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Why does *Gila elegans* have a bony tail? A study of swimming morphology convergence

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ABSTRACT

Caudal-fin-based swimming is the primary form of locomotion in most fishes. As a result, many species have developed specializations to enhance performance during steady swimming. Specializations that enable high swimming speeds to be maintained for long periods of time include: a streamlined body, high-aspect-ratio (winglike) caudal fin, a shallow caudal peduncle, and high proportions of slow-twitch ("red") axial muscle. We described the locomotor specializations of a fish species native to the Colorado River and compared those specializations to other fish species from this habitat, as well as to a high-performance marine swimmer. The focal species for this study was the bonytail (*Gila elegans*), which has a distinct morphology when compared with closely related species from the Southwestern United States. Comparative species used in this study were the roundtail chub (*Gila robusta*), a closely related species from low-flow habitats; the common carp (*Cyprinus carpio*), an invasive cyprinid also found in low-flow habitats; and the chub mackerel (*Scomber japonicus*), a model high-performance swimmer from the marine environment. The bonytail had a shallow caudal peduncle and a high-aspect-ratio tail that were similar to those of the chub mackerel. The bonytail also had a more streamlined body than the roundtail chub and the common carp, although not as streamlined as the chub mackerel. The chub mackerel had a significantly higher proportion of red muscle than the other three species, which did not differ from one another. Taken together, the streamlined body, narrow caudal peduncle, and high-aspect-ratio tail of the bonytail suggest that this species has responded to the selection pressures of the historically fast-flowing Colorado River, where flooding events and base flows may have required native species to produce and sustain very high swimming speeds to prevent being washed downstream.

1. Introduction

In fishes, a suite of specializations is associated with the ability to swim rapidly for long periods of time (henceforth termed "high-performance swimming") (Bernal et al., 2001; Westneat and Wainwright, 2001; Walker et al., 2013). Externally, these modifications are most apparent in the axial body and tail (caudal) fin, the primary propulsive structures for the majority of fishes. In fishes that can swim rapidly for long periods of time, morphological adaptations such as body streamlining and a forked, semi-lunate or lunate (crescent-moon shaped) caudal fin shape assist in sustained high-velocity swimming (Nauen and Lauder, 2002).

In many high-performance caudal-fin-based swimmers, neural and hemal spines of the vertebral column are depressed posteriorly, or are absent altogether, in the region of the body termed the caudal peduncle. These neural and hemal spines are, respectively, dorsal and ventral projections from the vertebral centra that serve as locations for axial muscle attachment. Axial muscles allow for the transmission of force to the vertebral column (Lindsey, 1978), resulting in body-bending. In caudal-fin-based swimmers, a posterior-moving 'wave' of bending passes along the body towards the caudal fin. In high-performance caudal-fin-based swimmers, the angle of the neural and hemal spines decreases in the caudal peduncle region and the last set of spines radiates from the ultimate vertebra to form the hypural plate (Westneat and Wainwright, 2001). This morphology forms a shallow caudal peduncle that further streamlines the body. However, reduction of neural and hemal spine length also reduces the surface area on which muscles can attach. The Scombridae have developed a great lateral tendon that does not attach to the vertebral elements in the caudal pedun-

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cle but instead transmits force directly to the tail (Westneat and Wainwright, 2001). The reduction of muscular attachments in the caudal peduncle is rare and has thus far only been observed in the Scombridae.

Some scombrids are also known for modifications to the swimming musculature. Most of the axial body of a fish consists of white muscle (fast glycolytic fibers) (Jayne and Lauder, 1994), which is used to generate rapid accelerations that are typical of escape responses and burst and glide methods of locomotion (Westneat and Wainwright, 2001). The proportion of red muscle (slow oxidative fibers) in scombrids, as well in as a handful of other long-distance, high-speed swimmers (Egginton and Sidell, 1989), has been enlarged, moved medially (internalized), or both. Because red muscle is used to produce steady swimming (e.g., Altringham and Block, 1997), the increase in the proportion of red muscle allows these species to generate and maintain high sustained swimming speeds.

The majority of work that has been conducted on high-performance fishes has utilized pelagic marine species, for obvious reasons. The freshwater cyprinid fishes (carps and their relatives) are typically not known for producing high sustained swimming speeds. However, in very large rivers, cyprinids could experience selective pressures for high-performance swimming in order to maintain position during periods of high flow, or because high-velocity movements are required over long periods of time to travel great distances during migrations. In fact, some cyprinids that evolved in large, fast-flowing rivers show convergence in key anatomical features with scombrid fishes. For example, *Gila elegans*, once native to the swift-flowing mainstem Colorado River, appears to have an exceptionally shallow caudal peduncle and a high-aspect-ratio (wing-like) caudal fin (see Table 1) – a morphology that has given rise to its common name: bonytail.

