Swimming performance in early life stages of three threatened Iberian Leuciscidae

Daniel Mameri[1] • Carla Sousa-Santos[2] • Joana Isabel Robalo[2] • Fátima Gil[3] • Ana Margarida Faria[2]

Abstract

Rivers are dynamic systems where flow is constantly changing, making early fish life stages with lower swimming abilities potentially vulnerable to rapid changes in water velocity. In this study, we evaluated the response of critical young life stages of three Iberian leuciscids – *Achondrostoma occidentale*, *Iberochondrostoma lusitanicum*, and *Iberochondrostoma almacai* – to increasing water velocities, by determining their critical swimming speed (U_{crit}) and its relation with morphometric traits potentially associated with better swimmers. Results suggest a positive relation between both fish length and body depth with U_{crit} and species-specific differences in swimming performance. Moreover, most fish could not withstand the maximum velocity tested (20 cm s^{-1}), which can be surpassed in the rivers they occur. This study highlights the importance of considering individual traits for future management of fish stocks in rivers.

Introduction

Freshwater organisms are currently facing several threats, which include water pollution and removal, changes in land use, introduction of exotic species, and obstruction and flow regulation by dams and weirs (Dudgeon et al. 2006; Vörösmarty et al. 2010). In this last scenario, rapid variations in flow caused by hydropower dams (e.g., hydropeaking releases) can be particularly harmful for fish species, especially at young life stages. Additionally, more intense rainfall events under the ongoing climate change scenario (Milly et al. 2002) can also lead to abrupt changes in river flow and to an increasing risk of fish drift downstream (Lechner et al. 2016).

✉ Daniel Mameri
dmameri@isa.ulisboa.pt

1 CEF - Forest Research Centre, School of Agriculture, University of Lisbon, Tapada da Ajuda, 1349-017 Lisbon, Portugal

2 MARE – Marine and Environmental Sciences Centre, ISPA – Instituto Universitário, Rua Jardim do Tabaco 34, 1149-041 Lisbon, Portugal

3 Aquário Vasco da Gama, Cruz Quebrada-Dafundo, Portugal

Fish are particularly vulnerable to these threats. Depending on the stage of their life cycle, they may need to perform upstream migrations along the river to reach suitable habitat areas for growth, feeding, refuge, reproduction, and spawning, meaning they will have to swim against the current. Furthermore, these populations are highly dependent on the annual recruitment, which is in turn related to the survival of larvae and young of the year (Magalhães et al. 2003; Schmutz et al. 2016). In this context, species' swimming abilities need to be included in dispersal models, providing managers with information for decisions on flow regulation (Romão et al. 2012; Boavida et al. 2013) and fishway design (Adams et al. 2009; Peake 2008; Katopodis et al. 2019).

Since the 1960s, several studies addressed swimming performance in freshwater fish species (e.g., Brainbridge 1960; Brett et al. 1964; Cai et al. 2019; George et al. 2019; Tudorache et al. 2007), but until recently, most target species had relatively large ranges and low levels of conservation concern (e.g., common carp *Cyprinus carpio* Linnaeus, 1758 in Bainbridge 1960; roach *Rutilus rutilus* (Linnaeus, 1758) in Tudorache et al. 2007; bighead, silver and grass carps, invasive to North America, in George et al. 2018), despite some work already done in sturgeons (Deslauriers & Kieffer 2012; Katopodis et al. 2019; Verhille et al. 2014). Data on the swimming performance of fishes in biodiversity hotspots, such as the Mediterranean basin, considered one of the priority areas for biodiversity conservation (Myers et al. 2000), is still scarce.

Specifically for the Leuciscidae, a fish family that includes endemic Iberian fish species formerly included in Cyprinidae (Schönhuth et al. 2018), 24 out of the 31 species (77%) found in the Iberian Peninsula are endemic (IUCN 2019). Swimming performance studies conducted in this group have been restricted to a small number of species: the Iberian barbel *Luciobarbus bocagei* (Steindachner, 1864) (in Mateus et al. 2008; Silva et al. 2011; Alexandre et al. 2013), the Tagus nase *Pseudochondrostoma polylepis* (Steindachner, 1864), the bordello *Squalius caroliterti* (Doadrio, 1988) (in Romão et al. 2012), the southern straight-mouth nase *Pseudochondrostoma willkommii* (Steindachner, 1866) (in Alexandre et al. 2016), and the ruivaco *Achondrostoma oligolepis* (Robalo, Almada, Doadrio & Kottelat, 2005) (in Silva 2016). It should be noted that all these studies used adult individuals, meaning that the swimming performance of developmental stages of Iberian fish species remains yet unknown.

