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Size-related effects and the influence of metabolic traits and morphology on swimming performance in fish

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Abstract

Energy metabolism fuels swimming and other biological processes. We compared the swimming performance and energy metabolism within and across eight freshwater fish species. Using swim tunnel respirometers, we measured the standard metabolic rate (SMR) and maximum metabolic rate (MMR) and calculated the critical swimming speed (U_{crit}). We accounted for body size, metabolic traits, and some morphometric ratios in an effort to understand the extent and underlying causes of variation. Body mass was largely the best predictor of swimming capacity and metabolic traits within species. Moreover, we found that predictive models using total length or SMR, in addition to body mass, significantly increased the explained variation of U_{crit} and MMR in certain fish species. These predictive models also underlined that, once body mass has been accounted for, U_{crit} can be independently affected by total length or MMR. This study exemplifies the utility of multiple regression models to assess within-species variability. At interspecific level, our results showed that variation in U_{crit} can partly be explained by the variation in the interrelated traits of MMR, fineness, and muscle ratios. Among the species studied, bleak *Alburnus alburnus* performed best in terms of swimming performance and efficiency. By contrast, pumpkinseed *Lepomis gibbosus* showed very poor swimming performance, but attained lower mass-specific cost of transport (MCOT) than some rheophilic species, possibly reflecting a cost reduction strategy to compensate for hydrodynamic disadvantages. In conclusion, this study provides insight into the key factors influencing the swimming performance of fish at both intra- and interspecific levels.

Key words: body size, maximal metabolic rate, morphology, swimming efficiency

Swimming activity and other biological processes are fueled by energy metabolism (White et al. 2019) and, therefore, the energy budget of species plays a key role in many interactions with the physiology and ecology of organisms (Killen et al. 2010; Pang et al. 2019). The critical swimming speed test is the most common method for evaluating prolonged swimming performance (Kolok 1999). Critical swimming speed (U_{crit}) is defined as the highest swimming speed that a fish can maintain for a time period (Brett 1964). Although fish can rely on anaerobic metabolism while reaching U_{crit}, swimming is largely fueled by aerobic metabolism (Videler 1993; Hammer 1995). Two important metabolic traits describe the bounds of a fish's respiratory capacity: maximal metabolic rate (MMR), which is defined as the maximum rate of aerobic metabolism during swimming exercise (Nelson 2016; Norin and Clark

2016), and standard metabolic rate (SMR), which is the baseline energy required for maintenance measured in a post-absorptive, resting state (Chabot et al. 2016).

Body size is an important factor influencing the swimming capacity and energy metabolism of fish (Beamish 1978), and thus its effects must be accounted for before examining the variation of many traits. After accounting for body size effects, the swimming performance and metabolism of fish can vary remarkably; from inter-individual variability within species to differences among the diversity of taxonomic groups (Pettersen et al. 2018). Several studies have shown that metabolic rates such as SMR and MMR can vary two- to three-fold across individuals of the same body mass (e.g., Burton et al. 2011; Metcalfe et al. 2016), while Fisher et al. (2005) found up to 28% coefficient of variation in U_{crit} within the same species. On the other hand, because of the enormous diversity of fish species with different ecological lifestyles and behaviors, variations in metabolic rates and swimming capabilities across species are assumed to be much greater, for example, up to 40-fold difference observed by Killen et al. (2016). In general, species with a "fast" lifestyle often have higher metabolic rates and dispersal capacities than species with a "slow" lifestyle (Killen et al. 2010; Stoffels 2015; Killen et al. 2017; Pang et al. 2019).

The association between metabolic traits and how these are related to other aspects (e.g., morphology, behavior, and ecological correlates) have attracted interest in active areas of research in ecological and evolutionary physiology. While a mechanistic link between SMR and MMR has been observed in fish (Norin and Malte 2012; Killen 2014; Zhang et al. 2014), the causes of this link are still unclear. Nevertheless, there is compelling evidence that the consequences resulting from the covariation of these traits affect biological processes such as survival, growth, predation, and reproductive output (Killen et al. 2007; Burton et al. 2011; Auer et al. 2015). Additionally, MMR (and to a lesser extent SMR) has been positively associated with U_{crit} at both intra- and interspecific levels (Binning et al. 2015; Yan et al. 2013; Pang et al. 2015), thus suggesting that these traits are not entirely independent from one another. Previously, Bennett and Ruben (1979) proposed the aerobic capacity model in endotherms. Here, the authors speculated that an increased locomotor performance favors the evolution of costly physiological traits. More recently, this hypothesis has been tested in ectotherms and suggests that selection for a high aerobic capacity to maintain intense and sustained activity is functionally supported by an increase in metabolic costs of maintenance, thereby increasing SMR (Killen et al. 2016; Pang et al. 2019). Due to their high diversity, teleost fish constitute an excellent group with which to investigate phenotypic variation in performance traits. As such, exploring the interrelationships between swimming capacity, metabolic and morphological traits may provide new insights into the mechanisms by which the locomotor performance of fish is supported.

Among the morphological traits that can affect swimming capabilities, some of the best predictors are likely to be fineness ratio (Webb 1975; Scarnecchia 1988; Ohlberger et al. 2006; Walker et al. 2013; Rubio-Gracia et al. 2020), caudal peduncle depth factor, propulsive ratio, and muscle ratio (Fisher et al. 2000; Fisher and Hogan 2007; Nanami 2007). Swimming capacity is generally enhanced with a streamlined body shape, a shallow caudal region, and an elevated proportion of muscle fibers (Webb 1984; Ohlberger et al. 2006; Nanami 2007; Domenici et al. 2008). Moreover, morphological features can influence swimming efficiency because energetic costs depend on drag forces and propulsion (Webb 1984; Videler 1993). It has been shown that streamlined bodies tend to maximize

thrust and minimize drag and recoil energy losses (Webb 1975; Ohlberger et al. 2006; Langerhans 2009; Langerhans and Reznick 2010). Therefore, to facilitate the understanding of swimming performance and the energetic costs of species, morphological traits must be taken into consideration.