We hypothesize that historically high-flow conditions in the Colorado River led to selection for morphological characteristics in *G. elegans* that are similar to those seen in high-performance swimmers. Thus, we expect that individuals of *Gila elegans* will demonstrate a body morphology that is convergent with that of high-performance swimmers. To test this hypothesis, we examined bonytail, *Gila elegans* (Cypriniformes: Cyprinidae), and compared individuals from this species to individuals from three other species representing a range of locomotor abilities. *Gila elegans* is native to the mainstem Colorado River, which once experienced high flows during seasonal flooding events. *Gila robusta*, the roundtail chub, is closely related to *G. elegans* and evolved in the tributaries of the Colorado River, but appears to lack the distinct body and tail morphology exhibited by *G. elegans*. A non-native fish that has been introduced to nearly all waterways of the Colorado River basin is the common carp, *Cyprinus carpio* (Cypriniformes: Cyprinidae). *Cyprinus carpio* has a deep body and is regarded as a slow-speed swimmer (1–2 body lengths (BL) s^{-1}) that typically exploits low-flow habitats (De Boeck et al., 2006). Chub mackerel (henceforth, mackerel), *Scomber japonicus* (Perciformes: Scombridae) serves as an example of a high-performance swimmer for comparative purposes. *Scomber japonicus* is a semi-pelagic species that has documented morphological specializations for high-performance swimming, including a shallow caudal peduncle, a high proportion of red muscle, a streamlined body, and a high-aspect-ratio caudal fin (Kafuku, 1950). Additionally, *S. japonicus* spans the same size range as the other three species tested here (Collette, 1978).

Based on our overarching hypothesis of functional convergence, we predict that *G. elegans* will be similar to *S. japonicus* in body shape, tail shape, vertebral column morphology in the caudal peduncle region and have a similar red-to-white muscle ratio in the axial body. Additionally, we predict that *G. elegans* has significantly diverged from its close cyprinid relative to converge on a morphology associated with swimming at high velocity. Indeed, previous work within the Cyprinidae has shown that body shape can change in response to changing flow regimes (Cureton and Broughton, 2014). We also predict that *G. robusta* will be similar to *C. carpio* because both species inhabit slower-moving waters when compared to *G. elegans* (Tyus, 1989), which must contend with the higher flows of the mainstem Colorado River.

2. Materials and methods

2.1. Fish specimens

Fish specimens were obtained from several institutions. *Gila elegans* ($n = 5$; 197.5–202 mm standard length (SL)) were donated by the museum of the Southwest. *Gila robusta* ($n = 5$; 195.6–208.8 mm SL) were donated by David Ward and the USGS. *Cyprinus carpio* ($n = 5$; 198–203 mm SL) were purchased from the aquarium trade. *Scomber japonicus* ($n = 5$; 192.2–209.6 mm SL) were donated by Kathryn Dickson (California State University Fullerton). All fish analyzed for this study were 200 ± 10 mm (Table 1). Measurements of the body and tail were taken from photographs of frozen and defrosted specimens (1.0 cm x 1.0 cm grid was placed behind every fish for scale) using the program ImageJ (Abràmoff et al., 2004). To allow detailed visualization of the vertebral column, the caudal peduncle region of the *G. elegans, G. robusta, C. carpio* and *S. japonicus* specimens was cleaned using a dermestid beetle colony.

2.2. Morphological calculations

To test the prediction that *G. elegans* has a body shape different from that of *G. robusta* and more similar to that of *S. japonicus,* we measured fineness ratio (Fig. 1B), which is considered a metric of streamlining. A streamlined body provides a hydrodynamic advantage for fishes that swim at high speeds or for long distances (Webb, 1984). Here, fineness ratio was calculated by dividing the standard length of the fish by the greatest body depth, which was typically just anterior to the dorsal fin.

To test the prediction that *G. elegans* has a tail shape different from that of *Gila robusta* and more similar to that of *S. japonicus*, we calculated caudal fin aspect ratio (Fig. 1A), which describes the shape of the fin. High values describe fins built for speed and low values describe fins built for maneuverability (Westneat and Wainwright, 2001). Fishes that travel long distances or achieve high speeds typically have high-aspect-ratio lunate tails (Westneat and Wainwright, 2001). Caudal fin aspect ratios were calculated by squaring the fin span (measured from the dorsal tip to the ventral tip of the caudal fin) and dividing this number by the fin area (this area is defined as the caudal fin, excluding the caudal peduncle). These measurements were taken from photos of defrosted specimens using ImageJ software. Prior to taking each photo, the caudal fin was maximally extended and pinned down to ensure the full caudal fin span and area was photographed.

To test the prediction that *G. elegans* is similar to *S. japonicus* in the proportion of red muscle, we divided the cross-sectional area of red muscle by the cross-sectional area of the same section of body excluding the body cavity and the vertebral centra (Fig. 1C). Red muscle is the primary muscle that powers the body during sustained swimming. Red muscle is exclusively used during sustained swimming in many of the scombrids (Shadwick et al., 1998). Following Wakeling and Johnston (1999), fish were transversely sectioned at 10% SL increments starting at the back of the head (as defined by the posterior edge of the opercular). Each section was photographed and images were imported into ImageJ. Using ImageJ, we measured the area of the red muscle and divided it by the area of the white muscle to yield a red:white muscle ratio for each section of the body. Red muscle was differentiated from white by

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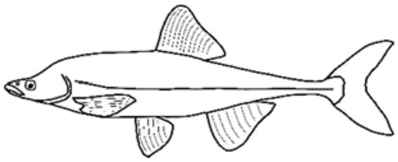
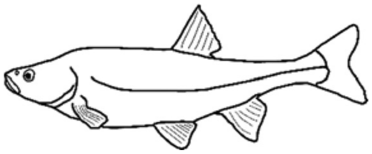
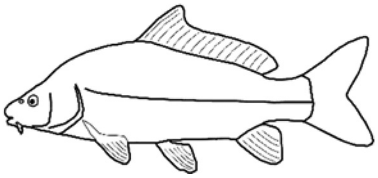
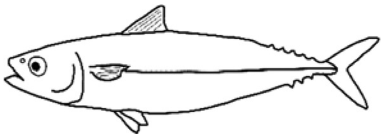
Table 1
Species of interest were chosen to represent fish lineages from different natural ranges with distinct body types.