In this study, we sought to measure the critical swimming speed (U_{crit}) in three-threatened Iberian leuciscid species: the western ruivaco *Achondrostoma occidentale* (Robalo, Almada, Sousa Santos, Moreira & Doadrio, 2005), the Portuguese nase *Iberochondrostoma lusitanicum* (Collares-Pereira, 1980), and the southwestern nase *Iberochondrostoma almacai* (Coelho, Mesquita & Collares-Pereira, 2005). Swimming performance was tested by measuring the critical swimming speed, U_{crit}, defined by Brett (1964) as the maximum velocity that a fish can maintain for a certain period of time, variable among species and among developmental stages. Several authors have suggested that U_{crit} is as an ecologically relevant measurement (e.g., Plaut 2001; Faria et al. 2014) and a good indicator of their maximum aerobic performance (Hammer 1995; Drucker 1996), allowing fish to perform rapid vertical movements to face different water currents (Fisher and Leis 2009). Additionally, the role of morphometric variables as predictors of U_{crit} was also evaluated, as their importance in determining individual swimming performance has already been demonstrated in other freshwater fish species (minnows: Bestgen et al. 2010; Iberian leuciscids: Mateus et al. 2008).

Material and methods

Test subjects

A total of 49 fish were retrieved from captive stocks currently undergoing a captive breeding program for Portuguese native leuciscids (Sousa-Santos et al. 2014a): 17 *A. occidentale*, 20 *I. lusitanicum*, and 12 *I. almacai*, from the rivers Safarujo, Grândola, and Odelouca, respectively. These are small river basins, with main river courses ranging between 18 km (Safarujo) and 92 km (Odelouca). Due to different availability of early juvenile fish in these captive stocks, *A. occidentale*

and *I. lusitanicum* were tested in November 2017, while *I. almacai* juveniles were tested in June 2018. Fish stocks in this captive breeding program are reared following a "naturalistic approach," aiming to preserve the natural behavioral patterns of the species, such as escape from predators and search for food (Sousa-Santos et al. 2014a). To achieve this, four conditions were established at the start of the program: (1) naturally occurring spawnings; (2) availability of refuge areas for fry and juveniles; (3) natural conditions of light and temperature; and (4) minimal human intervention (Sousa-Santos et al. 2014a).

Critical swimming speed was measured in a swimming chamber made of clear Perspex with 6 parallel swimming lanes, each 30 mm wide, 50 mm high, and 180 mm long. (Fig. 1). Water was retrieved from a PVC tank (200 L capacity) through a pump and redistributed equally in the six lanes composing the swimming chamber (Fig. 1; for further details see Faria et al. 2009). Fish were placed in an aerated container kept at the same temperature as the swimming chamber (20.0 ± 1.0 °C) 1 hour before each trial, to acclimate and recover from any potential handling stress. Fish were then introduced into the swimming chamber (Fig. 1), one fish per lane and left to acclimate at a constant velocity of 5 cm s^{-1} for 5 min. If a
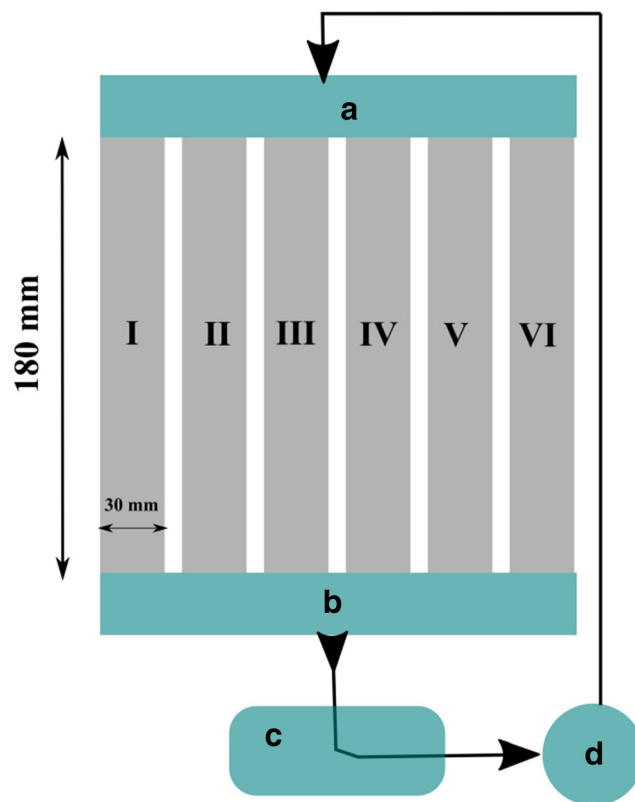
Fig. 1 Schematics of the swimming chamber: (**A**) water input, equally distributed to the six lanes (I–VI), each 180 mm long and 30 mm wide; (**B**) outflux; (**C**) source tank to where the water drops; (**D**) pump connected to the tank and the pipe circuit, redistributing the water back to the swimming chamber