Here, we compared eight freshwater fish species that present marked differences in body size and morphological traits. The species tested were bleak *Alburnus alburnus* (Linnaeus 1758), Catalan chub *Squalius laietanus* Doadrio, Kottelat, and de Sostoa 2007, Mediterranean barbel *Barbus meridionalis* Risso 1827, minnow *Phoxinus septimaniae* Kottelat 2007, roach *Rutilus rutilus* (Linnaeus 1758), pumpkinseed *Lepomis gibbosus* (Linnaeus 1758), Spanish toothcarp *Aphanius iberus* (Valenciennes 1846), and the eastern mosquitofish *Gambusia holbrooki* Girard 1859. The main objectives of this study were to: 1) examine intra- and interspecific variation in swimming performance and energy metabolism after accounting for body size and 2) investigate to what extent interspecific variation in swimming performance is explained by a suite of morphological and physiological traits.

Material and Methods

Experimental fish and holding conditions

A total of 8 species were collected between 2014 and 2017. The samples of bleak ($N = 17$), Catalan chub (chub, hereafter) ($N = 12$), roach ($N = 14$), and pumpkinseed ($N = 17$) were caught from the Muga River (42°16′30.5″ N 3°02′38.8″ E). The sample of Mediterranean barbel (barbel, hereafter) ($N = 16$) was caught from the Fluvià River (42°21′75″ N 2°57′42″ E), and the sample of minnow ($N = 21$) was caught from the Brugent River (42°00′09.3″ N 2°36′28.4″ E), a tributary of the Ter River. The different rivers were selected because the differences in the distribution ranges of the species made it difficult to collect a sufficient number of individuals from the same stream. Nonetheless, the sampling reaches were similar in terms of hydrological conditions and the specific habitat characteristics were assumed to have a negligible influence on swimming performance. In the field, fish sampling was conducted by trained personnel using electrofishing techniques. Spanish toothcarp (toothcarp, hereafter) individuals were originally collected from La Rubina salt marshes in the Alt Empordà, north-eastern Iberian Peninsula (42°15′38.7″ N, 3°8′38.9″ E) in 2012. The sample of toothcarp ($N = 41$) used for this study represents the fifth generation raised in captive conditions at the University of Girona. Data on swimming capacity and metabolism for mosquitofish were obtained from our previous study (Srean et al. 2017). In total, 60 mosquitofish were originally collected from the Ter Vell lagoon in L'Estartit (42°02′44″ N 3°11′41″ E) in 2014 using dip nets (1-mm mesh size).

Upon arrival at the University of Girona, cyprinids and pumpkinseed were initially held in 200 L rectangular tanks, whereas toothcarp and mosquitofish were initially held in 90 L rectangular tanks. Tanks were supplied with recirculated, filtered freshwater (particle filtered and ozone sterilized) and vigorous aeration. Water changes (ca. 30% of the total volume) were conducted twice a week in each tank to assist with maintaining water quality. During the holding period, the water temperature was set to $20 \pm 1°C$ for cyprinids, pumpkinseed, and toothcarp, whereas the temperature was $25 \pm 1°C$ for mosquitofish (Srean et al. 2017). A natural photoperiod cycle was used during the acclimation period. Fish were fed every day with frozen bloodworms (*Chironomus* sp.) using a meal size of approximately 1.5–2% of their body mass. This amount of food was enough to maintain the body condition of fish throughout

the experiment, but was still below satiation levels. To avoid post-prandial metabolism, fish were subjected to a fasting period of at least 24 h prior to the experiments (Secor 2009). No mortalities occurred during the holding period and visually all fish remained in good health. Experiments were always conducted between autumn and early spring to avoid the breeding seasons of the species. In accordance with the regional legislation (Law 42/2007, Spanish Government), alien species (roach, bleak, minnow, pumpkinseed, and mosquitofish) were euthanized after the experiments had taken place following a standardized protocol using concentrated MS222 in an aerated-water holding tank. Native species, on the other hand, were released at the same place they were captured. The experiments in this study were conducted in compliance with the Autonomous Government of Catalonia (Expedient PNAE 2017PNA TAAEAUT075) and the Commission of Animal Experimentation (Ref. CEA-OH/9673/1) guidelines.

Respirometer set-up

Swimming speeds and rates of oxygen consumption by 8 freshwater fish species were obtained using two Blazka-style swim tunnel respirometers (Loligo® Systems, Viborg, Denmark). Both swim tunnels have a compact design that allows fish enough space for "free" swimming and an adequate volume for reliable oxygen consumption measurements. Flow inside the respirometer was made rectilinear by a honeycomb plastic screen situated at the entrance of the swimming section. The continuous laminar flow was generated by a propeller connected to the motor outside of the respirometers. Swim tunnels were connected to an optical fiber instrument (Witrox 1; Loligo® Systems, Tjele, Denmark) that allowed us to record dissolved oxygen concentration mg·l^{-1} at 1 Hz. A temperature probe (Pt1000 temperature sensor; Witrox 1; Loligo® Systems) was also used for the automated compensation of oxygen data to changes in temperature and barometric pressure in real time. Rates of oxygen consumption were measured using computerized, intermittent-flow respirometry. Swim tunnel respirometers were periodically flushed with aerated water for 2 min followed by a 1-min closed mixing period and then 20 min of closed respirometry.

A large swim tunnel respirometer was used for cyprinids and pumpkinseed (range of standard length, SL$=3.7 - 15.2$ cm). The respirometer consisted of a rectangular measuring recirculation system equipped with a 5-L swimming chamber (30 cm length$\times$7.5 cm height$\times$7.5 cm width). The external water bath connected to the respirometer (25 L) was equipped with an automated Eheim pump that constantly flushed aerated water at a rate of 10 l min^{-1}. Thus, we ensured the complete mixing of the respirometer water between flush cycles. We additionally connected the external water bath of the swim tunnel to a plastic supply tank containing 300 L of air-saturated freshwater. An automated Eheim pump continuously provided freshwater from the supply tank to the external water bath and then water was recirculated again through a decantation system. The supply tank was equipped with an automated liquid cooler (85 W, 972.46 BTU/h, J.P. Selecta®) to maintain the temperature at 20°C.

A small swim tunnel respirometer was used for toothcarp and mosquitofish (range SL$=1.2 - 3.6$ cm). The respirometer consisted of a 170-mL tubular swimming chamber (100 mm length$\times$26.4 mm internal diameter) immersed in an external water bath containing 25 L of clean, aerated water. The respirometer was darkened on the outside with black plastic to prevent external disturbances. An automated Eheim pump replaced freshwater inside the chamber at a rate

of 5 L min^{-1}. For mosquitofish, the water temperature was directly controlled at 25 ± 1°C using an Eheim heater placed in the external water bath.