Species	Taxonomy	Location	Role in study	Illustration	Sample size
Gila elegans	Order: Cypriniformes Family: Cyprinidae Genus: *Gila* Species*: elegans*	Native to mainstem Colorado River	Hypothesized high-performance swimmer		5
Gila robusta	Order: Cypriniformes Family: Cyprinidae Genus: *Gila* Species*: robusta*	Native to Colorado River tributaries	Closely related low-performance swimmer		5
Cyprinus carpio	Order: Cypriniformes Family: Cyprinidae Genus: *Cyprinus* Species*: carpio*	Invasive to the Colorado River and tributaries	Distantly related low-performance swimmer		5
Scomber japonicus	Order: Perciformes Family: Scombridae Genus: *Scomber* Species*: japonicus*	Marine fish found in the pelagic zone	High-performance swimmer from the marine environment		5

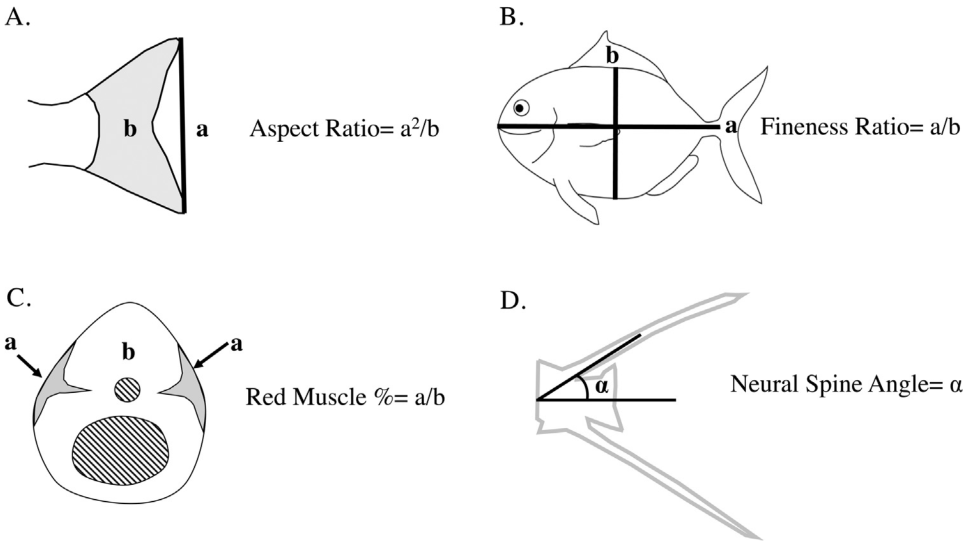


Fig. 1. In this study, four morphological variables were measured from bonytail (*Gila elegans*), roundtail chub (*Gila robusta*), common carp (*Cyprinus carpio*), and chub mackerel (*Scomber japonicus*) as follows: (A) aspect ratio (tail fin area^2/fin span), (B) fineness ratio (body length/depth), (C) red muscle proportion (cross-sectional measure of the area of red muscle/area of the entire body section, excluding the body cavity and vertebral centra), and (D) neural spine angle (angle of the spine as it projects away from the vertebral column, relative to the vertebral column chord).

backlighting each section and discerning the distribution of muscle that contained red pigmentation vs. the distribution of muscle that did not contain red pigment.

To test the prediction that neural spine angle is similar in *G. elegans* and *S. japonicus,* we calculated the angle of the neural spine as it projects dorsally from the vertebra (Fig. 1D). A narrow caudal peduncle contributes to body streamlining and creates minimal disturbance to the water as it passes by the body towards the tail. This allows the tail to push against a relatively undisturbed sheet of water (Nauen and Lauder, 2002). A shallow caudal peduncle is seen in fishes that reach high speeds and can be created by either reducing/eliminating the neural and hemal spines or having them folded posteriorly. Spine angle calculations were made from whole specimens that were cleaned using a dermestid beetle colony (Fig. 2). We measured the fifth-to-last vertebra as an indicator of caudal peduncle depth and as representative of the morphology of the vertebrae in this region of the vertebral column. Measurements of the neural spine angle were taken relative to the axis of the vertebral column (following Ashley-Ross et al., 2014). All measurements were taken from photos of the prepared skeletons using the program ImageJ.