fish was pulled over to the back wall of the lane during this period, it was removed from the experiment.

Each trial consisted of a 4-step series of constant water speed increments (5, 10, 15, and 20 cm s^{-1}), lasting 5 min each. Whenever a fish was in the back wall and unable to swim against the current, the time and the water velocity were recorded. If during the trials fish displayed unsteady swimming, i.e., moved back and forward in the chamber (Mateus et al. 2008), they would not be considered for the analyses. After each trial, fish were photographed for subsequent morphometric measurements and placed in an aerated container before returning to their original tanks. No fish died during the experimental procedures. Morphometric measures were taken on calibrated photographs (one photograph per fish, lateral view). Pictures were taken after putting each fish in a transparent aquarium of $15 \times 5 \times 10$ cm (camera model: Canon Powershot SX160 IS), and measures were obtained using the software ImageJ (version 1.52d) and included standard length ("SL"), fork length ("FL"), total fish length ("TL"), body depth ("BD," measured from the insertion of the dorsal fin to the ventral edge of the fish profile), and caudal peduncle height ("CP").

U_{crit} determination

U_{crit} was determined following the formula proposed by Brett (1964): $U_{crit} = U + [(t/t_i) \times U_i)]$, where U is the penultimate speed a fish is able to maintain, U_i the velocity increment, t the time swam in the final velocity increment, and t_i the time interval for each velocity increment. As 20 cm s^{-1} was the maximum velocity step that was possible to attain in this experimental design (due to the pump and swimming chamber constraints), a U_{crit} of 25 cm s^{-1} was assumed for all fish that successfully concluded the trials (as velocity increment = 5 cm s^{-1}).

Data analyses

Data normality was assessed with the Shapiro-Wilk test and distribution observation through histograms, while heteroscedasticity was evaluated using the F-test implemented in the R software (function *var.test*, R Core Team 2018). Comparison of the U_{crit} obtained for the three target fish species was performed with an ANOVA test, followed by a Tukey post hoc test to account for pairwise comparisons. Additionally, a generalized linear model (GLM) for U_{crit} was built taking into account the morphometric variables (TL, BD, and CP). To reduce bias related to individual body length, we standardized U_{crit} for species comparison and model fit according to total body length: relative critical swimming speed (TL s^{-1}), expressed in body lengths per second (cm/cm s^{-1}). FL

and SL measures were excluded due to their strong correlation with TL ($r = 0.994$), while CP was removed from the analyses due to its correlation with BD, thus preventing collinearity issues in fitted models (see below).

A backwards stepwise regression was computed from a GLM following a Gaussian distribution, with TL, BD, and CP to retrieve the most adequate model, i.e., the one with the lowest Akaike Information Criterion (AIC) score and an AIC difference (Δi) of 2.0, following the recommendations of Burnham and Anderson (2002). For the GLM and stepwise analyses, U_{crit} values obtained for the three groups were pooled together. A significance of 0.05 was considered for all analyses, which were performed in R (R Core Team 2018, version 3.5.1), using the function *step. AIC* from the package *MASS* (Vernables and Ripley 2002).

