



UNIVERSIDADE DE ÉVORA
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INSTITUTO SUPERIOR DE AGRONOMIA
UNIVERSIDADE TÉCNICA DE LISBOA

Determinação das velocidades críticas de natação da boga-comum (*Pseudochondrostoma polylepis* Steindachner, 1865) e do escalo do Norte (*Squalius carolitertii* Doadrio, 1988)

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ORIENTAÇÃO: Professor Doutor Pedro Raposo de Almeida

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Esta tese não inclui as críticas e sugestões feitas pelo júri

MESTRADO EM GESTÃO E CONSERVAÇÃO DOS RECURSOS NATURAIS

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Licenciado em Biologia

Tese apresentada à Universidade de Évora para obtenção do grau de Mestre em Gestão e
Conservação dos Recursos Naturais.

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AGRADECIMENTOS

Ao professor Pedro Raposo de Almeida , pela sua constante disponibilidade e supervisão e também por toda a confiança que depositou em mim, a qual tentarei sempre retribuir.

Ao Doutor Bernardo R. Quintella, pela sua constante supervisão e por todos os conhecimentos que me transmitiu ao longo desta etapa. A sua presença constituiu a base do meu sucesso.

À Catarina Mateus pela sua disponibilidade, apoio e informação que foram essenciais para o desenvolvimento do meu trabalho.

Aos meus colegas de trabalho: Carlos Alexandre, Silvia Pedro e Vera Canatheiro. À Marta Alves pelo ajuda na realização da componente prática.

A todas as pessoas e investigadores do Centro de Oceanografia que sempre se disponibilizaram para me ajudar.

Aos meus pais e irmãos por todo o seu apoio e por tudo o que representam na minha vida.

À Rita Gonçalves por todo o apoio, compreensão e toda a coragem que me inspirou.

Critical swimming speed of two Iberian cyprinids (*Pseudochondrostoma polylepis* Steindachner, 1865) and (*Squalius carolitertii* Doadrio, 1988)

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ABSTRACT

Critical swimming speed (U_{crit}) was determined for the Iberian nase (*Pseudochondrostoma polylepis* Steindachner, 1865) and for the Iberian chub (*Squalius carolitertii* Doadrio, 1988) two endemic cyprinids of the Iberian Peninsula. Fish were tested in a Brett's type swimming tunnel, using a standard U_{crit} procedure. From a total of 80 nases tested, the mean (\pm S.D.) U_{crit} observed was 0.78 ± 0.15 m/s (c. 3.74 ± 0.93 bl/s). The 72 chubs tested presented a mean (\pm S.D.) U_{crit} of 0.54 ± 0.1 m/s (c. 4.43 ± 0.72 bl/s). Significant differences were found between the U_{crit} of these species in terms of interspecific comparisons. However the analysis from the comparison of the two species swimming performance suggests that the relation between the U_{crit} and size of the individuals varies similarly with the increasing body length on both species. Intraspecific comparisons between the U_{crit} and the following variables – size, gender, factor, gonadosomatic index – were also accessed. Size of individuals influences their U_{crit} . Conversely, the gender, the condition factor and the gonadosomatic index apparently do not influence the swimming performance of the two cyprinids tested, exception made for the *S. carolitertii* where significant differences between the U_{crit} of both sexes were found. The prime output of this study is to serve as baseline information in the definition of the water velocity criteria in fishways and culverts. If properly used, the information gathered in this study will improve the passage efficiency of the fishways negotiated by these species during their migrations.

KEYWORDS: Maximum aerobic capacity, cyprinids, U_{crit} , fishways, migration, Portugal.

