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

Clinton J. Moran [a,*], Lara A. Ferry [b], Alice C. Gibb [a]

[a] *Biological Sciences, Northern Arizona University, 617 S. Beaver St., Flagstaff, AZ 86011, USA*
[b] *School of Mathematical and Natural Sciences, Arizona State University, 4701 W. Thunderbird Rd., Glendale, AZ 85306, USA*

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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.

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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-

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