Results

A total of 5 fish (2 *A. occidentale*, 2 *I. lusitanicum*, and 1 *I. almacai*) were removed after the acclimation period due to pulling over to the back wall, while 8 fish (2 *A. occidentale*, 3 *I. lusitanicum*, and 3 *I. almacai*) displayed poor rheophilic behavior (i.e., did not try to swim against the current) and were not considered for analyses. Overall, 36 tested fish were considered for analyses: 13 *A. occidentale*, 15 *I. lusitanicum*, and 8 *I. almacai*, ranging from 24 to 53 mm total length (see **Table S1** in Electronic Supplementary Material for further details). Twenty-two fish could not withstand the final velocity step (20 cm s^{-1}): 5 *A. occidentale* (38%), 11 *I. lusitanicum* (73%), and 7. *almacai* (88%). The measured morphometric variables and U_{crit} (absolute and relative) values for the three species are summarized in Table 1.

Significant differences in U_{crit} values were found when comparing the three species ($F = 6.347$, $p = 0.009$), with *I. almacai* having the lowest average relative critical swimming speed value: 4.5 TL s^{-1} (Table 1). Post hoc comparisons revealed significant differences of the U_{crit} values between *I. almacai* and both *A. occidentale* (mean deviation = 1.523, $p = 0.017$) and *I. lusitanicum* (mean deviation = 1.527, $p = 0.014$); in contrast, the U_{crit} values obtained for these last two species did not differ (mean deviation = 0.004, $p = 0.999$).

The fitted model for U_{crit} retained both morphometric variables entered in the model and significantly related to the response variable (Table 2), total fish length and body depth; with the second being positively related with swimming performance, more "robust" fish (i.e. with higher body depths) were more likely to attain higher relative U_{crit} (Fig. 2). In contrast, relative U_{crit} was negatively correlated with total fish length, but absolute U_{crit} was higher in longer fish (Fig. 2).

Table 1 Minimum, maximum, and mean values with standard deviations for total fish length (TL), body depth (BD), caudal peduncle height (CP), and absolute and relative U_{crit} for *A. occidentale*, *I. lusitanicum*, and *I. almacai*

	A. occidentale	*I. lusitanicum*	*I. almacai*
N	13	15	8
TL (mm)			
Mean ± SD	38.8 ± 4.8	34.7 ± 4.9	43.8 ± 6.7
Range	30.6–46.8	26.7–44.3	33.6–53.4
BD (mm)			
Mean ± SD	7.6 ± 0.5	5.7 ± 0.7	7.5 ± 1.3
Range	7.1–8.5	4.6–6.8	5.7–8.0
CP (mm)			
Mean ± SD	3.4 ± 0.2	2.8 ± 0.3	3.7 ± 0.6
Range	3.5–3.8	2.1–3.2	2.9–3.9
Absolute U_{crit} (m s^{-1})			
Mean ± SD	23.2 ± 4.2	20.5 ± 3.7	19.8 ± 4.7
Range	10.4–25.0	13.6–25.0	11.3–25.0
Relative U_{crit} (TL s^{-1})			
Mean ± SD	6.0 ± 1.3	6.0 ± 1.1	4.5 ± 1.1
Range	3.1–8.2	3.3–8.0	2.7–6.0

Discussion

This study provided the first data on the swimming performance of young developmental fish stages of three small leuciscid species, endemic to the Iberian Peninsula. As this geographic area is part of the Mediterranean basin biodiversity hotspot, the protection of the endemisms is crucial for the maintenance of biodiversity within this diverse fish family.