Determination of swimming performance and metabolic traits

Essentially, we followed the same methodology and procedures used in our previous work with mosquitofish (Srean et al. 2017). After at least 2 weeks of being held under experimental conditions, fish were then individually transferred into the swim tunnel respirometer. Any effects from the stress of being handled were potentially minimized by transferring fish into the swimming flume without exposing them to air and providing them with a 1-h acclimation period at a speed of 0.5 BL s^{-1} (body length, taken as the standard length of the fish). A critical swimming speed (U_{crit}) test was performed with step-wise increases in flow speed of approximately 1 BL s^{-1} with a time interval of 20 min until the fish fatigued. Fatigue was defined as having occurred when the fish could no longer swim against the current continuously (Farrell 2008). We calculated U_{crit} according to Beamish (1978)

$$U_{crit} = U_f\ + U_i T_f T_i^{-1},$$

where U_f is the highest velocity maintained for the entire swimming period, U_i is the speed increment (cm s^{-1}), T_f is the time elapsed at fatigue speed, and T_i is the set interval time (min). When the calculated cross section of the fish was more that 10% of the swimming tunnel cross section, swimming speed was corrected for the solid blocking effect (Bell and Terhune 1970). The relative U_{crit} was calculated by dividing U_{crit} values by standard length.

Measurements of oxygen consumption of individual fish were recorded during swimming. Linear regressions were fitted from the decline in oxygen concentration in the respirometers over time between flush cycles. The 20:2 min measurement: flush cycle produced clear slopes of oxygen concentration during the measurement period. Regression slopes were then used to calculate oxygen consumption rates

$$\dot{M}_{O_2} =\ -(\Delta Of\ -\ \Delta Ob) \times\ V \times 60,$$

where ΔOf and ΔOb are the slopes of the regression (mg O$_2$ L^{-1} min^{-1}) due to fish respiration and microbial respiration, respectively, V is the volume of the respirometer (after subtracting the fish volume), and 60 was used to change units to mg O$_2$ h^{-1}. The highest value of $\dot{M}_{O_2}$ during the swimming trial was defined as the MMR (Nelson 2016; Norin and Clark 2016). At the end of each swimming trial, the respirometer was left without fish for 10 min to calculate the background respiration associated to microbial activity.

The exponential function generally resulted in higher regression coefficients than the power function did and was therefore used as the model to describe the relationship between $\dot{M}_{O_2}$ (log-transformed) and swimming speed (U) (Brett 1964; Webb 1975; Beamish 1978; Tudorache et al. 2008)

$$\dot{M}_{O_2} =\ SMR\ \times\ e^{bU},$$

where SMR is the estimated SMR at zero swimming speed and b an estimated constant that can be used as an index of swimming efficiency; that is, the higher the value of b, the more marked the increase in the swimming $\dot{M}_{O_2}$ with increased swimming speed. The mass-specific cost of transport (MCOT)

was calculated by dividing the obtained $\dot{M}_{O_2}$ values by the corresponding speed and body mass. MCOT values were then converted into energy units using an oxycaloric value of 14.1 J mgO$_2^{-1}$ (Hepher 1988).

Fish morphology

Following the swimming trials, individuals were weighed to the nearest 0.1 mg and some morphological measurements were obtained from digital images using tpsDig2 software (Rohlf 2015). These measurements included lengths (standard length and total length), depths (maximum body depth and least depth of caudal peduncle), and areas (body, muscle, and propulsion areas). Some morphometric ratios were then calculated following Fisher and Hogan (2007): fineness ratio (ratio between standard length and maximum body depth), caudal peduncle depth factor (ratio between caudal peduncle depth and maximum body depth), propulsive ratio (ratio between propulsive area and body area), and muscle ratio (ratio between muscle area and body area).

Data analysis

Statistical analyses were performed in the R software environment (R Development Core Team 2018). The individual effects of body mass and total length on U_{crit}, MMR, and SMR were analyzed by linear regression. Following Srean et al. (2017), we performed multiple linear regressions using total length, MMR, or SMR as covariates, once body mass has been accounted for, thus allowing us to assess potential independent effects of body mass and an additional covariate (independent variables). When the two regression coefficients were significant, we repeated the same model separately by sexes to account for sex-dependent effects. The suitability of different models was assessed by the significance of regression coefficients and the likelihood ratio tests. The effects of body size on swimming $\dot{M}_{O_2}$ were evaluated by linearizing the exponential function (i.e., $\dot{M}_{O_2}$ was log$_{10}$-transformed). Analysis of covariance (ANCOVA) was applied to compare $\dot{M}_{O_2}$ across different body mass ranges within species using swimming speed as the covariate. ANCOVA was also applied to test for differences in U_{crit}, MMR, and SMR among fish species using body mass as the covariate. Regression slopes were only compared between the 5 cyprinids and pumpkinseed because of the enormous difference in size between these species and the other 2 remaining species (toothcarp and mosquitofish). In addition, ANCOVA was not applied to compare toothcarp and mosquitofish due to differences in origin (i.e., captive-bred stock and wild population) and experimental temperature. Tukey's multiple comparison test was applied to elucidate differences in covariate-adjusted means among species. Metabolic rates were standardized to the mean of body mass according to $\dot{M}_{O_2(4.65\ g)} = \dot{M}_{O_2observed} \times (4.65/M)^b$, where b is a common scaling coefficient of 0.75 used for all individuals (e.g., Reidy et al. 2000). Interrelationships between swimming capacity, metabolic traits, and morphometric ratios were evaluated using linear regression analysis and Pearson-product moment correlations. Individual fractions of variation explained by "species" and morphometric ratios (all of them pooled) were tested using variation partitioning (the "varpart" function of the vegan package in R). Significance of testable fractions was determined using 999 permutation tests with the "anova.cca" function (Oksanen et al. 2017).