A MANOVA was used as a preliminary multivariate approach to identify morphological differences between species. Pillai's crite-

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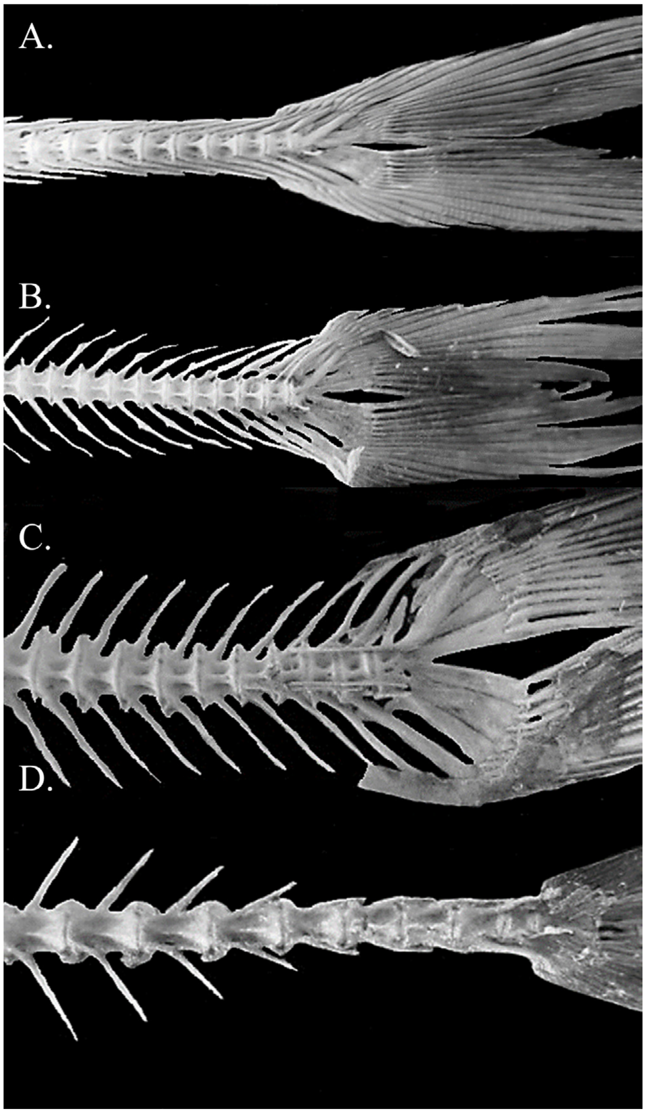

Fig. 2. Photos from cleared specimens demonstrate the variable morphologies of the dorsal and neural spines in the caudal peduncle for the four species considered here: (A) bonytail (*G. elegans*), (B) roundtail chub (*G. robusta*), (C) common carp (*C. carpio*), and (D) chub mackerel (*S. japonicus*). *G. elegans* has posteriorly depressed neural and hemal spines throughout the caudal peduncle. *S. japonicus* has reduced posteriorly depressed neural and hemal spines (absent on the last 3–4 vertebrae). Both *G. robusta* and *C. carpio* have neural and hemal spines that protrude from the vertebra at a significantly larger angle when compared to *G. elegans* and *S. japonicus*.

rion was used to establish multivariate significance. This analysis was followed by one-way ANOVAs within each morphological variable to consider the potential effect of species. All four species, *S. japonicus*, *G. elegans*, *G. robusta* and *C. carpio*, were included in all analyses. Following the ANOVA, Tukey's least significant difference (LSD) post hoc tests were conducted to determine which species differed from one another for a given variable. All statistical analyses were conducted in SPSS version 21 (IBM Corp., Armonk, NY, USA) with an alpha of 0.05.

3. Results

There were significant differences among species based on the fineness ratio, caudal fin aspect ratio, angle of the fifth neural spine and red muscle proportion (Pillai's trace = 2.041, $p < 0.0001$). The fineness ratios (which quantify streamlining of the body) were different between all species tested ($p < 0.05$). The most streamlined body was found in *S. japonicus*, followed by *G. elegans*, *G. robusta* and *C. carpio*. *G. elegans* had the most streamlined body of the cyprinids considered here (Table 2).

When measurements were taken from the prepared skeletons, *G. elegans* had the lowest angle (mean ± S.D. = 13.73 ± 1.22) for the fifth-to-last neural spine and this angle was not significantly different from that of the neural spine angle seen in *S. japonicus* (mean ± S.D. = 19.69 ± 2.18, $p > 0.05$). However, neural spine angle for these species was less than that in *G. robusta* (mean ± S.D. = 32.50 ± 6.06), and *G. robusta* had a smaller angle than *C. carpio* (mean ± S.D. = 46.97 ± 2.09, $p < 0.05$) (Fig. 3). The low spine angle in the fifth-to-last vertebra is associated with an overall narrowing of the caudal peduncle.

G. elegans and *S. japonicus* had highly forked tails when compared to *C. carpio* and *G. robusta*. When comparing caudal fin aspect ratios, the species tested here sorted into two groups. *S. japonicus* had the highest average aspect ratio (mean ± S.D. = 3.33 ± 0.24, highly forked), but this did not differ significantly from that of *G. elegans* (mean ± S.D. = 3.02 ± 0.08, $p > 0.05$). Both of these species had a larger caudal fin aspect ratio than *G. robusta* (mean ± S.D. = 1.77 ± 0.1) and *C. carpio* (mean ± S.D. = 2.11 ± 0.17, $p < 0.001$) (Table 2). *G. robusta* and *C. carpio* were not significantly different from one another and had an aspect ratio that is indicative of a more square-shaped tail with a large area and small span ($p > 0.05$, Fig. 3).