Our results show that most fish could not withstand the last water velocity step (20 cm s^{-1}), which can be surpassed under natural conditions throughout the year in Portuguese rivers, such as the Odelouca River, where *I. almacai* occur (Pires et al. 2008). Particularly in early summer, water velocities in this river can vary between 10 and 50 cm s^{-1} (Pires et al. 2008). Even when regulation by dams and subsequent discharges (e.g., hydropeaking events) are not taking place, larvae and young juvenile fish must rely on refuges to avoid higher velocities, namely, during flood events (Lechner et al. 2016). *I. almacai* was the species that showed the lowest average relative U_{crit} among the three target species, which may indicate that it may be more susceptible to higher water

velocities. In a study conducted by Pires et al. (2008) in the Odelouca River, field surveys revealed a decrease in abundance of *I. almacai* following a flood event in late summer-early fall. Though we are aware that some individuals may be able to surpass the U_{crit} threshold of 25 cm s^{-1} assumed in this study, the information gathered here can be used, for instance, to determine the total habitat suitability, taking into account suitable water velocity (Santos and Ferreira 2008; Boavida et al. 2013), and the definition of criteria for ecological flow discharges in dams and weirs in regulated rivers (Romão et al. 2012).

For the three species studied, at least for captive bred individuals, fish body length and body depth seem to be determinant traits for U_{crit} of early juvenile stages, accordingly with previous literature targeting other small minnows (Bestgen et al. 2010) and also the Iberian leuciscid species *L. bocagei* (Mateus et al. 2008). Indeed, body size is among the most important characteristics that influence swimming performance (Beamish 1978; Hammer 1995, Plaut 2001). Previous studies have also shown that absolute swimming speed (i.e., U_{crit} expressed in cm s^{-1}) increases with size; contrastingly, the relative speed (U_{crit} expressed in body lengths per second) tends to decrease as size increases (Brett 1965; Hammer 1995; Mateus et al. 2008). The results obtained in this study for three different leuciscid species are concordant with these patterns, which were also found for the Iberian barbel *L. bocagei* (Mateus et al. 2008).

Following these results, future studies should also address intraspecific morphological differences between populations of the same species, as morphological features may be responsive to local habitat conditions (Alexandre et al. 2013; Haas et al. 2015). A previous study on the growth rate of *A. occidentale*

Table 2 AIC scores and differences (Δi) for the tested models for relative U_{crit} (TL s^{-1}). The most fit model included the two morphometric traits that were considered for these analyses (TL and BD)

Predictors	AIC	Δi
TL, BD (full model)	113.0	–
TL	115.4	2.4
BD	123.8	10.8
none (null model)	124.0	11.0

Fig. 2 Correlation plots for (**a**) total length (mm) and absolute U_{crit} (cm s^{-1}); (**b**) total length (mm) and relative U_{crit} (TL s^{-1}); (**c**) body height (mm) and absolute U_{crit} (cm s^{-1}), and (**d**) body height (mm) and relative U_{crit} (TL s^{-1}); different point labels refer to the three species considered: *A. occidentale* (red triangles); *I. lusitanicum* (green dots) and *I. almacai* (blue crosses)
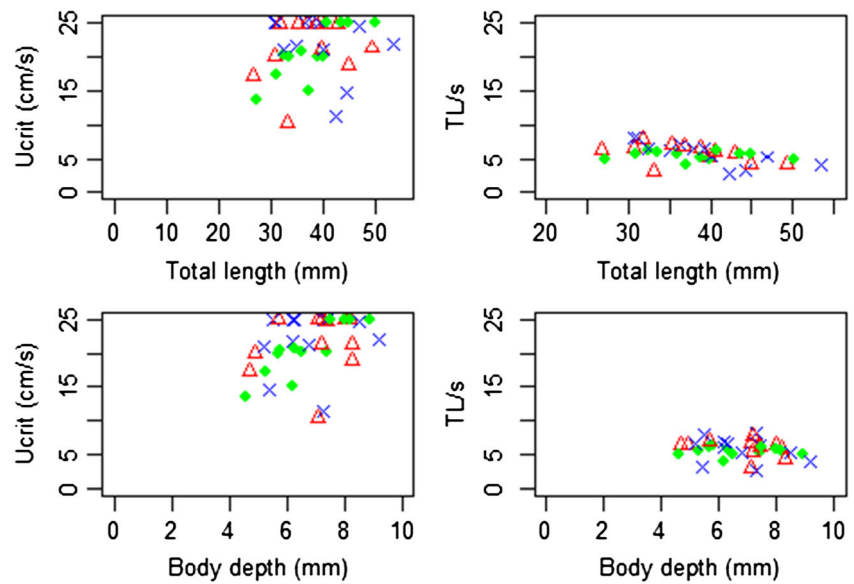
(Mameri et al. 2018) revealed differences in growth and length at age between the three wild populations of this species, and also an overall higher growth rate in the stocks bred in captivity compared with the wild ones. This is most likely due to the fact that fish experience much less stressful conditions in captivity than in their natural habitat. Studies using captive bred Iberian leuciscids have so far provided valuable insights for the knowledge of their ecology and reproduction (Gil et al. 2010; Sousa-Santos et al. 2014b) but may not fully represent the response that wild individuals would have to certain stressors, such as water velocity increases. Thus, it would be interesting to assess if the pattern of swimming performance herein described is similar for wild-caught individuals, to clarify how differently captive and wild individuals cope with increasing water velocities. Additionally, although we tried to select individuals with similar body length, *I. almacai* was tested in the early summer, while *A. occidentale* and *I. lusitanicum* were tested in late fall, after the breeding season. Therefore, a possible effect of different somatic condition between these seasons, which was not assessed in this study, should be taken into consideration in future studies.

