

RESEARCH ARTICLE

Behavioral and physiological adaptations to high-flow velocities in chubs (*Gila* spp.) native to Southwestern USA

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ABSTRACT

Morphological streamlining is often associated with physiological advantages for steady swimming in fishes. Though most commonly studied in pelagic fishes, streamlining also occurs in fishes that occupy high-flow environments. Before the installation of dams and water diversions, bonytail (Cyprinidae, *Gila elegans*), a fish endemic to the Colorado River (USA), regularly experienced massive, seasonal flooding events. Individuals of *G. elegans* display morphological characteristics that may facilitate swimming in high-flow conditions, including a narrow caudal peduncle and a high aspect ratio caudal fin. We tested the hypothesis that these features improve sustained swimming performance in bonytail by comparing locomotor performance in *G. elegans* with that of the closely related roundtail chub (*Gila robusta*) and two non-native species, rainbow trout (*Oncorhynchus mykiss*) and smallmouth bass (*Micropterus dolomieu*), using a Brett-style respirometer and locomotor step-tests. *Gila elegans* had the lowest estimated drag coefficient and the highest sustained swimming speeds relative to the other three species. There were no detectable differences in locomotor energetics during steady swimming among the four species. When challenged by high-velocity water flows, the second native species examined in this study, *G. robusta*, exploited the boundary effects in the flow tank by pitching forward and bracing the pelvic and pectoral fins against the acrylic tank bottom to 'hold station'. Because *G. robusta* can station hold to prevent being swept downstream during high flows and *G. elegans* can maintain swimming speeds greater than those of smallmouth bass and rainbow trout with comparable metabolic costs, we suggest that management agencies could use artificial flooding events to wash non-native competitors downstream and out of the Colorado River habitat.

KEY WORDS: Endemism, Native, Caudal peduncle, *Gila robusta*, Colorado River, Swimming performance

INTRODUCTION

Certain body morphologies are consistently associated with particular habitats and locomotor specializations in teleost fishes. For example, many fishes from still-water habitats are deep-bodied, maneuverability specialists, while fishes that live in high-flow environments are more often streamlined, steady-swimming specialists (Poff and Allan, 1995; Ohlberger et al., 2006; Langerhans, 2008; Langerhans and Reznick, 2010). Because a

streamlined body will minimize pressure drag by reducing the pressure gradient along the body and decrease the turbulent wake behind a swimming animal (Vogel, 1981), a streamlined, or fusiform, body shape can facilitate swimming at high speeds with minimal energetic costs (Lighthill, 1969; Weihs and Webb, 1983; Webb, 1993, 1975; Scarnecchia, 1988; Peterson and Bayley, 1993; Poff and Allan, 1995; Ohlberger et al., 2006). Indeed, the energetic advantage of a streamlined body shape has been demonstrated empirically using both within- and among-species comparisons. When comparing the deep-bodied (higher-drag) common carp (*Cyprinus carpio*) with the streamlined (lower-drag) roach (*Rutilus rutilus*), Ohlberger et al. (2006) found that roach were able to reach higher sustainable speeds at a lower cost of transport. Similarly, when comparing standard metabolic rates of dimorphic crucian carp (*Carassius carassius*), Pettersson and Brönmark (1997) found that the streamlined morphs had lower active metabolic rates than the deeper-bodied morphs.

Metabolic activity has been used to evaluate fitness and locomotor capabilities in fishes that occupy a variety of habitats. Aerobic metabolism, cost of transport (energy needed to travel a given distance) and aerobic scope have all been used to estimate energy usage associated with locomotion (Fry, 1947; Claireaux et al., 2000, 2006; Hvas et al., 2017). Perhaps the most informative measurement of whole-organism energy budgets during locomotion is aerobic scope. This measurement is estimated as the difference between the maximum aerobic active metabolic rate and standard metabolic rate (Fry, 1947). As such, this measurement is a quantification of oxygen available for fitness-related traits during locomotion (Priede, 1985; Claireaux and Lefrancois, 2007). Steady-swimming specialists usually have high aerobic scopes because they are able to maintain continuous aerobic swimming at high speeds (Clark et al., 2013).

Cyprinids from the Lower Colorado River (USA) exhibit specialized morphological features associated with locomotion (Miller, 1946; La Rivers, 1962; Portz and Tyus, 2004). For example, the bonytail, has a high aspect ratio (fin height²/fin area) caudal fin that is attached to the body by a long, shallow caudal peduncle (Moran et al., 2016). This swimming morphology is even more extreme than the swimming adaptations previously documented in other Cyprinids. In fact, features exhibited by *G. elegans* are characteristic of high-performance steady-swimming fishes, most of which are marine, open-water species (Webb, 1984b; Moran et al., 2016). These morphological features, atypical in freshwater fishes, may have enabled the ancestors of *G. elegans* to cope with seasonal flooding in the Colorado River, where flow historically reached velocities from 31 to 200 cm s⁻¹ during summer monsoons and spring snow-melt events (Graf, 1997).

Based on the observation that *G. elegans* exhibit some locomotor morphologies characteristic of high-performance, steady-swimming fishes, we hypothesized that individuals of *G. elegans* would experience reduced drag relative to other species present in the Lower Colorado River Basin. Furthermore, we predicted that the

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streamlined body, in combination with a shallow caudal peduncle and a high aspect ratio tail, would allow individuals of *G. elegans* to maintain high swimming speeds – speeds that enabled their ancestors to maintain position in the Colorado River during historic flooding events. To assess the swimming performance of *G. elegans* relative to that of other native and non-native fish species of the Colorado River, we compared swimming behavior and performance in *G. elegans* with that of a close relative that lives in smaller tributaries of the Colorado River, the roundtail chub (*Gila robusta*), and two non-native fishes that have been introduced to the Lower Colorado River basin within the last 100 years, smallmouth bass (Centrarchidae, *Micropterus dolomieu*) and rainbow trout (Salmonidae, *Oncorhynchus mykiss*). We measured the maximum sustainable swimming speed and oxygen consumption of these four species to test our prediction that axial and tail morphology of *G. elegans* enable individuals of this species to maintain high speeds with low metabolic cost (i.e. a lower cost of transport), relative to another native cyprinid and to two introduced non-native fishes.