The red muscle in *S. japonicus* was located more medially (closer to the vertebral column) relative to the red muscle distribution seen in the other three species. The red muscle proportions were also significantly higher in *S. japonicus* than in the other species considered here ($p < 0.05$) along all regions of the body. No significant differences in red muscle proportion for each section of the body were present among the three cyprinids ($p > 0.05$, Fig. 4, Table 2). As has been documented in previous studies (Shadwick et al., 1998), the contribution of red muscle to the axial musculature increased along the anterior to posterior axis in *S. japonicus*. This pattern was only seen in *S. japonicus* and was not seen in any of the other species tested here.

Based on observations of prepared skeletons for the four species considered here, species with shallow spine angles have shallow caudal peduncles (Figs. 2 and 3). *G. elegans* has compressed neural and hemal spines in the caudal peduncle. This is similar to *S. japonicus*; however, in *S. japonicus* spines are reduced or absent near the tail. The spine orientation seen in *G. elegans* (13.73 ± 1.22) is very different from that seen in the closely related *G. robusta* (32.50 ± 6.06) (Table 2). The angle of the spines as they protrude from each vertebra is directly correlated with the depth of the caudal peduncle.

4. Discussion

G. elegans and *S. japonicus* display similarities in key aspects of their locomotor morphologies, which suggests functional convergence in features that produce high-performance swimming behaviors. For example, both *G. elegans* and *S. japonicus* have high-aspect-ratio caudal fins. High-aspect-ratio caudal fins are typically lunate (shaped like a crescent moon) or forked, and have been described in mackerels and tunas, as well as in other marine vertebrates such as whales and dolphins. Such tails have a higher efficiency during steady swimming than low-aspect-ratio caudal fins because less drag (force opposite to direction of motion) is induced per unit lift (force perpendicular to direction of motion) (Magnuson, 1978). A reduction in drag while maintaining thrust and lift increases the hydrodynamic efficiency of aquatic organisms with high-aspect-ratio tails.

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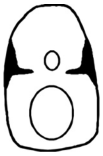
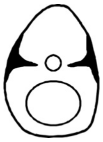
Table 2
Morphological measurements (mean ± standard error) for key variables measured from five individuals representing four teleost species.

Species	Fineness ratio (Mean ± S.E.)	Caudal fin aspect ratio (Mean ± S.E.)	Angle of 5th neural spine (°) (Mean ± S.E.)	Red muscle% per *section of body* (Mean ± S.E.)	Cross-sectional line drawing
Gila elegans	4.38 ± 0.1	3.02 ± 0.08	13.73 ± 1.22	*30%*: 3.15 ± 0.09 *40%*: 4.26 ± 0.30 *50%*: 4.09 ± 0.06 *60%*: 3.68 ± 0.64 *70%*: 5.19 ± 0.69 *80%*: 6.31 ± 1.15 *90%*: 5.27 ± 1.20	
Gila robusta	4.01 ± 0.063	1.77 ± 0.1	32.50 ± 6.06	*30%*: 2.85 ± 0.25 *40%*: 2.99 ± 0.41 *50%*: 3.26 ± 0.16 *60%*: 3.48 ± 0.54 *70%*: 3.01 ± 0.46 *80%*: 4.89 ± 0.31 *90%*: 5.89 ± 0.45	
Cyprinus carpio	3.56 ± 0.17	2.11 ± 0.17	46.97 ± 2.10	*30%*: 3.22 ± 0.22 *40%*: 5.85 ± 0.28 *50%*: 6.10 ± 0.01 *60%*: 6.96 ± 0.23 *70%*: 7.54 ± 0.40 *80%*: 7.52 ± 0.45 *90%*: 5.11 ± 0.52	
Scomber japonicus	5.36 ± 0.09	3.33 ± 0.24	19.694 ± 2.18	*30%*: 6.46 ± 1.04 *40%*: 11.33 ± 1.68 *50%*: 12.12 ± 0.81 *60%*: 12.01 ± 0.70 *70%*: 15.37 ± 0.56 *80%*: 20.04 ± 0.75 *90%*: 18.09 ± 1.76	