Determinação das velocidades críticas de natação da boga-comum (*Pseudochondrostoma polylepis* Steindachner, 1865) e do escalo do Norte (*Squalius carolitertii* Doadrio, 1988)

RESUMO

Neste estudo foi determinada a velocidade crítica de natação (U_{crit}) da boga-comum (*Pseudochondrostoma polylepis* Steindachner, 1865) e do escalo do Norte (*Squalius carolitertii* Doadrio, 1988). Estes ciprinídeos endémicos da Península Ibérica foram testados num tanque de natação do tipo Brett, utilizando um procedimento padronizado de determinação do U_{crit} . Das 80 bogas testadas o U_{crit} médio (\pm D.P.) determinado foi 0.78 ± 0.15 m/s ou 3.74 ± 0.93 CT/s. Para os 72 escalos testados o U_{crit} médio (\pm D.P.) foi 0.54 ± 0.1 m/s ou 4.43 ± 0.72 CT/s. Foram encontradas diferenças significativas entre os U_{crit} de ambas as espécies. No entanto, a análise comparativa do desempenho de natação das duas espécies, sugere que a relação entre o U_{crit} e o tamanho dos indivíduos varia de forma semelhante com o aumento do comprimento do corpo para ambas as espécies. Comparações intraespecíficas entre o U_{crit} e as seguintes variáveis – comprimento, sexo, condição corporal, índice gonadossomático – também foram avaliadas. O tamanho dos indivíduos influencia de forma determinante o U_{crit} . Em contrapartida, o sexo, o factor de condição corporal e o índice gonadossomático, parecem não influenciar o desempenho natatório dos dois ciprinídeos testados, com excepção para *S. carolitertii*, onde foram encontradas diferenças significativas entre os U_{crit} de ambos os sexos. O principal objectivo deste estudo é servir como informação de base na definição dos perfis de velocidade nas passagens para peixes. A informação reunida neste estudo, se utilizada correctamente, permitirá melhorar a eficiência das passagens de peixes que são utilizadas por estas espécies durante as suas migrações.

PALAVRAS-CHAVE: Capacidade máxima aeróbia, ciprinídeos, U_{crit} , passagens para peixes, migração, Portugal.

INTRODUCTION

Swimming performance is considered a main character determining survival in many species of fish. It is assumed that the maximal swimming performance may strongly influence the ability of fish to obtain food, find a mate, avoid unfavorable conditions, suggesting that swimming capability is a major trait affecting Darwinian fitness (Drucker, 1996; Plaut, 2001).

Fishes swimming performance are classified into three categories: sustained, prolonged, and burst. Each reflects not only the constraints imposed by time, but also on the biochemical processes which supply the fuel for their application (Beamish, 1978).

Sustained swimming occurs at relatively low speeds, and can be maintained for long periods (>200 min) without interruption (Beamish, 1978). The energy used to support this activity is generated through aerobic metabolic pathways and is supported by the well-perfused red musculature (Hammer, 1995; Kieffer, 2000; Peake, 2008). Naturally, it includes cruising speed (e.g. migrating fish) and speeds for routine activity (Reidy *et al.*, 2000).

Prolonged swimming involves moderate speeds that require some anaerobic energy, and therefore eventually ends in swimming failure after 20 seconds to 200 min (Peake, 2008). By nature, prolonged activity is a relatively uneven activity and is frequently associated with periods of cruising and occasional burst (Hammer, 1995). Prolonged speeds are most accurately measured in the laboratory in swimming flumes (Beamish, 1978).

High speed locomotion is classified as burst swimming, activity that is exclusively anaerobic (glycolysis within the white muscle) in nature and relatively short-lived (< 20 s) (Kieffer, 2000; Peake, 2008). These speeds are characterized by an initial acceleration phase of unsteady swimming followed by a steady phase hereafter termed “sprint” (Beamish, 1978). Burst swimming speed is used when trying to catch prey or avoid predator attack, as well as in any other situation of sudden disturbance and maneuvering through strong current fields (Reidy *et al.*, 2000).

There are several methods of measuring swimming capability of fishes (Plaut, 2001). The main three methods used to measure this parameter in laboratorial flumes are: critical swimming speed (Brett, 1964), endurance (Beamish, 1978) and gait transition speed (Drucker, 1996) (for details on the methods not applied in this study see Appendix - I.1).