Results

Intraspecific variation

Body mass was largely the best predictor of U_{crit}, SMR, and MMR (R^2 values were always higher for body mass than for total length). The inclusion of a second predictor such as total length or MMR in addition to body mass markedly increased the explained variation of U_{crit} (range = $6.7 - 480\%$ increase), whereas the inclusion of SMR improved the explained variation of MMR (range = $12 - 135\%$ increase) in several species (Table 1). Additionally, we found that body mass and total length were both significant for U_{crit} in minnow and body mass and MMR were both significant for U_{crit} in toothcarp and mosquitofish (Table 1). U_{crit} was only affected independently by the 2 predictors in minnow and mosquitofish. This result therefore indicates that, for instance, longer minnow individuals of similar body mass had lower U_{crit}. When testing this model separately for each sex, we found that the 2 predictors were only significant in minnow males (log$_{10}$ U_{crit} = $3.43 + 1.38$ log$_{10}$ $M - 2.82$ log$_{10}$ TL; R^2_{adj} = 0.80). Moreover, we found that body mass and SMR were both significant for MMR in mosquitofish (Table 1). When testing this model separately for each sex, we found that the 2 predictors were only significant in mosquitofish females (log$_{10}$ MMR = $-0.13 + 0.40$ log$_{10}$ $M + 0.26$ log$_{10}$ SMR; R^2_{adj} = 0.76), indicating that individuals of the same body mass with higher SMR also had higher MMR.

Oxygen consumption was highly correlated with swimming speed, with the speed exponent b ranging from 0.01 to 0.09 (Supplementary Table S1). The value of the speed exponent generally tended to decrease with increasing body mass, which indicates that heavier fish can optimally swim faster. Importantly, species showed high intraspecific variation in $\dot{M}_{O_2}$ across mass-range groups (Figure 1). ANCOVA showed significant effects of body mass on $\dot{M}_{O_2}$ in six fish species, with the exception of minnow ($F_{1,160}$ = 0.03, P = 0.97) and toothcarp ($F_{1,213}$ = 1.48, P = 0.22).

Interspecific variation

ANCOVA showed a significant mass×species interaction for U_{crit} for barbel (P = 0.003) but not for the rest of species, which had similar slopes (Table 1 and Supplementary Figure S1a). After accounting for body mass effects, minnow and bleak had higher U_{crit} than chub (Tukey's test, P = 0.02 and P = 0.04, respectively), and cyprinids had significantly higher U_{crit} than pumpkinseed (ANCOVA, $F_{4,75}$ = 85.29, P < 0.001). In addition, bleak had the lowest SMR ($F_{5,90}$ = 11.16, P < 0.001) (Supplementary Figure S1b). MMR values were generally higher in barbel and chub, although ANCOVA showed a significant mass×species interaction for these species (barbel: P = 0.03; chub: P = 0.01) (Supplementary Figure S1c). Minnow had higher MMR than bleak (Tukey's test, P < 0.002), and cyprinids had higher MMR than pumpkinseed ($F_{3,64}$ = 18.13, P < 0.01). Toothcarp and mosquitofish attained the highest MCOT at a comparable workload, whereas bleak showed the lowest MCOT (Figure 2). Interestingly, pumpkinseed attained lower MCOT than some cyprinids at a comparable workload.

We found that SMR and MMR were positively correlated (Figure 3A), following the general relation log$_{10}$ MMR = $0.45 + 0.34$ log$_{10}$ SMR (P < 0.001, R^2 = 0.14) after adjusting for body mass. Further, U_{crit} and MMR were also positively correlated (Figure 3B), following the general relation log$_{10}$ MMR = $-0.17 + 0.78$ log$_{10}$ U_{crit} (P < 0.001, R^2 = 0.40), after adjusting for body mass. Linear models without mosquitofish (the only species measured at 25°C) showed similar explained variation as the models including all the species (R^2 = 0.15 and 0.40). The adjusted estimates of SMR and MMR and

Table 1. Simple and multiple linear regression analyses of the swimming performance and metabolic traits in 8 freshwater fish species

	Dependent variable	Independent variables		a	b_1	b_2	R^2_{adj}
Bleak	U_{crit}	M		1.30***	0.66*		0.42[a]
	U_{crit}	M	TL	0.54	0.36	1.0	0.44[a]
	U_{crit}	M	MMR	1.41***	0.36	0.24	0.47[a]
	MMR	M		−0.47	1.27***		0.51[a]
	MMR	M	TL	0.07	1.48*	−0.70	0.49[a]
	MMR	M	SMR	−0.61	1.39**	−0.14	0.49[a]
Catalan chub	U_{crit}	M		1.46***	0.36***		0.85[a]
	U_{crit}	M	TL	1.17***	0.23	0.4	0.85[a]
	U_{crit}	M	MMR	1.42***	0.31	0.11	0.84[a]
	MMR	M		0.39**	0.41**		0.60[a]
	MMR	M	TL	0.5	0.46	−0.15	0.56[a]
	MMR	M	SMR	0.41**	0.31*	0.3	0.64[a]
Mediterranean barbel	U_{crit}	M		1.65***	0.13**		0.44[a]
	U_{crit}	M	TL	0.7	−0.26	1.30*	0.61[b]
	U_{crit}	M	MMR	1.65***	0.13	−0.01	0.40[a]
	MMR	M		0.29**	0.63***		0.78[a]
	MMR	M	TL	−0.64	0.26	1.27	0.78[a]
	MMR	M	SMR	0.37*	0.51*	0.15	0.77[a]
Minnow	U_{crit}	M		1.30***	0.83***		0.75[a]
	U_{crit}	M	TL	3.28***	1.26***	−2.56*	0.80[b]
	U_{crit}	M	MMR	1.30***	0.79***	0.04	0.74[a]
	MMR	M		−0.05	0.92***		0.52[a]
	MMR	M	TL	−1.82	0.54	2.29	0.52[a]
	MMR	M	SMR	−0.04	0.80**	0.15	0.51[a]
Roach	U_{crit}	M		1.38***	0.52**		0.50[a]
	U_{crit}	M	TL	3.57	1.54	−3.11	0.50[a]
	U_{crit}	M	MMR	1.51***	−0.01	0.44**	0.73[b]
	MMR	M		−0.29	1.22***		0.68[a]
	MMR	M	TL	−2.96	−0.02	3.79	0.67[a]
	MMR	M	SMR	−0.44	1.40**	−0.13	0.67[a]
Pumpkinseed	U_{crit}	M		0.76	0.46		0.05[a]
	U_{crit}	M	TL	4.26	2.14	−5.54	0.03[a]
	U_{crit}	M	MMR	1.41**	−0.33	0.47*	0.29[b]
	MMR	M		−1.38**	1.69***		0.50[a]
	MMR	M	TL	−0.81	1.96	−0.9	0.47[a]
	MMR	M	SMR	−1.79*	2.09**	−0.21	0.49[a]
Spanish toothcarp	U_{crit}	M		1.22***	0.40**		0.22[a]
	U_{crit}	M	TL	−0.65	−0.51	3.03	0.27[a]
	U_{crit}	M	MMR	1.39***	0.34**	0.29***	0.43[b]
	MMR	M		−0.43***	0.43*		0.11[a]
	MMR	M	TL	−3.48*	−1.10	4.88*	0.17[b]
	MMR	M	SMR	−0.08	−0.18	0.42***	0.40[c]
Mosquitofish	U_{crit}	M		1.28***	0.19**		0.15[a]
	U_{crit}	M	TL	1.25*	0.18	0.03	0.13[a]
	U_{crit}	M	MMR	1.48***	−0.20**	0.71***	0.63[b]
	MMR	M		−0.29***	0.55***		0.57[a]
	MMR	M	TL	0.45	0.91**	−1.09	0.58[a]
	MMR	M	SMR	−0.14*	0.40***	0.22**	0.64[b]