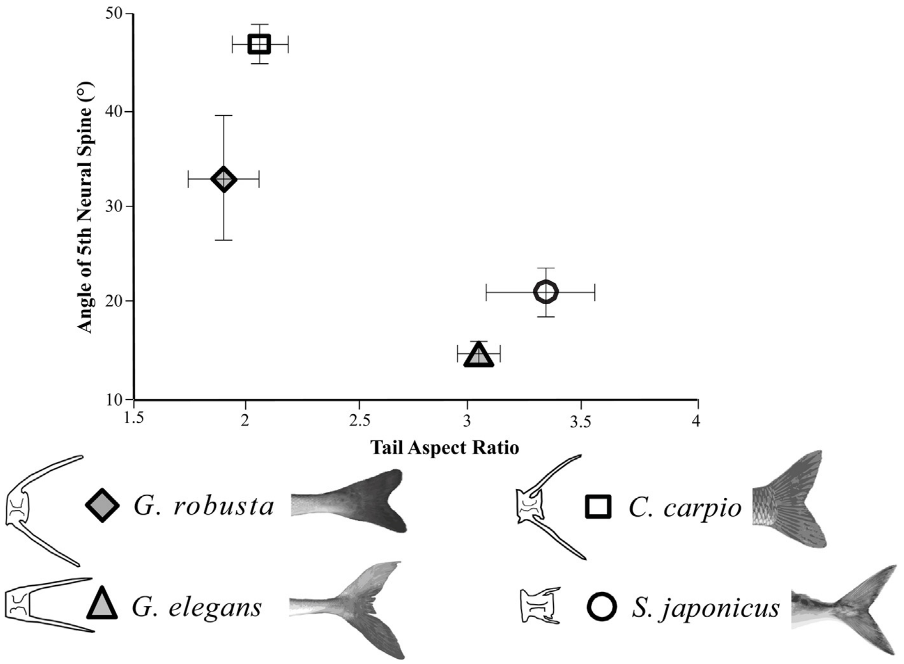


Fig. 3. *G. elegans* and *S. japonicus* are characterized by high-aspect-ratio caudal fins and shallow caudal peduncles, as quantified here by the angle of the fifth neural spine relative to the vertebral column. Shown here are mean values (± SE) from five individuals of each species. Open symbols (circle: *S. japonicus*; square: *C. carpio*) represent a model high-performance swimmer and an introduced freshwater species (respectively). Filled symbols (diamond: *G. robusta*; triangle: *G. elegans*) represent two species native to the Southwestern United States. Pictured next to each species are graphics depicting the fifth vertebra with the neural and hemal spines (left) and the overall shape of the tail (right).

Another way in which *G. elegans* and *S. japonicus* are similar is that they both possess a shallow caudal peduncle. From scombrids to cetaceans, the shallow caudal peduncle is another morphological trait that characterizes high-performance steady swimmers. The shallow caudal peduncle has been shown to decrease drag as the caudal fin is moved laterally through the water during a tail beat, both through mathematical modeling (Lighthill, 1975) and digital particle image velocimetry, a process by which the force imparted

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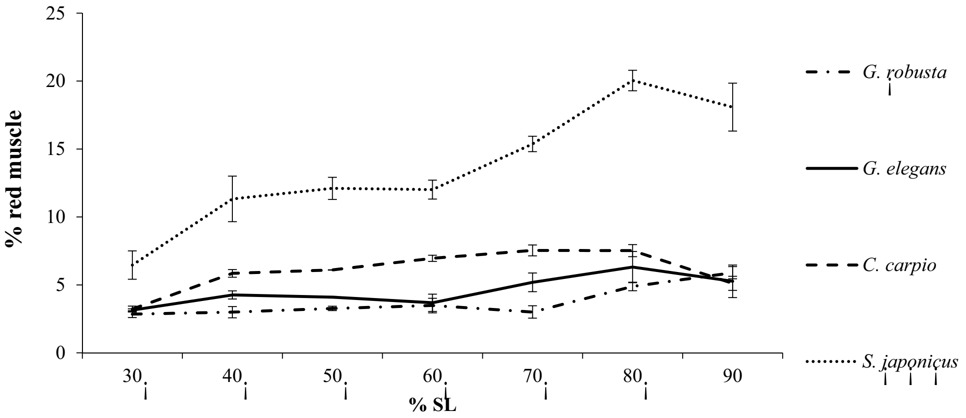

Fig. 4. *S. japonicus* has a higher proportion of red muscle along the body length relative to all of the cyprinids measured here. Shown here are the mean values (± SE) of red muscle proportions posterior to the head (which accounted for ~30% of SL for all species).

to the water during aquatic locomotion is quantified (Nauen and Lauder, 2002). In species with this morphological modification, the shallow caudal peduncle "cuts" through the water, thus reducing water disturbance; this then allows the caudal fin to push against a relatively undisturbed sheet of water. Pushing against a laminar sheet of water is hydrodynamically advantageous for steady swimming because it allows the caudal fin to produce maximum thrust during a tail stroke (Nauen and Lauder, 2002).

G. elegans and *S. japonicus* possess similar caudal fin and peduncle shapes. These two morphological specializations may help *G. elegans* in achieving sufficient swimming velocity to hold position during periods of high flow in the Colorado River during seasonal flooding. Individuals of *S. japonicus* can maintain maximum swimming speeds of over 100 cm s^{-1} (4–5 BL s^{-1}) (Sepulveda and Dickson, 2000; Dickson et al., 2002) in a flow tunnel. Preliminary data collected for 200 mm individuals of *G. elegans* indicate that they can maintain speeds exceeding 120 cms^{-1}, or 6 BL s^{-1} in a flow tunnel (C.J.M., personal observation). Average base flows from Lees Ferry to the confluence of the Little Colorado River, which is *G. elegans* habitat, typically generate water velocities in this reach of approximately 31 cm s^{-1} (Graf, 1997). However, the largest flooding event is estimated to have generated water velocities of approximately 220 cm s^{-1} through this same stretch of river, although it is important to note that flow velocity will vary according to both base flow (m^3/s) and river morphology (width and depth of the channel). Although we cannot predict the exact flow speeds that a fish may encounter during flooding events, the high water velocities produced during flooding in this region may have served as a selective pressure on locomotor morphology.