The information gathered in this study can provide important guidelines for the conservation and management of wild stocks of these endemic species, by allowing the establishment of regional water velocity criteria for fishways and habitat restoration measures that promote refuge availability for juveniles and fry (e.g., plant aquatic macrophytes and native riparian tree species with submerged roots acting as shelters), so that sudden instream flow changes would be negligible stressors and species recruitment would not be compromised.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Human and animal rights and informed consent This study was performed in accordance with the European directive 2010/63/UE for the protection of animals used for scientific purposes and undertaken under the supervision of an accredited expert in laboratory animal science (following FELASA category C recommendations). The experiments were approved by ISPA's Animal Welfare Body (Permit Number 01/2019) and all methods were performed in accordance with the relevant guidelines and regulations.

References

Adams SR, Hoover JJ, Killgore KJ (2009) Swimming performance of the Topeka shiner (*Notropis topeka*) an endangered Midwestern minnow. Am Midl Nat 144:178–186. https://doi.org/10.1674/0003-0031(2000)144[0178:SPOTTS]2.0.CO;2

Alexandre CM, Quintella BR, Ferreira AF, Romão FA, Almeida PR (2013) Swimming performance and ecomorphology of the Iberian barbell *Luciobarbus bocagei* (Steindachner, 1864) on permanent and temporary rivers. Ecol Freshw Fish 23(2):244–258. https://doi.org/10.1111/eff.12073

Alexandre C, Branca R, Quintella B, Almeida PR (2016) Critical swimming speed of the southern straight-mouth nase *Pseudochondrostoma willkommii* (Steindachner, 1866), a potamodromous cyprinid from southern Europe. Limnetica 35(2):365–372. https://doi.org/10.23818/limn.35.29

Bainbridge R (1960) Speed and stamina in three fish. J Exp Biol 37:129–153

Beamish FWH (1978) Swimming capacity. Volume 7. In: Hoar WS, Randall DJ (eds) fish physiology. academic press, New York, pp 101–187

Bestgen KR, Mefford B, Bundy JM, Walford CD, Compton RI (2010) Swimming performance and fishway model passage success of Rio Grande silvery minnow. Trans Am Fish Soc 5(2):433–448. https://doi.org/10.1577/t09-085.1

Boavida I, Santos JM, Pinheiro NA, Ferreira MT (2013) Fish-habitat response to hydropeaking. In: Proceedings of the 35th IAHR world congress, 8–13 September, Chengdu, China

Brett JR (1964) The respiratory metabolism and swimming performance of young sockeye salmon. J Fish Res Board Can 21:1183–1226

Brett JR (1965) The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (Oncorhynchus nerka). J Fish Res Board Can 23:1491–1501

Burnham K, Anderson D (2002) Model selection and multimodel inference, 2nd edn. Springer, New York

Cai L, Hou Y, Katopodis C, He D, Johnson D, Zhang P (2019) Rheotaxis and swimming performance of perch-barbel (Percocypris pingi, Tchang, 1930) and application to design of fishway entrances. Ecol Eng 132:102–108. https://doi.org/10.1016/j.ecoleng.2019.04.009