MATERIALS AND METHODS

Fish specimens

Gila robusta S. F. Baird & Girard 1853 and *Gila elegans* S. F. Baird & Girard 1853 were hatchery raised at the Aquatic Research and Conservation Center (ARCC) in Cornville, AZ, USA (Arizona Game and Fish Department, AGFD). *Oncorhynchus mykiss* (Walbaum 1792) were collected from hatchery-raised stocks in the Page Springs Trout Hatchery in Cornville, AZ, USA (AGFD). Specimens of *Micropterus dolomieu* Lacépède 1802 were captured by electro-fishing from Clear Creek, AZ, USA. All fishes (5 of each species) were size matched (13.0–16.2 cm standard length; Table 1) and held at ARCC; these holding tanks were maintained at temperatures of 20±1°C. Fishes were fed earthworm flake food (Brine Shrimp Direct, Ogden, UT, USA) once every other day; food was withheld 48 h prior to a swimming trial to reduce the effects of specific dynamic action on metabolic rate. All specimens were captured and maintained according to AGFD protocols.

Morphology

Fineness ratios, theoretical drag coefficients and least caudal peduncle depths were measured and calculated to test the

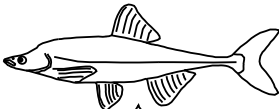
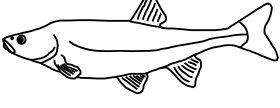
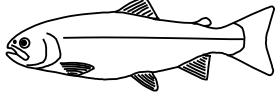

prediction that *G. elegans* have a more streamlined body shape than the other species tested here (Webb, 1975; Fish, 1996). Following Pettersson and Brönmark (1997), we captured still images from video taken of fish swimming at 1.5 body lengths s⁻¹ ($L_B s^{-1}$) during respirometry experiments. Images were scaled to fish length and analyzed using ImageJ (NIH; Abràmoff et al., 2004). From five individuals per species, fish mass, total length, greatest dorsoventral depth, greatest lateral width, fineness ratio (total length/greatest depth), least caudal peduncle depth (dorsoventral depth of the caudal peduncle at the narrowest segment) and drag coefficient were measured and calculated (Table 1). Fineness ratio is a metric commonly used to estimate streamlining, but ratios can vary from 3 to 7 with only a 10% increase in drag (Webb, 1975). Therefore, we also calculated theoretical drag coefficients to better assess the hydrodynamic effects of streamlining because increased drag, the opposing force to forward thrust during swimming, would be a hydrodynamic disadvantage in steady-swimming fishes (Webb, 1975; Pettersson and Brönmark, 1997). To make this calculation, we measured the surface area of one side of the fish from a photo of the lateral aspect of the fish, excluding the paired, dorsal and anal fins (fins were excluded from the lateral surface area because their shapes were variable within and among speeds). Total surface area was calculated as twice the lateral surface area as measured from the photo. Dorsal and ventral surface area were not measured, equating to an underestimate of wetted surface area; however, this technique was used across all species, which provided a consistent approximation of wetted surface area. Assuming a rigid body, theoretical drag D at a given speed was calculated using the equation:

$$D = 1/2\rho \times S \times U^2 \times C_T, \quad (1)$$

where ρ is the density of water (1.0 g cm⁻³), S is the estimated lateral surface area of the fish, U is the velocity and C_T is the drag coefficient (Webb, 1975). C_T is composed of the frictional drag coefficient C_f and the pressure drag coefficient C_p . Because we were interested in the differences in body shape, velocity was 1.0 for all drag coefficient calculations. C_T was calculated using the equation:

$$C_T = C_f \times [1 + 1.5(d/L)^{3/2} + 7(d/L)^3]. \quad (2)$$

Table 1. Morphology and habitat of the fishes used in this study

Species	Illustration	Total length (cm)	Mass (g)	Width (cm)	Depth (cm)	Peduncle depth (cm)	Fineness ratio	Drag coefficient
<i>Gila elegans</i>		15.98±0.15	30.1±1.04	1.72±0.05	3.36±0.05	0.67±0.02 ^a	4.76±0.08 ^a	1.56±0.05 ^a
<i>Gila robusta</i>		16.24±0.12	37.86±1.05	1.88±0.05	3.1±0.04	1.22±0.04 ^b	5.11±0.04 ^b	1.8±0.06 ^b
<i>Oncorhynchus mykiss</i>		15.34±0.31	41.24±1.54	1.84±0.04	3.7±0.02	1.47±0.03 ^d	4.22±0.02 ^c	2.0±0.12 ^b
<i>Micropterus dolomieu</i>		15.6±0.1	44.59±3.07	2.15±0.06	3.56±0.1	1.74±0.09 ^c	4.34±0.18 ^c	1.8±0.04 ^b

Data are means±s.e.m. Lowercase letters indicate statistical significance ($P<0.05$) for examined variables.

