass have larger eyes and maximum anatomical gapes per unit length, relative to the Colorado pikeminnow, the only native piscivore from the Colorado River and its tributaries. The cross-hatched boxes represent the discrepancy in eye diameter and maximum anatomical gape for a size matched (400 mm) individual of both species. (**A**) A 400 mm Colorado pikeminnow is anticipated to have an eye diameter of 10 mm, while a 400 mm striped bass will have an eye diameter of 15 mm (50% larger). (**B**) A 400 mm Colorado pikeminnow is anticipated to have a gape-depth of approximately 30 mm, while a 400 mm striped bass will have an eye diameter of 60 mm (again, approximately 50% larger). These morphological differences are anticipated to provide an advantage to a striped bass feeding on other fishes in the clear waters of dammed sections of the Colorado River.

Management improvements

Recently, management agencies have made a commitment to better understanding morphological, physiological, and behavioral influences on native fish survival. Here, we highlight a few success stories in native fish propagation/stocking efforts and outline where further improvements might be made.

In an attempt to reduce the vulnerability of stocked native fishes to predation by non-native piscivores, the Arizona Game and Fish Department (AZDGF) has partnered with the Bureau of Reclamation Lower Colorado River Multi-Species Conservation Program to study the utility of pheromone-based anti-predator conditioning to improve the survival of hatchery-reared fish stocked into the wild (Suboski and Templeton 1989; Griffin et al. 2000). All fishes in the family Cyprinidae (many of the endangered species in the Southwest) produce an alarm substance which is embedded in the skin. Termed "Schrekstoff", this substance is released when an individual's skin has been damaged (Mathuru et al. 2012) and has been shown to elicit a "fright" reaction in conspecifics. In a laboratory setting, this substance can be isolated as a skin extract and mixed into water (Brown et al. 2000). This liquid preparation can be used to train fish to recognize potential predators using classical aversive conditioning (Suboski and Templeton 1989; Griffin et al. 2000).

Recently, researchers used classical aversive conditioning techniques and exposed naïve razorbacks (*Xarauchen texanus)* and bonytail to physically hindered largemouth bass and channel catfish (*Ichtalurus punctatus*) (both of which are known to prey on native fishes) in the presence of the alarm pheromone. Native fish exposed to the control (no alarm substance) displayed very little agitation, whereas native fish exposed to the pheromone became extremely agitated during the conditioning process. In addition, conditioned fish would typically school several feet from predators during survival trials, while unconditioned fish would use cover occupied by predators or actually seek out predators as cover. Consequently, following the predator-avoidance-conditioning, there was a significant increase in survival of bonytail and razorback sucker.

In addition to the predator training by O'Neill and Stewart (2014), AZDGF, along with colleagues at the Bureau of Reclamation, are working to create physically "fitter" fish for stocking into the wild. Ward and Hilwig (2004), Mueller et al. (2007), and Senger and Sjöberg (2010) found that by creating flow in grow out tanks to exercise fish, they were able to cultivate individuals that could maintain higher steady swimming speeds than those raised without in-tank flow. By increasing the sustainable swimming speeds of fishes stocked into the wild, managers are producing fishes that can better cope with high flows in both steady and flood-flow environments. An experimental stocking of unconditioned and flow conditioned razorback suckers suggested that flow-conditioned fish are less likely to move downstream after being stocked in a small stream (Avery et al. 2011). This technique is being used at AGFD's Aquatic and Research Conservation Center to better prepare hatchery-raised spikedace and loach minnow (*Rhinichthys cobitis*) for stocking into stream environments (P. N. Walters, pers comm. 2019).