The 2 regression coefficients were not significant in models with SMR as the dependent variable, hence linear regression functions have been omitted from the table. The different lowercase letters show significant differences between models (likelihood ratio tests, $P < 0.05$). M, body mass; MMR, maximal metabolic rate; SMR, standard metabolic rate; TL, total length; and U_{crit}, critical swimming speed. All variables were $\log_{10}$-transformed (*$P \leq 0.05$, **$P \leq 0.01$, and ***$P \leq 0.001$).

the relative U_{crit} showed a 15-, 19-, and 7-fold interspecific difference between minimum and maximum values, respectively, which highlights high variation in metabolic traits and swimming capabilities across fish species. The mean values of the morphometric ratios for each species are presented in Table 2. The linear relationships of the adjusted estimates of SMR and MMR and the relative U_{crit} with morphometric ratios are presented in Table 3. The adjusted MMR was significantly correlated with the muscle and fineness ratios (Figure 4A, B). "Species" (18%; $F_{7,148} = 8.22$, $P = 0.001$), and morphometric ratios and "species" together (23%; $F_{4,155} = 12.23$, $P = 0.001$) significantly contributed to explaining the variation in MMR (variation partitioning). The relative U_{crit} was also significantly correlated with the muscle and fineness ratios (Figure 4c, d). "Species" (9%; $F_{7,150}=5.72$, $P = 0.001$), morphometric ratios (2%;
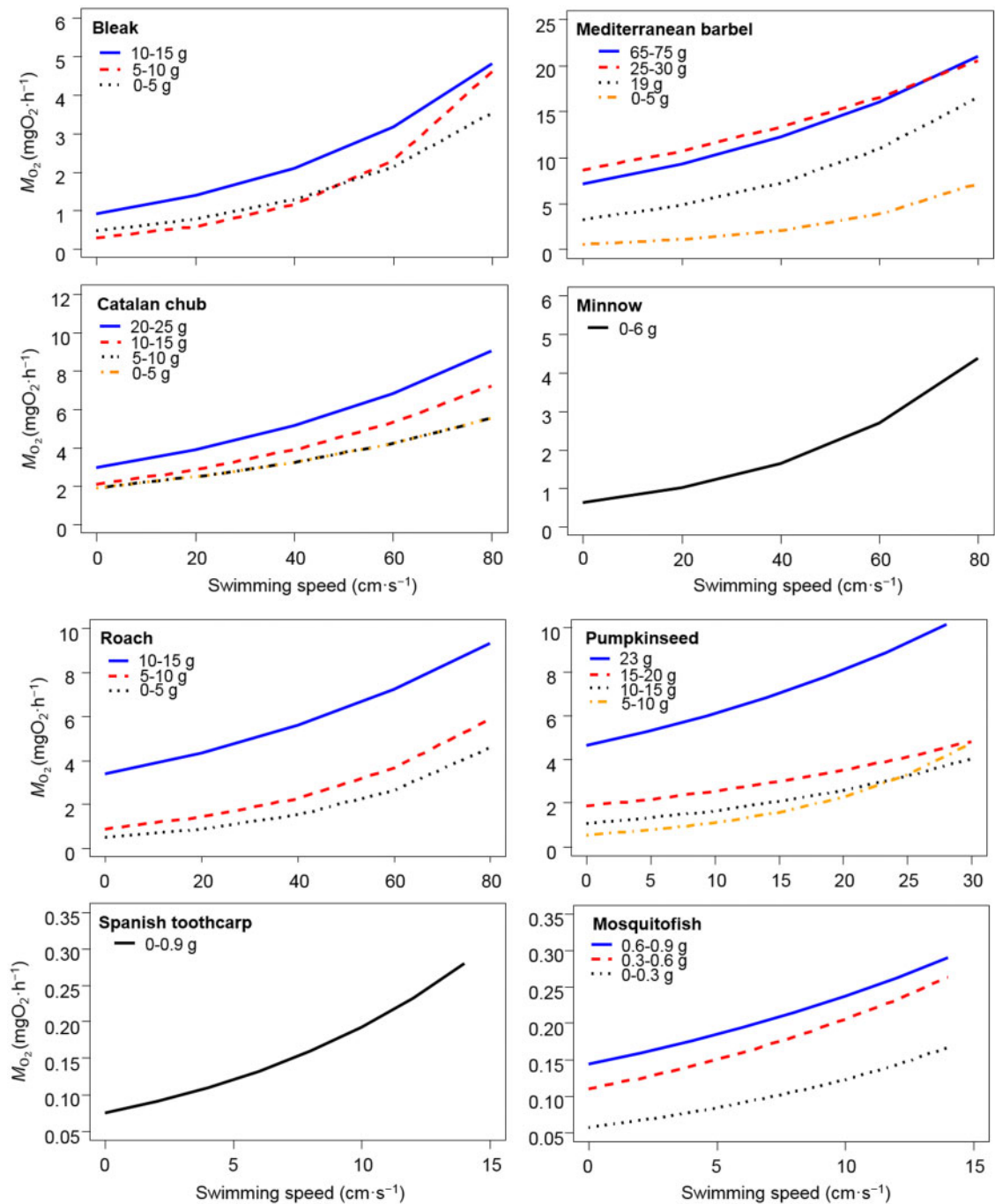
Figure 1. Metabolic rates ($\dot{M}_{O_2}$) as a function of swimming speed measured in 8 freshwater fish species. Within each species, fish were grouped into different mass-range groups according to their respective body mass: ranges of 5 g for bleak, Catalan chub, Mediterranean barbel, roach, and pumpkinseed; 2 g for minnow, and 0.3 g for Spanish toothcarp and mosquitofish. An exponential function is shown for each range of body mass within species when there were significant differences. For $\log_{10}$-transformed regression equations, see Supplementary Table S1.