The term d is the mean value of maximum width and maximum depth of the fish body and L is the total length of the body. C_f is dependent on the flow regime, which is characterized by the Reynolds number Re , and varies between $1.33Re^{-0.5}$ and $0.072Re^{-0.2}$ for turbulent and laminar flow, respectively. We chose an arbitrary intermediate value to describe C_f :

$$C_f = 0.74 \times Re^{-0.3}, \quad (3)$$

where the Reynolds number is a function of the length (L), velocity (U) and the kinematic viscosity of water (ν , $1.2 \times 10^{-2} \text{ s}^{-1} \text{ cm}^2$) (Webb, 1975):

$$Re = (L \times U)/\nu. \quad (4)$$

Respirometry

Using a Brett-type swimming tunnel respirometer (a closed-system, recirculating flow tunnel with an oxygen electrode), the rate of oxygen consumption (\dot{V}_{O_2}) was measured during swimming step-tests using methods similar to classic studies by Videler (1993) and Rome (1995). The working space for the swim tunnel was $13.5 \times 13.5 \times 50.8 \text{ cm}$. The cross-sectional area of the largest fish used in this study was $<10\%$ of the cross-sectional area of the chamber, so potential blocking effects were not considered (Brett, 1964; Webb, 1971). This tunnel continuously recirculated a total volume of 35 l and the velocity of the water was controlled by a variable-speed pump that drove a propeller. Before the trials were conducted, a flow meter (Marsh McBirney Model 2000, Loveland, CO, USA) was placed in the center of the working space to enable us to calibrate flow speed relative to motor speed.

Prior to each step-test, the respirometer was opened and flushed with oxygenated water to restore oxygen levels to $7.0 \pm 0.3 \text{ mg l}^{-1}$. Following the flushing period, the tunnel was closed so that metabolic rate of oxygen consumption (\dot{M}_{O_2}) could be measured. During the trials, water oxygen concentration (mg l^{-1}) was measured continuously with a YSI 55 oxygen probe (Yellow Springs, OH, USA). Assuming the average density of fish is equal to that of water, the mass-specific \dot{M}_{O_2} at each speed was calculated using the equation:

$$\dot{M}_{O_2} = R[(V_{\text{flume}} - V_{\text{fish}})/M], \quad (5)$$

where R is the change in water oxygen concentration over time, V_{flume} is the flume volume in liters, V_{fish} is the volume displaced by the fish and M is the body mass of the fish (Kendall et al., 2007).

Five individuals of each species were used in the swimming step-tests. Each fish acclimated to the flow tunnel while swimming at a speed of $1.0 L_B \text{ s}^{-1}$ for 30 min. After 30 min, step-tests began at increments of $0.5 L_B \text{ s}^{-1}$. Swimming speed intervals lasted 15 min, during which \dot{M}_{O_2} measurements were recorded from the middle 10 min of the session. Temperature was maintained at $20 \pm 1^\circ \text{C}$ during swimming trials. Step-tests continued until continuous swimming was no longer maintained, following methods outlined in Sepulveda and Dickson (2000). The speed at which fish could no longer maintain a steady swimming behavior (U_{max}), resorting to a burst-and-glide gait, suggests that this is the point at which fish begin to recruit anaerobic muscle fibers (Videler, 1993; Rome, 1995).

To test the hypothesis that *G. elegans* is able to swim faster with less metabolic output than the other species tested here, we measured metabolic rate and maximum sustainable swimming speed (U_{max}) and made estimates of net cost of transport (COT_{Net}), standard metabolic rate (SMR) and aerobic scope. Metabolic rate

was calculated as $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$. U_{max} was defined as the highest speed at which the fish was able to continuously swim without resorting to the burst-and-glide mode of locomotion (Rome, 1995). COT_{Net} was calculated from the slope of the linear regression of mass-specific metabolic rate and swimming speed in m h^{-1} ($\text{mg O}_2 \text{ kg}^{-1} \text{ m}^{-1}$) (Bennett, 1985; Sepulveda and Dickson, 2000). Individual slope units were converted to $\text{J kg}^{-1} \text{ m}^{-1}$ by multiplying by the oxycaloric constant of $13.54 \text{ J mg}^{-1} \text{ O}_2$. The y -intercept for the regression lines of metabolic rate and speed was used as an estimate of SMR (Fry and Hochachka, 1970; Sepulveda and Dickson, 2000). Aerobic scope was calculated as the difference between maximum aerobic metabolic rate and SMR.

Behavior and kinematics

High-speed video recorded at $600 \text{ frames s}^{-1}$ was analyzed to test the hypothesis that swimming kinematics are different among the four species examined here. Orientation angle [angle of the body relative to horizontal (0 deg)], tail beat amplitude (distance the caudal fin moved during one tail beat), tail beat frequency (number of tail beats per second) and yaw (lateral displacement of the head) were measured for every speed during sustained swimming. Using ImageJ, all linear measurements taken during the trials were scaled to fish length to generate size-independent performance parameters (e.g. tail beat frequency in $L \text{ s}^{-1}$). Measurements of fin and head movements were made for five complete fin beat cycles and averaged for a given speed.

Statistical analysis

Prior to statistical analyses, the data collected during the swimming trials were examined for outliers and violations of the assumptions of ANOVA. Log-transformed data were used for the analysis of metabolic rate, tail beat amplitude and yaw because log-transformed data for these variables fitted the assumptions of normality and homogeneity of variances, while untransformed data did not. The statistical alpha level was 0.05 in all tests and SPSS (v. 21) was used to conduct all statistical analyses. Raw data are available from the corresponding author on request.

One-way ANOVAs were used to compare morphological variables, U_{max} and COT_{Net} among species. Mixed-model ANOVAs were used to evaluate metabolic rate, tail beat amplitude, tail beat frequency, yaw and orientation angle for potential main effects of speed and species, as well as the potential interaction between speed and species. A balanced design is required for this analysis, so only data for the first four speed intervals were analyzed in the ANOVAs. Under circumstances where the assumption of sphericity (as determined by Mauchly's test of sphericity) was violated, Greenhouse–Geisser results were used to determine significance. Following a significant ANOVA result, LSD *post hoc* tests were conducted to determine which speeds or species were different from one another, as appropriate.

RESULTS

Morphology

Body fineness ratio differed among the species tested here. *Gila robusta* had the greatest fineness ratio ($P < 0.05$) followed by *G. elegans* ($P < 0.05$). Fineness ratios between *O. mykiss* and *M. dolomieu* did not differ. Theoretical hydrodynamic drag differed among the species tested here; *G. elegans* had the lowest drag coefficient ($P < 0.05$) but values were not different among the other three species. Least caudal peduncle depth differed among all species, with *G. elegans* having the narrowest peduncle and *M. dolomieu* having the deepest peduncle (Table 2).