Populations of razorback sucker in the lower Colorado River are sustained with an effort involving a half dozen state and federal hatcheries, private consulting firms, multiple management agencies, various park, land, and water management efforts, and huge financial expense (MSCP LCR 2019). These programs stock tens of thousands of fish annually into the lower Colorado River to maintain a "wild" (free-living) population of a few thousand fish (MSCP LCR 2019). In an effort to increase survivorship, Marsh and Brooks (1989) proposed increasing the size of stocked individuals. Initial fish target size was between 250 and 300 mm TL, which produced mixed results. Marsh et al. (2005) observed a positive relationship between size at release and survivorship; however, Karam et al. (2008) reported a survival rate of just 16% during the first year for fish that were stocked at an average size of 381 mm. Of 19 fish lost in Year one of the study by Karam et al. (2008), 16 were lost due to predation. Striped bass were the likely predators because they were able to consume fish >400 mm (Karam et al. 2008). Despite these early mixed results, managers believe that stocking larger fish with greater body depth will reduce the ability of predators to consume native fish as prey.

We suggest the following suite of management strategies to promote self-sustaining populations of native fishes in Southwestern waterways. Because Southwestern native fishes have been shown to outperform non-native fishes in a high-flow environment, stocking fish into a more natural flow regime should provide a selective advantage for native fishes, relative to non-natives. Because their specialized swimming morphologies, physiologies, and behaviors provide an advantage in higher-flow conditions, it is important to stock native fishes into habitats that experience flows as similar to historical conditions as possible. Stocking native fishes into more turbid waterways will also increase the probability of their survival because reduced light transmission will inhibit the ability of visual predators to locate and target native fish as prey items. In addition, while we recognize the added cost of raising fishes to larger sizes in a hatchery setting, releasing physically larger fish into Southwestern waterways should allow native fish individuals to be morphologically excluded from the diets of some non-native piscivores simply because they are physically too large to be consumed. Furthermore, an expansion of native fish high-flow and predator-aversion training could allow managers to stock more "fit" and "experienced" fish into the wild—fish that can maintain position in high flow environments and recognize and avoid potential predators.

One potential complication with this suite of recommendations is posed by the presence of introduced catfishes in the waterways of the Southwest. Members of the catfish family (Ictaluridae) are omnivores that are highly successful in turbid environments because they do not rely on vision to identify their prey. Given the similarly sized eyes between catfish and native fishes, it is clear that these highly predatory fishes have evolved to feed in low visibility environments (Moran et al. 2018b). In fact, channel (*Ictalurus punctatus*), blue (*Ictalurus furcatus*), and flathead (*Pylodictis olivaris*) catfish have olfactory projections (Morita and Finger, 1998), barbels lined with taste buds (Hansen et al. 2003), as well as neuromasts on the head—all of which can aid in locating prey in turbid environments. Thus, even if stocking procedures are modified as suggested above, introduced catfishes may continue to present a problem for native fish survival in the wild.

However, even in the presence of introduced catfishes, low visibility environments in the Southwest may be a refuge from the detrimental effects of introduced, non-native fishes. Parts of Lake Mead (NV) that have consistent inflow from the Colorado River, Virgin/Muddy rivers, and Las Vegas Wash all have self-sustaining (albeit low) populations of endangered razorback sucker (Albrecht et al. 2010, 2017). These habitats are known to have high sediment loads, high primary production, and diverse niche availability (Karp and Mueller, 2002; Kaemingk et al., 2007; Hines, 2011). Riverine sediment input might be the biggest contributing factor to sustained populations in these localized habitats because increased turbidity likely reduces the predation pressure of non-natives on native fishes (Johnson and Hines 1999; Albrecht et al. 2010; Ward et al. 2016). Importantly, razorback sucker use these inflow habitats year round suggesting that they are refuges during months of high and low sediment loads (Albrecht et al. 2017).

In conclusion, we have presented many morphological, physiological, and behavioral mechanisms that can be used to assist in the repatriation of Southwestern endangered native fishes. While we highlighted some of the successes above, the outlook for these fishes is dismal. As highlighted by some of the success stories above, understanding how organisms are influenced by all environmental variables is crucial in accounting for how variations might impact a species of concern. Unfortunately, not enough is being done to restore these natural environmental variables. While further fundamental research is needed, this serves as a bridge between pure and applied researchers with a common goal to restore native populations of Southwestern endemic fishes.

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