Deslauriers D, Kieffer JD (2012) The effects of temperature on swimming performance of juvenile shortnose sturgeon (Acipenser brevirostrum). J Appl Ichthyol 28(2):176–181. https://doi.org/10.1111/j.1439-0426.2012.01932.x

Drucker EG (1996) The use of gait transition speed in comparative studies of fish locomotion. Am Zool 36:555–566

Dudgeon D, Arthington AH, Gessner MO, Kawabata Z-I, Knowler DJ, Lévêque C, Naiman RJ, Prieur-Richard AH, Soto D, Stiassny ML, Sullivan CA (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. Biol Rev 81(2):163–182. https://doi.org/10.1017/s1464793105006950

Faria A, Ojanguren A, Fuiman L, Gonçalves E (2009) Ontogeny of critical swimming speed of wild-caught and laboratory-reared red drum Sciaenops ocellatus larvae. Mar Ecol Prog Ser 384:221–230

Faria AM, Borges R, Gonçalves EJ (2014) Critical swimming speeds of wild-caught sand smelt Atherina presbyter larvae. J Fish Biol 85(3):953–959. https://doi.org/10.1111/jfb.12456

Fisher R, Leis JM (2009) Swimming speeds in larval fishes: from escaping predators to the potential for long distance migration. Pp. 333-373. In: Fish locomotion: an eco- ethological perspective (Ed. CRC press and Paolo Domenici). United States of America

George AE, Garcia T, Stahlschmidt BH, Chapman DC (2018) Ontogenetic changes in swimming speed of silver carp, bighead carp, and grass carp larvae: implications for larval dispersal. PeerJ 6:e5869. https://doi.org/10.7717/peerj.5869

Gil F, Sousa-Santos C, Almada V (2010) A simple and inexpensive technique for the Ex Situ reproduction of critically endangered cyprinids Achondrostoma occidentale as a case study, Journal of the world aquaculture Society. 41(4):661–664. https://doi.org/10.1111/j.1749-7345.2010.00408.x

Haas TC, Heins DC, Blum MJ (2015) Predictors of body shape among populations of a stream fish (Cyprinella venusta, Cypriniformes: Cyprinidae). Biol J Linn Soc 115(4):842–858. https://doi.org/10.1111/bij.12539

Hammer C (1995) Fatigue and exercise tests with fish. Comparative biochemistry and physiology part a. Physiology 112(1):1–20

IUCN (2019). The IUCN red list of threatened species. Version 2018-2. ISSN 2307-8235. URL: http://www.iucnredlist.org. Accessed on 28 January 2019

Katopodis C, Cai L, Johnson D (2019) Sturgeon survival: the role of swimming performance and fish passage research. Fish Res 212: 162–171. https://doi.org/10.1016/j.fishres.2018.12.027

Lechner A, Keckeis H, Humphries P (2016) Patterns and processes in the drift of early developmental stages of fish in rivers: a review. Rev Fish Biol Fish 26(3):471–489. https://doi.org/10.1007/s11160-016-9437-y

Magalhães MF, Schlosser IJ, Collares-Pereira MJ (2003) The role of life history in the relationship between population dynamics and environmental variability in two Mediterranean stream fishes. J Fish Biol 63(2):300–317. https://doi.org/10.1046/j.1095-8649.2003.00148.x

Mameri D, Sousa-Santos C, Robalo JI, Magalhães MF (2018) Growth and age structure in captive and wild stocks of the endangered western ruivaco Achondrostoma occidentale (Cyprinidae). Limnetica 37(1):105–115. https://doi.org/10.23818/limn.37.09

Mateus CS, Quintella BR, Almeida PR (2008) The critical swimming speed of Iberian barbel Barbus bocagei in relation to size and sex. J Fish Biol 73(7):1783–1789. https://doi.org/10.1111/j.1095-8649.2008.02023.x

Milly PCD, Wetherald RT, Dunne KA, Delworth TL (2002) Increasing risk of great floods in a changing climate. Nature 415:514–517. https://doi.org/10.1038/415514a

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858. https://doi.org/10.1038/35002501