Table 2. ANOVA statistics for morphological, kinematic and metabolic data with accompanying least significant difference (LSD) *post hoc* analyses

Model	Dependent variable	d.f.	F-statistic	P-value	LSD
One-way ANOVA					
	Fineness ratio	3,16	30.55	<0.001	e<r<m=d
	Drag	3,16	6.455	0.0045	e<r=m=d
	Peduncle depth	3,16	64.666	<0.001	e<r<m<d
	COT _{Net}	3,16	0.288	0.833	
	SMR	3,16	0.386	0.765	
	U _{max}	3,16	28.318	<0.001	e>m>d>r
	Aerobic scope	3,16	3.265	<0.05	e>d
Mixed-model ANOVA					
	Metabolic rate				
	Species	3,16	2.006	0.154	
	Speed	3,48	33.731	<0.001	1<2<3<4
	Orientation angle				
	Species	3,16	23.14	<0.001	e=d<r<m
	Speed	4,48	36.154	0.001	2=3=1(1>4)
	Tail beat amplitude				
	Species	3,16	8.915	0.001	d<(e<r)=m
	Speed	1.8,28.8	9.142	0.001	1=2<3=4
	Tail beat frequency				
	Species	3,16	0.631	0.606	
	Speed	3,48	<0.001	25.874	1<2<3<4
	Species×speed	9.48	0.005	3.137	*
	Yaw				
	Species	3,16	8.026	0.002	d<e=r=m
	Speed	3,48	13.967	<0.001	1<2<3<4

e, *G. elegans*; r, *Gila robusta*; m, *O. mykiss*; d, *M. dolomieu*. COT_{Net}, net cost of transport; SMR, standard metabolic rate; U_{max}, maximum sustainable swimming speed.

*Interaction term comparisons: *G. robusta*: 1=2, 1<3=4, 2<4; *O. mykiss*: 1=2=3, 1=2<4; *M. dolomieu*: 1<2=3=4.

Respirometry

There was no significant interaction between speed and species and no main effect for species when considering the log of metabolic rate during steady swimming (mixed-model ANOVA). However, there was a significant main effect of speed. Metabolic rate of all four species consistently increased with increasing swimming speed (Table 2, Fig. 1, Table 3). COT_{Net} and estimates of SMR did not

differ among species; however, *G. elegans* had a higher aerobic scope than *M. dolomieu* (Table 2, Fig. 2).

All species voluntarily swam in the center of the working area of the flow tank and did not gravitate toward the bottom or sides of the flow tank, with one exception: *G. robusta* at the highest speed interval. At the highest flow speeds (>2.5 L_B s⁻¹), *G. robusta* individuals would flatten their paired fins on the bottom of the swim tunnel. Once their pectoral and pelvic fins were positioned against the bottom of the swim tunnel, fish would re-orient their bodies to an angle of ~20–30 deg relative to the bottom of the flow tunnel. This station-holding behavior was associated with a decrease in metabolic rate for *G. robusta* (Fig. 3).

Wild fish have been shown to perform better at higher speeds relative to hatchery-reared fish in some previous studies (e.g. McDonald et al., 1998); therefore, one potentially confounding variable in our study was the fact that we used three hatchery-raised fish species and one wild-caught species. However, the wild-caught *M. dolomieu* sustained comparable swimming speeds with similar metabolic rates to those of some of the hatchery-raised fish. This suggests that the one wild-caught species included in this study did not have a performance or metabolic advantage over the three species of hatchery-reared fish.

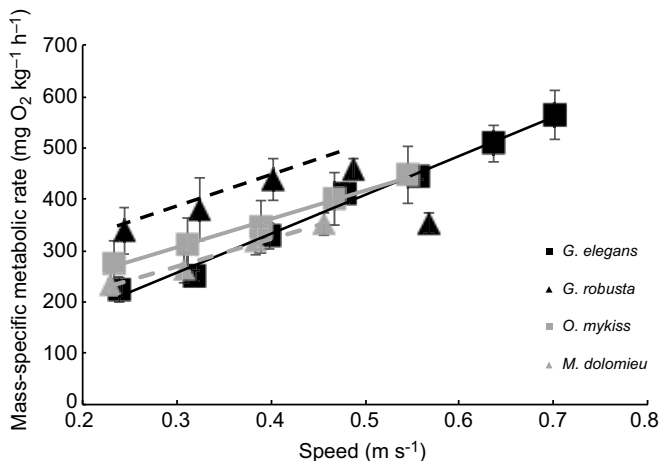


Fig. 1. Metabolic rate of the study species. Metabolic rate increased with increasing speed but there were no differences among species. The mixed-model ANOVA was conducted on log-transformed data for the first four speed intervals. Black symbols and lines denote native fish species (*Gila elegans* and *Gila robusta*) while gray symbols and lines denote non-native fish species (*Oncorhynchus mykiss* and *Micropterus dolomieu*). Squares represent mainstem Colorado River fishes while triangles represent fishes from Colorado River tributaries. No significant differences among species were detected; however, metabolic rate increased significantly with speed ($P<0.01$) ($n=5$ /species). Data are means±s.e.m. Regression statistics are listed in Table 3.

Table 3. Equations and associated error measurements for regression lines in Fig. 1

Species	Regression equation	Slope s.e.m.	y-intercept s.e.m.	R ²	P-value
<i>G. elegans</i>	$y=6.116x+95.338$	1.274	66.234	0.99	<0.001
<i>G. robusta</i>	$y=5.926x+193.643^*$	1.109	78.877	0.99	0.015
<i>O. mykiss</i>	$y=5.678x+135.607$	0.643	47.889	0.97	<0.001
<i>M. dolomieu</i>	$y=4.639x+129.834$	1.664	65.625	0.96	0.006

*Regression line did not include the last data point for *G. robusta* on Fig. 1.