Although closely related, *G. elegans* and *G. robusta* demonstrated different locomotor morphologies, suggesting that the two morphologies reflect differences in the abiotic parameters of their respective habitats. The fineness ratio of *G. elegans* was significantly greater (indicating that it is more streamlined), relative to that of the closely related *G. robusta*. Similarly, *G. elegans* has a shallower caudal peduncle and a more lunate caudal fin than *G. robusta*. This suggests that flow may have played a role in selecting for a streamlined body, as *G. robusta* is typically found in slower-moving tributaries of the Colorado River and the small waterways of the Lower Colorado River Basin. Historically, these habitats experienced lower flows and less flow variability than the Colorado River (Rinne, 1976). Preliminary data we have collected for *G. robusta* suggests that 200 mm individuals cannot maintain position in water that is moving in excess of 3 BL s^{-1} in a flow tunnel (C.J.M., personal observation). Assuming preliminary flow tank results are substantiated, *G. elegans* may prove to be able to sustain swimming speeds that are twice as fast as those sustained by *G. robusta*. Given estimated flow velocities during flooding events in the Colorado River, it is likely that the morphological divergence between *G. robusta* and *G. elegans* has allowed bonytail to survive the high flow events of the main stem of the river.

In teleost fishes, the neural and hemal spines are bony projections that originate at the vertebral centra and facilitate the attachment of the axial musculature. These spines not only provide connections between muscles and bones, but may also provide energy storage and recovery during cycles of bending (Westneat and Wainwright, 2001). Most scombrids have significantly reduced neural and hemal spines at the peduncle (Westneat and Wainwright, 2001), but *G. elegans* does not (Fig. 2). We propose a possible explanation for these two distinct peduncle morphologies. Koch (1917) and Fierstine and Walters (1968) suggested that larger neural and hemal spines offer greater surface area, which would allow greater attachment of the musculature on the vertebrae. Scombrids have a great lateral tendon that transmits force from the axial musculature directly onto the hypural plate (Westneat and Wainwright, 2001). This tendon could reduce the need for musculature to insert onto the vertebral column within the caudal peduncle. Because *G. elegans* does not possess a specialized tendon, the neural and hemal spines presumably retain a connection to the axial muscle via collagen–fiber connections; this should facilitate the transmission of force through the peduncle onto the caudal fin.

Although *G. elegans* and *S. japonicus* share numerous morphological locomotor specializations, *G. elegans* may ultimately be limited in its sustained swimming performance by the lack of fatigue-resistant musculature. As seen in Fig. 4, *G. elegans* has a small proportion of red muscle when compared to *S. japonicus*. Red muscle is the primary muscle type used in sustained swimming (Fierstine and Walters, 1968). As a result, *G. elegans* may have a reduced ability to swim steadily for long periods of time at very high water velocities, relative to tunas and some mackerels. When compared to the relatively homogeneous habitat of the scombrids, the Colorado River is a complex environment made up of turbulent runs and low flow pools. *G. elegans* may rely on short periods of burst swimming (through a run) while maintaining position or moving up river (through a pool).

G. elegans is a critically endangered species for which current management strategies have been unsuccessful in generating self-sustaining populations in the wild. The implementation of hydroelectric dams along the mainstem Colorado River and predation by non-native fishes (Mueller and Marsh, 2002) have made it difficult for *G. elegans* to be reestablished in the Colorado River. However, it is possible that manipulation of flow regimes in the Colorado River may aid the recovery of *G. elegans*. Given their morphological specializations for swimming in a fast-flowing complex environment, periodic increases in flow volume in the Colorado River (to simulate a moderate natural flooding event) may promote the success of *G. elegans*, relative to some non-native species. Many of the non-native fish predators (particularly members of the Centrarchidae and Cyprinidae) are not adapted for a fast-flowing, spatially complex environment. *Micropterus salmoides,* for example, would likely be swept downriver; Peake (2004) found that subadult individuals of *M. salmoides* can only maintain a swimming speed of 3 BL s^{-1} for a short period of time (60 cm s^{-1} for a fish of 20 cm SL). Given that they rapidly fatigue at these speeds, it is unlikely that individuals of *M. salmoides* would be able to maintain position in the Colorado River during floods and baseflows. Unfortunately, current conditions in the Colorado River favor the non-native predators, as long stretches of the river are currently low-flow environments (< 50 cm s^{-1} flow speed) (Mueller and Marsh, 2002). By deliberately increasing river flow, habitat managers could potentially wash the non-native fish predators downstream, promoting the success of *G. elegans* in an environment free of non-native predators.

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References

Abràmoff, M.D., Magalhães, P.J., Ram, S.J., 2004. Image processing with ImageJ. Biophot. Intern. 11, 36–43.

Altringham, J.D., Block, B.A., 1997. Why do tuna maintain elevated slow muscle temperatures? Power output of muscle isolated from endothermic and ectothermic fish. J. Exp. Biol. 200, 2617–2627.

Ashley-Ross, M.A., Perlman, B.M., Gibb, A.C., Long, J.H., 2014. Jumping sans legs: does elastic energy storage by the vertebral column power terrestrial jumps in bony fishes? Zoology 117, 7–18.