U_{crit} , a special category of prolonged swimming, was first defined and employed by Brett (1964) to designate the maximum velocity fish could maintain for a precise time period (Beamish, 1978). For the measurement, a fish is placed in a water tunnel and forced to swim against water current at different velocities (Beamish, 1978). Critical swimming speed is calculated as the sum of the penultimate velocity attained and a fraction of the velocity increment proportional to the time spent swimming at the final velocity relative to the full time interval. This method has been widely used to assess the swimming performance of several fish species in the last decades (Beamish, 1978; Hammer, 1995; Kollok, 1999; Plaut, 2001; Peake, 2008; Mateus *et al.*, 2008).

Generally it is assumed that maximum oxygen uptake occurs at the critical swimming speed (Hammer, 1995). It is also presumed to be a relatively close measure of maximum aerobic capacity of the fish and gives a good estimate for swimming capacity in general, as it includes aerobic and anaerobic swimming (Tudorache, 2008). The maximum red muscle output occurs at U_{crit} , and maximum efficiency will occur at some lower level of activity (Hammer, 1995). It is frequently used to evaluate the effects of different factors on fish swimming ability, usually in order to predict their ecological effects on fishes and their habitat (Plaut, 2001) (see Appendix - I.2). One of the most important practical applications of critical swimming speed data is related to the establishment of water velocity criteria for fishways and culverts (Peake, 2008).

The information available about the swimming capacity of the most representative group of riverine fishes in the Iberian Peninsula, the cyprinids, is still scarce (Mateus *et al.*, 2008). The Iberian nase *Pseudochondrostoma polylepis* (Steindachner 1865) and the Iberian chub *Squalius carolitertii* (Doadrio 1988) are two cyprinids endemic of the Iberian Peninsula which occur in nearly all river basins from northern and central Portugal (Santos *et al.*, 2004; Kottelat & Freyhof, 2007; Ribeiro, 2007) (see Appendix I.3 and Appendix I.4).

The locomotion activity of these cyprinids is enhanced by the variation of the environmental parameters, mainly the rise of water temperature, and is associated to the proximity of the reproductive period and the search for appropriate spawning grounds (Cervia & Elvira, 1981; Doadrio, 2001; Maia *et al.*, 2006). With the approach of the reproductive period, which normally takes place from March to June, these species migrates upstream towards gravel substrates (Carmona & Doadrio, 2000; Santos *et al.*, 2004). They are both considered non-threatened species in Portugal (Cabral *et al.*, 2005), but in Spain *S. carolitertii* is classified as threatened (Doadrio, 2001).

Hydroelectric development is a ubiquitous occurrence in many Iberian rivers (Mateus *et al.*, 2008). The construction of a dam on a river can block or delay upstream fish migrations and thus contribute to the decline and even extinction of species that depend on longitudinal movements along the stream during certain phases of their life cycle. The migration of potamodromous species, whose entire life cycle is completed within inland waters of a river system, must be considered in the assessment and optimization of the fishways (Larinier, 2000). U_{crit} data may represent important information to conservately estimate maximum allowable water velocities in fishways (Peake, 2008).

The main objective of the present study was to determine and compare the swimming performance of two endemic cyprinids of the Iberian Peninsula. The influence of size, sex, condition factor and gonad maturation on the swimming performance of both species was also assessed.

MATERIAL and METHODS

Experimental animals and Critical Swimming Speed test

The Iberian nase specimens, used on the experiments were captured in River Tagus, and the Iberian chubs were captured in River Mondego, two river basins located at the central region of Portugal. Experimental fish were captured with an electric fishing gear (Hans Grassl EL 62 generator DC, 600 V). Between March and May of 2008, we evaluated the swimming performance of 80 Iberian nase (51 males, 26 females, 3 undetermined sex) with total lengths (Lt) ranging from 11 cm to 32 cm and total weight (Wt) between 10 g and 263 g. The swimming performance of 72 Iberian chubs (29 males, 39 females, 4 undetermined sex) was evaluated between March and May of 2009. Iberian chub Lt ranged from 5 cm to 21 cm and Wt varied between 1 g and 99 g.