Peake SJ (2008) Swimming performance and behaviour of fish species endemic to Newfoundland and Labrador: a literature review for the purpose of establishing design and water velocity criteria for fishways and culverts. Canadian manuscript report of fisheries and aquatic sciences 2843:v + 52p

Pires A, Magalhães MF, Moreira da Costa L, Alves MJ, Coelho MM (2008) Effects of an extreme flash flood on the native fish assemblages across a Mediterranean catchment. Fish Manag Ecol 15(1): 49–58. https://doi.org/10.1111/j.1365-2400.2007.00570.x

Plaut I (2001) Critical swimming speed: its ecological relevance. Comp Biochem Physiol A Mol Integr Physiol 131(1):41–50. https://doi.org/10.1016/S1095-6433(01)00462-7

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL:https://www.R-project.org/

Romão F, Quintella BR, Pereira TJ, Almeida PR (2012) Swimming performance of two Iberian cyprinids: the Tagus nase Pseudochondrostoma polylepis (Steindachner, 1864) and the bordello Squalius carolitertii (Doadrio, 1988). J Appl Ichthyol 28(1): 26–30. https://doi.org/10.1111/j.1439-0426.2011.01882.x

Santos JM, Ferreira MT (2008) Microhabitat use by endangered Iberian cyprinids nase Iberochondrostoma almacai and chub Squalius aradensis. Aquatic Sciences 70(3):272–281

Schmutz S, Jurajda P, Kaufmann S, Lorenz AW, Muhar S, Paillex A, Poppe M, Wolter C (2016) Response of fish assemblages to hydromorphological restoration in central and northern European rivers. Hydrobiologia 769(1):67–78. https://doi.org/10.1007/s10750-015-2354-6

Schönhuth S, Vukić J, Šanda R, Yang L, Mayden RL (2018) Phylogenetic relationships and classification of the Holarctic family Leuciscidae (Cypriniformes: Cyprinoidei). Mol Phylogenet Evol 127:781–799. https://doi.org/10.1016/j.ympev.2018.06.026

Silva AT, Santos JM, Ferreira MT, Pinheiro AN, Katopodis C (2011) Effects of water velocity and turbulence on the behaviour of Iberian barbel (Luciobarbus bocagei, Steindachner 1864) in an experimental pool-type fishway. River Res Appl 27(3):360–373. https://doi.org/10.1002/rra.1363

Silva SSR (2016) Variabilidade espacial e temporal da capacidade natatória de um ciprinídeo ibérico, o ruivaco, Achondrostomaoligolepis (Robalo, Doadrio, Almada & Kottelat, 2005). Universidade de Évora, MSc thesis Retrieved from: http://hdl.handle.net/10174/21807 [In Portuguese]

Sousa-Santos C, Gil F, Almada VC (2014a) Ex situ reproduction of Portuguese endangered cyprinids in the context of their conservation. Ichthyol Res 61(2):193–198. https://doi.org/10.1007/s10228-013-0383-6

Sousa-Santos C, Robalo J, Almada V (2014b) Spawning behaviour of a threatened Iberian cyprinid and its implications for conservation. Acta ethologica 17(2):99–106. https://doi.org/10.1007/s10211-014-0185-5

Tudorache C, Viaenen P, Blust R, de Boeck G (2007) Longer flumes increase critical swimming speeds by increasing burst-glide swimming duration in carp Cyprinus carpio, L. J Fish Biol 71(6):1630–1638. https://doi.org/10.1111/j.1095-8649.2007.01620.x

Verhille CE, Poletto JB, Cocherell DE, DeCourten B, Baird S, Cech JJ, Fangue NA (2014) Larval green and white sturgeon swimming performance in relation to water-diversion flows. Conservation Physiology 2(1):cou031–cou031

Vernables WN, Ripley BD (2002) Modern applied statistics with S, Fourth edn. Springer, New York

Vörösmarty CJ, McIntyre PB, Gessner MO, Dudgeon D, Prusevich A, Green P, Glidden S, Bunn SE, Sullivan CA, Liermann CR, Davies PM (2010) Global threats to human water security and river biodiversity. Nature 467(7315):555–561. https://doi.org/10.1038/nature09440