Bernal, D., Dickson, K.A., Shadwick, R.E., Graham, J.B., 2001. Review: Analysis of the evolutionary convergence for high performance swimming in lamnid sharks and tunas. Comp. Biochem. Phys. A 129, 695–726.

Collette, B.B., 1978. Adaptations and systematics of the mackerels and tunas. In: Sharp, G.D., Dizon, A.D. (Eds.), The Physiological Ecology of Tunas. Academic Press, New York, pp. 7–39.

Cureton II, J.C., Broughton, R.E., 2014. Rapid morphological divergence of a stream fish in response to changes in water flow. Biol. Lett. 10, 20140352, http://dx.doi.org/10.1098/rsbl.2014.0352.

De Boeck, G., Van der Ven, K., Hattink, J., Blust, R., 2006. Swimming performance and energy metabolism of rainbow trout: common carp and gibel carp respond differently to sublethal copper exposure. Aqua. Tox. 80, 92–100.

Dickson, K.A., Donley, J.M., Sepulveda, C., Bhoopat, L., 2002. Effects of temperature on sustained swimming performance and swimming kinematics of the chub mackerel *Scomber japonicus*. J. Exp. Biol. 205, 969–980.

Egginton, S., Sidell, B.D., 1989. Thermal acclimation induces adaptive changes in subcellular structure of fish skeletal muscle. Am. J. Physiol. Reg. Int. Comp. Physiol. 256, R1–R9.

Fierstine, H.L., Walters, V., 1968. Studies in locomotion and anatomy of scombroid fishes. Mem. S. Calif. Acad. Sci. 6, 1–31.

Graf, J.B., 1997. The Colorado River in Grand Canyon: how fast does it flow? US Geological Survey Fact Sheet FS, 168–197, http://pubs.usgs.gov/fs/FS-168-97/pdf/fs-168-97.pdf.

Jayne, B.C., Lauder, G.V., 1994. How swimming fish use slow and fast muscle fibers: implications for models of vertebrate muscle recruitment. J. Comp. Physiol. A 175, 123–131.

Kafuku, T., 1950. Red muscles in fishes. I. Comparative anatomy of the scombroid fishes of Japan. Jap. J. Ichthyol. 1, 89–100, in Japanese with English abstract.

Koch, J.C., 1917. The laws of bone architecture. Am. J. Anat. 21, 177–298.

Lighthill, J., 1975. Mathematical Biofluiddynamics. Soc. Ind. Appl. Math., Philadelphia.

Lindsey, C.C., 1978. Form, function and locomotory habits in fish. In: Hoar, W.S., Randall, D.J. (Eds.), Fish Physiology, vol. 7. Academic Press, New York, pp. 1–100.

Magnuson, J.J., 1978. Locomotion in scombroid fishes: hydrodynamics, morphology and behavior. In: Hoar, W.S., Randall, D.J. (Eds.), Fish Physiology, vol. 7. Academic Press, New York, pp. 239–313.

Mueller, G.A., Marsh, P.C., 2002. Lost, a Desert River and Its Native Fishes: a Historical Perspective of the Lower Colorado. River Information and Technology Report 2002-0010. US Geological Survey, Fort Collins, CO.

Nauen, J.C., Lauder, G.V., 2002. Hydrodynamics of caudal fin locomotion by chub mackerel, *Scomber japonicus* (Scombridae). J. Exp. Biol. 205, 1709–1724.

Peake, S., 2004. An evaluation of the use of critical swimming speed for determination of culvert water velocity criteria for smallmouth bass. Trans. Am. Fish. Soc. 133, 1472–1479.

Rinne, J.N., 1976. Cyprinid fishes of the genus *Gila* from the lower Colorado River basin. Wassman J. Biol. 34, 65–107.

Sepulveda, C., Dickson, K.A., 2000. Maximum sustainable speeds and cost of swimming in juvenile kawakawa tuna (*Euthynnus affinis*) and chub mackerel (*Scomber japonicus*). J. Exp. Biol. 203, 3089–3101.

Shadwick, R.E., Steffensen, J.F., Katz, S.L., Knower, T., 1998. Muscle dynamics in fish during steady swimming. Am. Zool. 38, 755–770.

Tyus, H.M., 1989. Habitat Use and Streamflow Needs of Rare and Endangered Fishes, Yampa River, Colorado (No. FWS-89/14). US Fish and Wildlife Service, Vernal, UT.

Wakeling, J.M., Johnston, I.A., 1999. White muscle strain in the common carp and red to white muscle gearing ratios in fish. J. Exp. Biol. 202, 521–528.

Walker, J.A., Alfaro, M.E., Noble, M.M., Fulton, C.J., 2013. Body fineness ratio as a predictor of maximum prolonged-swimming speed in coral reef fishes. PLoS One 8, e75422, http://dx.doi.org/10.1371/journal.pone.0075422.

Webb, P.W., 1984. Body form: locomotion and foraging in aquatic vertebrates. Am. Zool. 24, 107–120.

Westneat, M.W., Wainwright, S.A., 2001. Mechanical design for swimming: muscle, tendon, and bone. Fish Physiol. 19, 271–311.

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