After being caught, fish were directly transported to the laboratory and placed in an indoor 2000-L circular fiberglass tank with controlled photoperiod of 12h-light: 12h-dark. The holding tank was equipped with appropriate filtration, aeration systems and controlled water temperature ($16 \pm 2^\circ \text{C}$). Once captured all animals were allowed to recover for at least 2 days previous to the swimming performance tests and were not fed during the whole experimental stage. Each fish was tested only once.

To evaluate the aerobic swimming capacity of *P. polylepis* and *S. carolitertii* we calculated their critical swimming speed (U_{crit}). For this procedure we used a method conducted according to Brett (1964; 1967) in a modified Brett-type swim tunnel. The swim tunnel was designed as a re-circulating water tunnel incorporating a cylindrical acrylic plastic swim chamber (dimensions L x D: 720 x 250 mm) with metal grids at both ends. The water circulated throughout the system with the help of a submersible propeller motor (Model SR4620.410 HG; Flyght, Gesallvagen, Sweden) mounted on a semi-closed circuit built with 250 mm diameter PVC pipes (see Appendix II – figure II.1).

The current velocity could be tuned by the investigator with an adjustable frequency drive (Model mini AC drive Altivar 31; Telemecanique, Rueil Malmaison

Cedex, France Altiva) which controlled the frequency of rotation of the motor propeller. A linear regression was used to determine the relation between motor speed (y) and current velocity (x ; measured with a current meter, model RHCM; Hidro-bios, Kiel-Holtenau, Germany). The resulting equation ($y=0.029x-0.0125$; $r^2=0.99$, $P<0.001$) was used to calculate the motor speed required to achieve a desired velocity (see Appendix II - table II.1 and figure II.2). A consistent flow profile along the swim chamber was accomplished over the range of velocities at which fish were forced to swim (0-1.4 m/s). This was achieved by employing an appropriate and designed diffuser section block of small diameter (6 mm) tubes (i.e. collimator), which served to remove any significant turbulence by producing a streamlined flow of minutely turbulent water.

The swim tunnel was submersed in an indoor 4500 L fiberglass ambient tank (dimensions L x W x H: 3.0 x 1.5 x 1.0 m) equipped with suitable filtration systems. The water volume used in the swimming apparatus was around 0.85 m³ and was kept during the whole experimental period. The water temperature ranged from 16 to 22°C (measured with a VEMCO Minilog-T, Halifax, Nova Scotia, Canada). This temperature range is well within that experienced by this species in the wild during the spawning migration (i.e. March to June).

All tests were carried out with the same light intensity (only artificial light), to eliminate possible differential interferences on swimming behavior. The front section of the swimming chamber was covered with an opaque PVC tube which helped to reduce the stress of the tested fish by allowing them to use it for cover.

The Lt (to nearest 1 mm) of each fish was measured the day before the trial in order to avoid stress resulting from manipulation.

Preceding the tests, the fishes underwent 60 min conditioning period at low water speed, of 1.0 bl/s to recover from handling and to allow the orientation of the fish in the swim chamber. Following the acclimation period, the water velocity was increased at a prescribed increment (0.75 bl/s) for a set period (30 min) until exhaustion. According to Peake, (2008) time intervals as low as 2 min, and as high as 60 min are used in these trials, although values greater than 20 min are most common. Kollok, (1999) referred that time intervals are generally between 10 and 30 minutes. The several parameters set for the calculation of the U_{crit} test were defined according to the available

literature (Beamish, 1978; Hammer, 1995; Kolok, 1999; Plaut, 2001), and previous experience with another cyprinid species (see Mateus *et al.*, 2008).