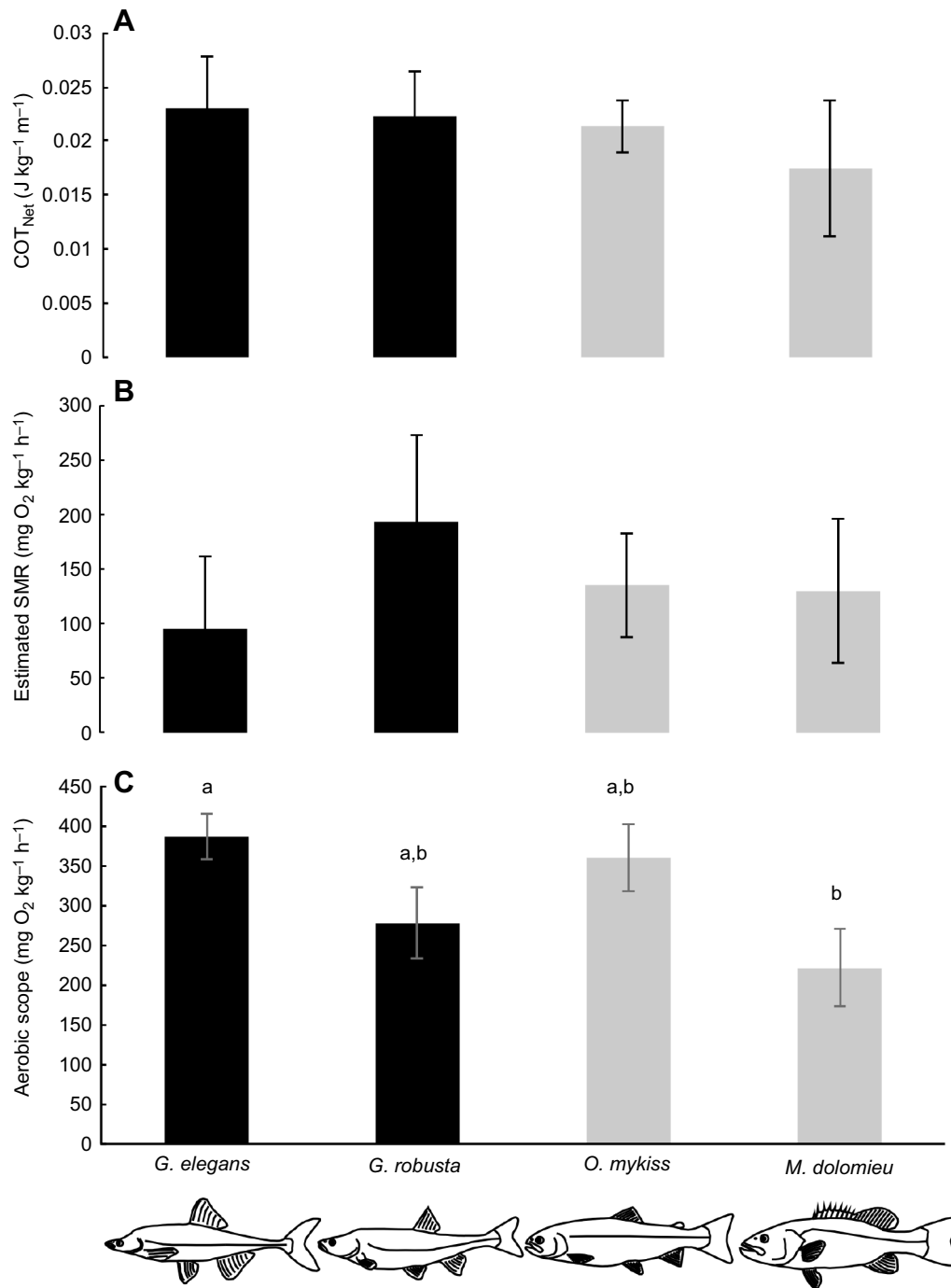


Fig. 2. Net cost of transport (COT_{Net}), standard metabolic rate (SMR) and aerobic scope of the studied species. All species had the same COT_{Net} (A) and estimated SMR (B); however, aerobic scope (C) was greater in *G. elegans* than in *M. dolomieu* ($P < 0.05$). Black bars denote native fish species while gray bars denote non-native fish species. Data are means \pm s.e.m. ($n=5$ /species). Significant ANOVA results are denoted by lowercase letters and summarized in Table 2.

Kinematics

Maximum sustainable swimming speeds (U_{max}) differed among all four species considered here (Table 2, Fig. 4). There was no significant speed \times species interaction term when considering orientation angle during steady swimming (mixed-model ANOVA); however, there were significant speed and species main effects. A *post hoc* test revealed that speed one and speed four were statistically different from one another; high positive orientation angles were more common at speed one, whereas orientation angles approaching zero (0 deg) were more common at speed four. *Post hoc*

analysis of the main species suggests that *G. robusta* and *O. mykiss* consistently used greater (more positive) orientation angles relative to *G. elegans* and *M. dolomieu*, which had orientation angles closer to zero (Fig. 5A).