$F_{4,150}=2.38$, $P=0.048$), and both predictors together (47%; $F_{4,157}=38.49$, $P=0.001$) were found to be significant. The interrelationships between MMR, U_{crit}, and morphometric ratios reflected a gradient of performance among species described by pumpkinseed < toothcarp < mosquitofish < cyprinids (pooled). In contrast, the variation in SMR was only explained by the contribution of "species" (18%; $F_{7,149}=6.18$, $P=0.001$), with morphometric ratios having negligible effects.

Discussion

Although body mass and total length are both indicators of size in fish (Beamish 1978), we found stronger positive relationships between body mass and both U_{crit} and metabolic traits. The effects of body mass on metabolic traits are not surprising as energy turnover varies according to body constituents (Killen et al. 2010; White et al. 2019). Nevertheless, some previous studies have used total length for predicting U_{crit} in fish (Ojanguren and Braña 2003;

Hogan et al. 2007; Mateus et al. 2008). It appears, however, that body mass may better predict fish swimming performance because it is directly related to body volume and, consequently, to swimming thrust (Ohlberger et al. 2005; Srean et al. 2017). We also observed that body mass influenced the swimming efficiency of most of the species studied, indicating that heavier fish are able to optimize energetic costs per unit of mass and distance due to a more favorable ratio of body volume to body surface in larger fish (Webb 1975; Beamish 1978; Videler 1993). However, toothcarp and minnow did not show differences in metabolic rates across individuals of different body mass. For minnow, this fact could be related to the restricted size range of individuals analyzed, as this species is notably smaller than the rest of cyprinids studied, and it would have also been necessary to use minnow juveniles in a smaller swim tunnel. In contrast, we used a relatively similar body size range for toothcarp and mosquitofish and, surprisingly, body mass markedly
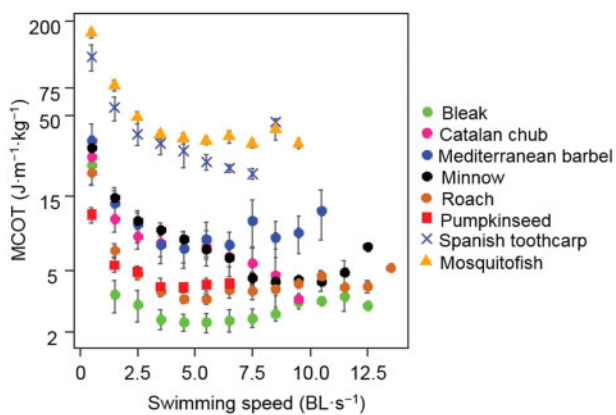

Figure 2. Mass-specific cost of transport (MCOT) as a function of swimming speed measured in 8 freshwater fish species. MCOT was negatively related with swimming speed ($P < 0.001$). Metabolic rates (in J m^{-1} kg^{-1}) are shown as means and error bars at each swimming speed presented as body length per second (BL s^{-1}). Note that data represent oxygen uptake at a comparable workload, but not necessarily at a comparable speed. Y-axis is on a log$_{10}$ scale. Cyprinid species are represented by circles. Colored symbols are available in the online version.

influenced the metabolic rates only in mosquitofish. This latter species also showed higher swimming efficiency (i.e., lower speed exponents) than toothcarp, indicating that these two species might differ in the way energy metabolism is used while swimming. In agreement with this, Rubio-Gracia et al. (2020) tested the 2 species at 25°C and found that mosquitofish can optimally swim without excessively increasing energetic costs over a wider range of swimming speeds. In short, this study shows the importance body mass has on influencing swimming performance and energy use.

In this study, U_{crit} was affected independently by body mass and total length in minnow and by body mass and MMR in mosquitofish. These results, along with other studies evaluating swimming performance in some fish species (e.g., Ohlberger et al. 2005; Srean et al. 2017), are consistent with the idea that, after accounting for body size, the sign of the relationships between swimming capacity and other traits may not always be positive. In relation to mosquitofish, Srean et al. (2017) pointed out that negative associations between U_{crit} and MMR can be related to the fact that females generally display more variability in body size and shape than males do. However, this is not likely to be the case for toothcarp, as females are generally larger than males. Instead, both sexes seem to have similar morphological traits related to swimming performance (Rubio-Gracia et al. 2020), and this would most likely explain the positive associations observed between traits. In short, this study opens a path to further investigate the sign and causes of the relationships between swimming capacity and metabolic traits in fish species, and the consequences trait covariation has on ecological interactions.

We found considerably high variation in SMR, even after standardizing to a common body mass. This could likely be related to the short acclimation period (1 h) used for the fish before starting the U_{crit} protocol. In general, several hours are needed to obtain the best accuracy of SMR estimates, although that said, the duration of acclimation period depends on the species (Chabot et al. 2016). Thus, taking this into consideration, SMR estimates (obtained from the $\dot{M}_{O_2}$-swimming curve) of species might have been somewhat overestimated. By contrast, estimates of U_{crit} were not likely affected by acclimation period since previous studies have shown that the U_{crit} protocol is relatively robust to variation in methodological
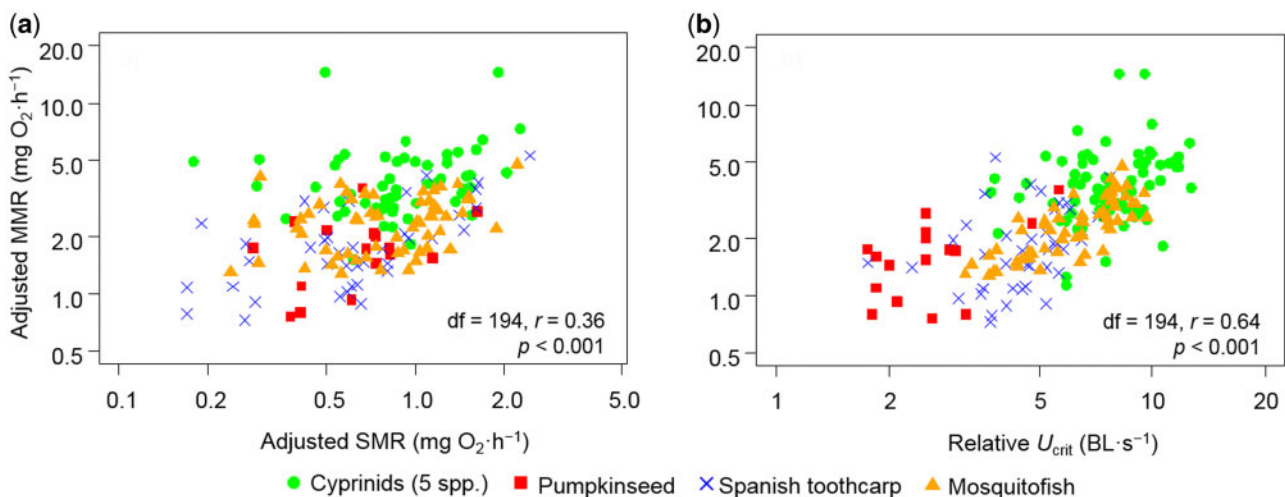

Figure 3. Relationships of adjusted standard metabolic rate (SMR) (A) and relative critical swimming speed (U_{crit}) (B) with adjusted maximal metabolic rate (MMR). Metabolic rates shown were standardized to the mean of body mass (4.65 g). For clarity, the 5 cyprinid species were pooled and shown as cyprinids. Relationships were significantly positive in both cases. Both axes are on a log$_{10}$ scale.
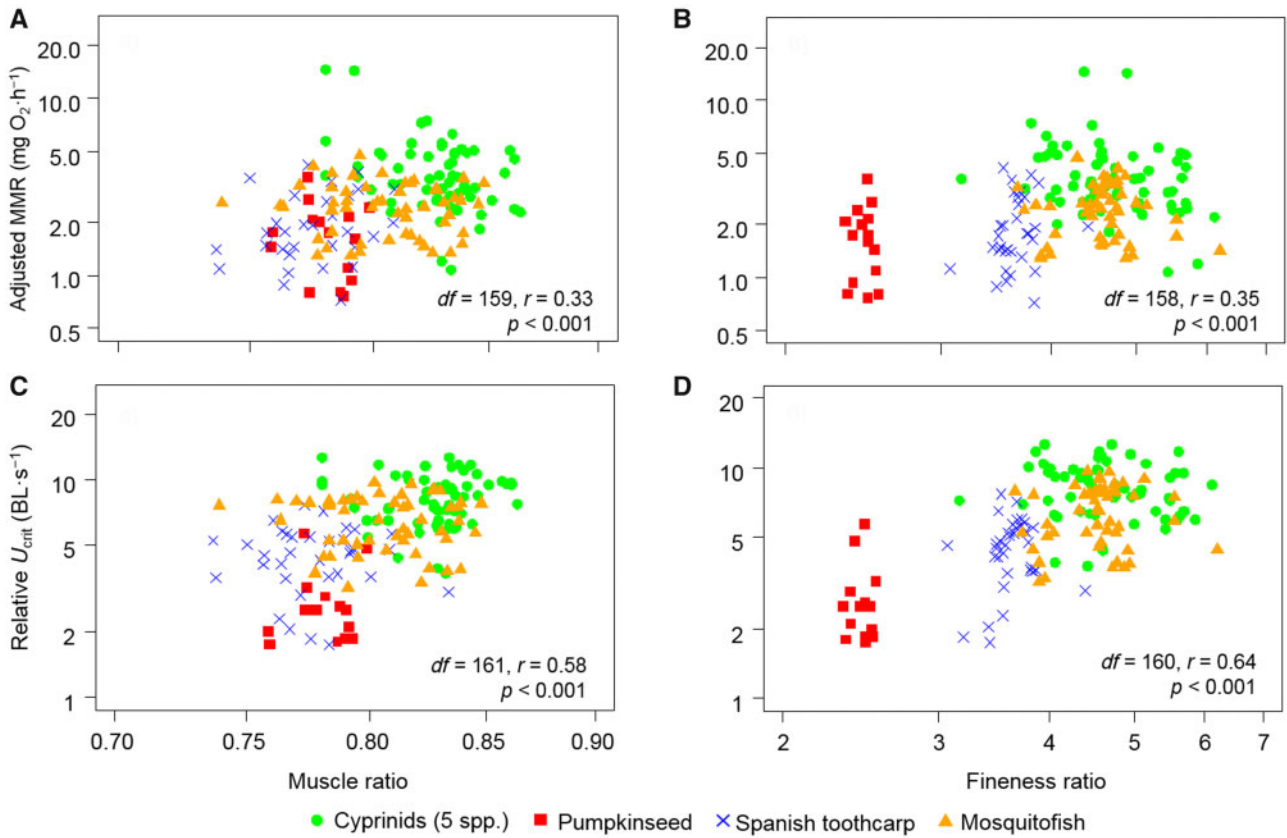
Figure 4. Interspecific variation in adjusted maximal metabolic rate (MMR) and relative critical swimming speed (U_{crit}) across 8 freshwater fish species in relation to 2 morphometric ratios. Adjusted estimates of MMR and U_{crit} plotted against muscle ratio (A, C) and fineness ratio (B, D). For clarity, the 5 cyprinid species were pooled and shown as cyprinids. All relationships were significantly positive (Table 3), indicating that these 2 morphological traits influenced swimming capacity and aerobic metabolism. Both axes are on a $\log_{10}$ scale.