There was no significant speed \times species interaction term when considering tail beat amplitude and yaw during steady swimming (mixed-model ANOVA). These kinematic variables demonstrated significant speed effects and increased with increasing swimming speed. Species and speed main effects were detected for both amplitude and yaw, with both measurements increasing with

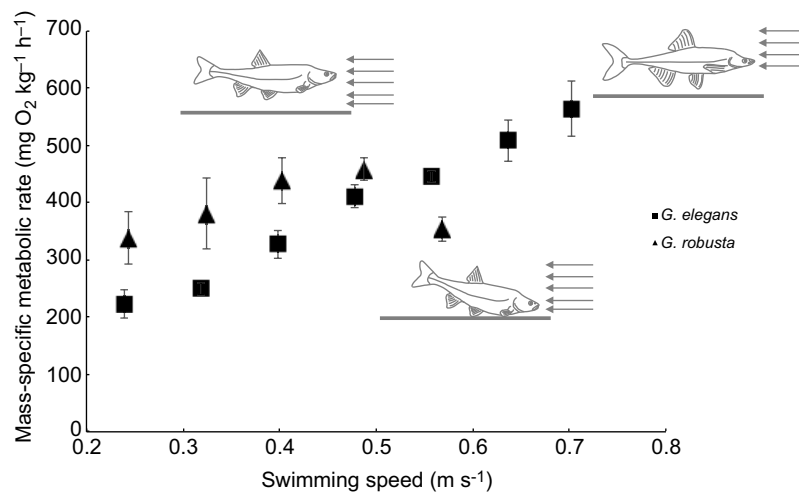


Fig. 3. Orientation angle. *Gila robusta* change orientation angle when flow velocity exceeds 0.4 m s^{-1} ($2.5 L_b \text{ s}^{-1}$, where L_b is body lengths). As a result, metabolic rate depression occurs at this speed. For comparison, the closely related *G. elegans* is included, which does not change its orientation angle during swimming. In addition to changing the orientation angle, *G. robusta* also uses the pectoral fins and pelvic fins to contact the bottom of the flow chamber and station hold. Data are means \pm s.e.m. ($n=5/\text{species}$).

increasing speed. Generally, *M. dolomieu* had the smallest average tail beat amplitude and yaw while *O. mykiss* had the greatest tail beat amplitude and yaw (Table 2, Fig. 5B,D). A significant interaction term was detected for tail beat frequency with a significant speed effect and a non-significant species effect. The significant interaction term was created by the unchanging fin beat frequency of *G. elegans* over the tested speeds and the increasing fin beat frequency for the other three species tested here (Table 2, Fig. 5C).

DISCUSSION

Gila elegans, a native Colorado River (USA) species, was able to sustain the highest maximum swimming speed (U_{max}) relative to the other three species examined in this study. Given the differences in sustained swimming performance and the overall similarities across species in swimming movements (kinematics) and physiology (respiration), how are *G. elegans* able to reach higher sustainable swimming speeds using similar amounts of energy? Differences in swimming ability may be attributed to the unusual morphology of *G. elegans*. A previous study (Moran et al., 2016) reported that *G. elegans* has morphological features similar to those of

high-performance swimmers from the marine environment. A shallow caudal peduncle, high body fineness ratio (approaching the optimal value of 4.5; Von Mises, 1945), low theoretical drag and a high aspect ratio caudal fin are features also exhibited by tunas, many shark species, cetaceans and even extinct swimming reptiles – all of these organisms are thought to be specialized for high-performance, sustained swimming (Webb, 1984a,b; Webb et al., 1984; Pettersson and Hedenström, 2000; Chapman et al., 2015; Baktoft et al., 2016). Additionally, the higher aerobic scope observed in *G. elegans* may allow this species to maintain higher aerobic swimming speeds than the other species tested here. *Gila elegans* tended to have a greater aerobic capacity than the closely related *G. robusta* and the introduced salmonid *O. mykiss*, although the difference was only significant for *M. dolomieu*. Aerobic scope can be an indication of the ability of an organism to cope with a given environment (Fry, 1947; Hvas et al., 2017). Not surprisingly, of the fishes sampled here, aerobic scope was greatest in those that can be found in the mainstem Colorado River, which requires a high capacity for aerobic steady swimming.

It appears that *G. elegans* locomotor behaviors and morphologies are modifications for life in the complex habitats of the Lower

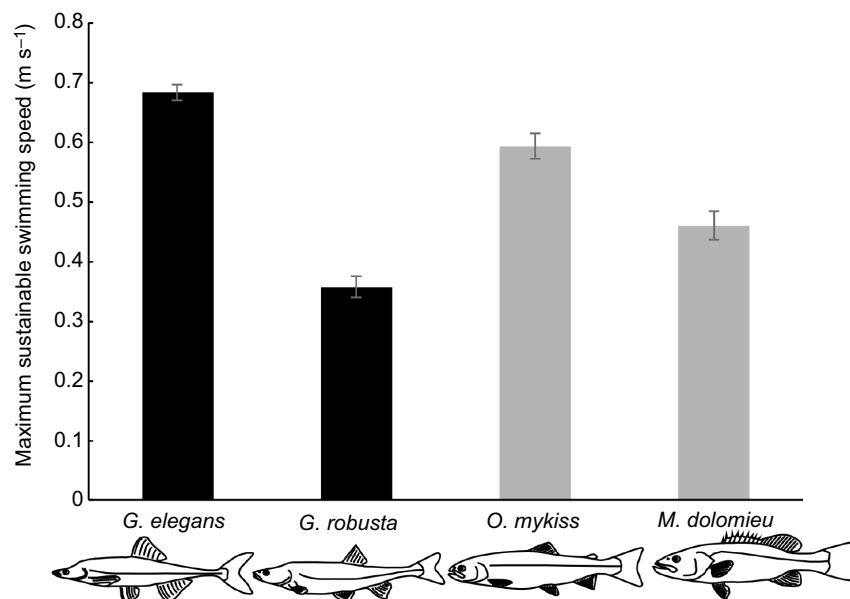


Fig. 4. Maximum sustainable swimming speed (U_{max}). *Gila elegans* had the highest U_{max} while the native *G. robusta* had the lowest U_{max} of the species tested here. There was a significant difference among all species (ANOVA, $P<0.05$, $n=5/\text{species}$). Black bars denote native species while gray bars denote non-native species. Data are means \pm s.e.m. Statistics are summarized in Table 2.