Table 2. Means ± standard deviations of various morphometric ratios measured in the 8 freshwater fish species studied

	N	Fineness ratio	Muscle ratio	Propulsive ratio	Caudal peduncle depth factor
Bleak	17	5.30±0.55	0.84±0.01	1.13±0.01	0.46±0.05
Catalan chub	7	4.58±0.25	0.81±0.02	0.99±0.02	0.46±0.03
Mediterranean barbel	6	4.43±0.38	0.79±0.02	1.03±0.02	0.49±0.02
Minnow	19	4.89±0.45	0.83±0.02	1.12±0.02	0.47±0.03
Roach	12	3.92±0.26	0.83±0.01	1.09±0.01	0.37±0.02
Pumpkinseed	15	2.46±0.07	0.78±0.01	1.23±0.01	0.32±0.01
Spanish toothcarp	34	3.63±0.22	0.78±0.02	0.96±0.02	0.60±0.04
Mosquitofish	52	4.56±0.46	0.81±0.02	1.05±0.02	0.64±0.06

Table 3. Linear relationships of relative critical swimming speed (U_{crit}), adjusted standard metabolic rate (SMR), and adjusted maximal metabolic rate (MMR) (metabolic rates were standardized to the mean of body mass, 4.65 g) with various morphometric ratios

	U_{crit} (BL s^{-1})					SMR (mg O$_2$ h^{-1})					MMR (mg O$_2$ h^{-1})				
	Estimate±SE	df	F	P	R^2	Estimate±SE	Df	F	P	R^2	Estimate±SE	df	F	P	R^2
Fineness ratio	0.303±0.029	160	111.4	***	0.41	0.022±0.031	159	0.51	0.48	0.003	0.149±0.031	158	22.62	***	0.13
Muscle ratio	0.036±0.005	161	47.11	***	0.23	−0.003±0.005	160	0.39	0.54	0.002	0.022±0.005	159	18.9	***	0.11
Propulsive ratio	−0.014±0.014	161	1.07	0.3	0.01	−0.014±0.011	160	1.4	0.23	0.009	0.003±0.012	159	0.04	0.84	<0.001
Caudal peduncle depth factor	0.072±0.040	160	3.21	0.07	0.02	0.039±0.033	160	1.34	0.25	0.008	−0.048±0.036	159	1.73	0.19	0.01

procedures (Hogan et al. 2007). Another important aspect is that mosquitofish swam at 25°C in the swim tunnel, which represents an experimental temperature 5 degrees warmer with respect to the

other species. Because of this, we avoided the direct comparison of mosquitofish with the rest of the species, since a potential bias of metabolic rates and swimming performance would be expected due

to the strong dependency of oxygen uptake with temperature in ectotherms (Fry and Hart 1948; Ohlberger et al. 2007). Nevertheless, we found that the explained variation of MMR by SMR was similar when removing mosquitofish from predictive models. This may be explained by the fact that mosquitofish is a highly eurythermal fish (Otto 2006) and metabolic rates are supposed to raise slowly as temperature increases (Schulte 2015), while abrupt changes in swimming performance seem to occur at more extreme temperatures (Wilson 2005). Therefore, this finding suggests that the strength of the relationship between metabolic traits may not be affected by small changes in temperature.

At the interspecific level, minnow and bleak displayed higher U_{crit} than other cyprinids and all cyprinids displayed higher U_{crit} and MMR than pumpkinseed for a given body mass. Thus, an improved swimming capacity was associated with higher metabolic capacity, as noted in previous studies (Yan et al. 2013). Differences in swimming capacity among species can be partly explained by the significant positive relationships between U_{crit} and the fineness and muscle ratios of species. Effects of these morphometric ratios on swimming capabilities have been previously reported in several fish species (Fisher et al. 2000; Ohlberger et al. 2006; Nanami 2007; Rubio-Gracia et al. 2020). Nanami (2007) pointed out that species with an elevated proportion of muscle fibers and slender body shape can generate more forward thrust and reach higher speeds. In addition to U_{crit}, we found that MMR was also positively correlated with fineness and muscle ratios, whereas the effects of these 2 morphometric ratios were negligible on SMR. Even though we are not certain whether the high variation observed in SMR may have counteracted the strength of the relationship between SMR and morphological traits, our results are compatible with much broader scale studies that explored the interrelationships of these traits in teleost fish. For instance, Killen et al. (2016) examined the interrelationships between metabolic and morphological traits among 92 fish species and found that some morphological traits (gill surface area, muscle protein, and caudal fin aspect ratio) had greater effects on MMR than on SMR. Interspecific variation may also be explained by the differences in ecological lifestyle among species (Killen et al. 2010; Stoffels 2015; Killen et al. 2017), since cyprinids are likely to be more rheophilic species than the other three species studied (Cano-Barbacil et al. 2020). However, differences in metabolic and dispersal rates among the species would likely be greater if we had studied a species with a clear fast-flow lifestyle. Species with benthic and benthopelagic behavior can have relatively similar metabolic traits, unlike species with pelagic behavior which clearly attain higher metabolic traits (e.g., Stoffels 2015). Taken together, this study shows that interspecific variation in U_{crit} can be partly explained by the variation in the interrelated traits of MMR, fineness, and muscle ratios.

Pumpkinseed, which is characterized by a very deep and laterally compressed body, attained lower MCOT than some cyprinids, which tend to have more fusiform or streamlined bodies, did. This finding may be explained by the relatively similar levels of SMR among the species. For instance, Pettersson and Brönmark (1999) found that deep-bodied fish did not experience any higher costs of transport than shallow-bodied fish because of their lower SMR, thereby compensating potential hydrodynamic disadvantages associated with high-drag morphs. Nevertheless, the cost of transport increases sharply in deep-bodied species when swimming speed is increased (Pettersson and Hedenström 2000), and therefore cyprinids are supposed to swim more efficiently at a wider range of speeds. Ultimately, other unexplored factors such as swimming mode and mechanics might also have influenced the swimming efficiency of the species (Fulton 2007). Species from the genus *Lepomis* often use median and paired-fin swimming (labriform swimming) (Jones et al. 2007), and previous studies have found that this type of swimming is energetically less costly than undulatory swimming (Korsmeyer et al. 2002), which is often employed by cyprinids at intermediate and high speeds. Therefore, this finding provides evidence supporting the idea that fish species with high-drag morphs may show cost reduction strategies to compensate for hydrodynamic disadvantages.

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Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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