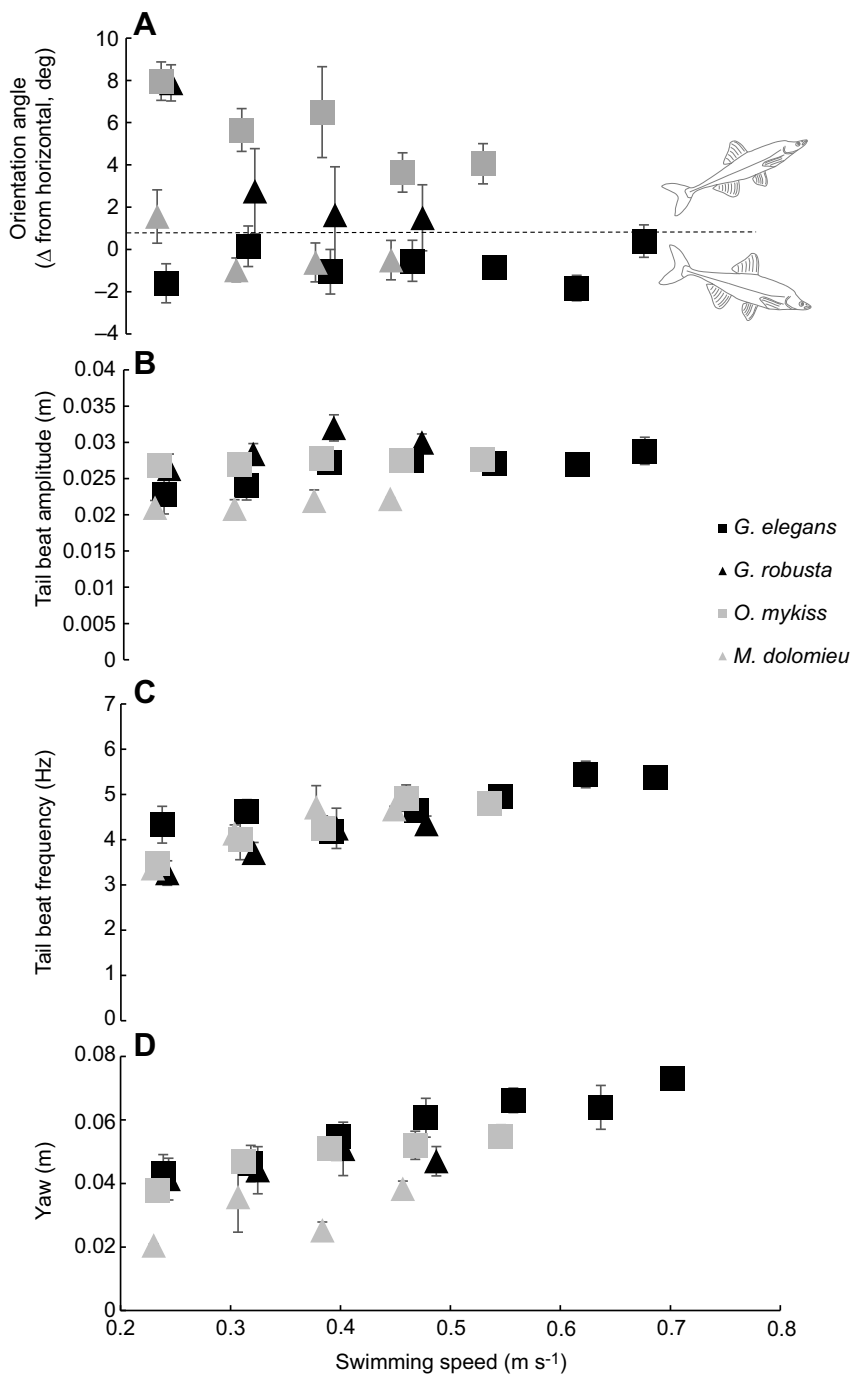


Fig. 5. Swimming kinematics. Swimming kinematics varied among species across speeds. (A) Change in orientation angle relative to horizontal (0 deg) across steady swimming speeds. (B) Tail beat displacement during one beat of the tail across steady swimming speeds. Statistics for tail beat amplitude were conducted on log-transformed data. (C) Frequency of the tail beat across steady swimming speeds. (D) Yaw (lateral displacement of the head during one tail beat) across steady swimming speeds. Statistics for yaw were conducted on log-transformed data. Black symbols denote native fish species while gray symbols denote non-native fish species. Squares represent mainstem Colorado River fishes while triangles represent fishes from Colorado River tributaries. Data are means \pm s.e.m. ($n=5$ /species). ANOVA statistics are summarized in Table 2.

Colorado River. Previous work documented similarities in locomotor morphologies between *G. elegans* and a high-performance swimmer from the marine environment, *Scomber japonicus* (Moran et al., 2016). When our data are compared with those for similarly sized *S. japonicus* reported by Donley and Dickson (2000), *G. elegans* has similar tail beat frequencies and amplitudes at matching swimming speeds. This result supports the findings of Bejan and Marden (2006), who documented a fundamental size dependence of kinematic variables during locomotion for flying, swimming and walking animals. However, despite similarities in tail movements, the role of the anterior body can vary among swimming fishes of different species. This becomes evident when waveforms on the body are measured for a swimming

fish. Donley and Dickson (2000) reported mean propulsive wavelengths of $\sim 120\%$ of total length for 16 cm *S. japonicus*, while *G. elegans* of the same size demonstrate a mean propulsive wavelength of 92% of total length ($n=5$) (C.J.M., personal observation), which suggests that the body of *G. elegans* bends more during locomotion than that of *S. japonicus*. In comparisons of anguilliform locomotion in swimming lamprey (*Ichthyomyzon unicuspis*) with carangiform locomotion in mackerel (*Scomber scombrus*), Tytell et al. (2010) found that anguilliform locomotion is more efficient at low speeds than carangiform locomotion. However, mackerel (carangiform swimmers) can reach higher speeds and are more efficient when swimming at higher speeds, relative to lamprey (anguilliform swimmers). The complex habitats

of the Lower Colorado River are primarily made up of pools (slow-moving deep water) and runs (swift, turbulent, shallow water). Locomotor morphologies and behaviors of *G. elegans* may allow for their success in both low- and high-flow environments.

Variation in body orientation among species raises the question, what are the consequences of a positive orientation angle during steady swimming? Negatively and neutrally buoyant fishes may tilt their body axis dorsally away from the substrate to compensate for negative or reduced lift at low speeds (Von Mises, 1945; Hoerner and Borst, 1975; Webb, 1993). Although it may enhance the production of lift, Webb (1993) predicted that tilting the body would increase pressure drag, and suggested that the propulsors must beat more rapidly in compensation to maintain forward thrust. However, despite a significant positive body tilt in *O. mykiss* and *G. robusta*, there were no differences in tail beat frequencies among species. COT_{Net} data for *G. robusta* and *O. mykiss* tended to be higher, but were not consistently greater, than those for the other two species considered here. Similar to Webb's (1993) studies of *O. mykiss*, we also observed a reduction in body tilting as speed increased. As flow speed increases, so does lift produced by the body (Webb, 1993). Consequently, adopting a horizontal orientation angle at high speeds likely compensates for reduced lift (relative to the lift produced at high speeds) in negatively or neutrally buoyant fishes. However, *G. elegans* maintained an approximately horizontal orientation at all speeds, which suggests that a tilting behavior is not required to produce sufficient lift to maintain forward thrust in this species. Colorado River fishes of the genus *Gila* have the greatest depth between the pectoral and pelvic fins. The forward location of the greatest depth acts like the wing of an aircraft to generate positive lift (Portz and Tyus, 2004). This could explain the lack of a positive orientation angle for *G. elegans* to generate lift. In addition, orientation angle does not appear to directly influence other aspects of steady swimming kinematics. For example, *O. mykiss* adopted a high orientation angle at low speeds, while *G. elegans* adopted one close to horizontal, but the two species did not differ in tail beat amplitude, yaw or metabolic rate.

Gila robusta used positive or near-horizontal orientation angles at low swimming speeds; however, individuals of *G. robusta* adopted negative body tilt at the highest speed (Fig. 5), which enabled them to station hold in high-velocity flows. Even though individuals of *G. robusta* ceased steady caudal fin-based locomotion at swimming velocities of $>2.5 L_B s^{-1}$, they could maintain their position in water flows $>5 L_B s^{-1}$ ($\sim 80 \text{ cm s}^{-1}$; C.J.M., personal observation) by using the paired fins and re-orienting the body relative to the substrate. Individuals of *G. robusta* not only maintained their position against high flow speeds but also lowered their metabolic rate by adopting this posture. This may be due in part to the reduced flow speeds near the substrate resulting from boundary layer effects (Bell and Terhune, 1970). Considering the smooth texture of the acrylic base of the working section of the flow tunnel, individuals of *G. robusta* may be able to withstand even higher flow speeds in the wild while holding onto rugged surfaces, such as rock faces or gravel bottoms. While this response to high flows has been described before in other species (see Brett, 1967; Webb et al., 1996; Adams et al., 1997; Peake and McKinley, 1998; Adams et al., 1999; Ward et al., 2003), we propose that the behavior serves a specific purpose in fishes native to Southwestern USA: it may allow individuals to resist being washed downstream during the flash flooding that occurs seasonally (Minckley and Meffe, 1987; Schultz et al., 2003).

Given that the native fishes of the American Southwest can behaviorally and physiologically cope with high flows, the

manipulation of flow regimes might help recover these rare and imperiled species in the Colorado River. Both a high sustainable swimming speed and station-holding ability would be beneficial in the historical conditions of the Southwestern USA, where seasonal flooding events generated extremely high river flows in the Colorado River before the installation of dams. Additionally, as seen in *G. elegans*, a high aerobic scope would allow this native species to outperform some of the non-native species in the Colorado River system. However, this method of non-native fish removal would likely not work against the non-native salmonids, which have proved to be well adapted to a life in flow, with high aerobic scopes and high proportions of aerobic axial musculature (Hudson, 1973; Hvas et al., 2017). During historical flooding events, flow in some stretches of the river exceeded 200 cm s^{-1} . However, modern water velocities average between 30 and 50 cm s^{-1} in many areas (just below the Glen Canyon Dam; Graf, 1999; Mueller and Marsh, 2002), which is only 25% of historic flows. Because native species are modified for these intermittent high flows, flow-regime alteration (a removal or reduction of this selective pressure) can allow for the proliferation of non-native species (Cucherousset and Olden, 2011). Correspondingly, anthropogenic modification of flows to mimic more natural conditions may enable native fishes to regain dominance over non-native fishes in regions downstream of engineered flooding events (Schmidt et al., 1998; Pool et al., 2010; Kiernan et al., 2012; Olden et al., 2014). Indeed, Ward et al. (2003) found that when flooding conditions were recreated in the lab, native fishes could cope with the rapidly changing conditions by using their mouths (in the case of the suckers from the Catastomidae) or pectoral fins to adhere to the substrate, while non-native fishes could not. If the Colorado River and its tributaries are manipulated to produce large, periodic, flooding events, native fishes may be retained, while the non-native, invasive species are washed downstream. This type of flow regime might facilitate the recovery of the unique native fish fauna of Southwestern USA aquatic habitats, including *G. elegans* and *G. robusta*, without expensive and time-consuming manual removal of non-native fish species.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: C.J.M., S.P.G., M.W.O., A.C.G.; Methodology: C.J.M., M.W.O.; Formal analysis: C.J.M., C.L.R., A.C.G.; Investigation: A.C.G.; Resources: M.W.O., A.C.G.; Writing - original draft: C.J.M.; Writing - review & editing: C.J.M., S.P.G., M.W.O., A.C.G.; Supervision: C.J.M., A.C.G.; Project administration: C.J.M.

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