Fish were discouraged from resting on the rear grid by an electric field (7-12 V, 4 A) that was turned on when the fish was in contact with the grid and was kept on for 2 s. This was sufficient to cause definitive avoidance without strong reaction, encouraging the fish to swim forward against the current. Exhaustion was taken as the point at which the fish was unable to remove itself from the grid despite consecutive 2 s electric stimulations throughout a maximum 10 s period (Brett, 1964). At this point the test ends and U_{crit} can be calculated.

The time and velocity at which the fish fatigue are used to calculate the critical swimming speed using the equation first described by Brett (1964):

$$U_{crit} = U_i + \left[U_{ii} \times \left(\frac{T_i}{T_{ii}} \right) \right]$$

where, U_i is the highest velocity maintained for the whole interval (m/s), U_{ii} is the velocity increment (m/s), T_i is the time elapsed at fatigue velocity (s) and T_{ii} is the prescribed interval time (s). Critical swimming speeds are presented as absolute swimming speed ($U_{crit/abs}$) in meters *per* second (m/s) and as relative swimming speed ($U_{crit/rel}$) in body lengths per second (bl/s).

The Relative critical swimming speed ($U_{crit/rel}$) expressed in body lengths per second (bl/s) was used in order to eliminate the influence of length variation among individuals of different species and also intraspecific size differences among individuals of distinct gender. Absolute swimming speed ($U_{crit/abs}$) expressed in meters *per* second (m/s) was used to determine if the U_{crit} varies with length, since in this case what is desired is to assess differences related to size variation.

The relative swimming speed (bl/s) was obtained from the absolute swimming speed (m/s) according to the equation:

$$U_{crit/rel} = \frac{U_{crit/abs}}{Lt}$$

The velocity, at which the fishes were swimming in the swim chamber, was corrected for the blocking effect. The fish itself, by blocking part of the cross-section area of the swim chamber causes a narrowing of the available water channel, resulting in an accelerated water flow and a different pressure regime in the vicinity of its own body (Plaut, 2001). Thus, an increase cross-sectional area of the fish leads to increased water velocity over the fish. This effect was corrected in accordance with the calculations described by Beamish (1978):

$$U_c = U_s \times \left[1 + \left(\frac{A_i}{A_{ii}} \right) \right]$$

where U_c is the corrected velocity, U_s is the velocity in the absence of the fish, A_i is the maximum cross-sectional area of the fish and A_{ii} is the cross-sectional area of the swim chamber. The cross-sectional area of the fish is assumed to approximate an ellipse and thus equal to $\pi \times (h/2) \times (w/2)$, where h and w represent the maximum body height and width, respectively.

At the end of trials fish were measured for Wt (to nearest 0.1g), for cross-sectional area, examined for sex determination and the gonads weighted.

Data analysis

Fulton's condition factor (k) was calculated in order to test its influence on U_{crit} . This factor is calculated (Bagenal & Tesh, 1978) from the relationship between the

weight of the fish and its length with the intention of describing the condition of that individual. K is given by the following expression:

$$K = \left(\frac{Wt}{Lt^b} \right) \times 100$$

where, Wt and Lt are the observed total weight (in g) and total length (in cm) and b is the coefficient achieved through the regression of weight and length (see appendix I figure I.2 and figure I.4). In order to test the influence of the condition factor we used the $U_{crit/rel}$ (bl/s) to eliminate the influence of length variation.

Gonadosomatic index (GSI) was determined in order to test its influence on U_{crit} . This index is calculated (Bagenal & Tesh, 1978) through the following expression:

$$GSI = \left(\frac{Wg}{Wt} \right) \times 100$$

where, Wg is the weight of the gonads.

Regression analysis can be used to answer the question of whether a statistically significant relationship exists between variation in a morphological or physiological trait and variation in the locomotor performance. Simple linear regression involving one trait and one performance variable is one of the simplest types of regression analysis and is the most common in fish literature (Kolok, 1999). Linear regressions were performed for *C. polylepis* and *S. carolitertii*, to examine possible relations between the following variables: $U_{crit/rel}$ vs Lt ; $U_{crit/abs}$ vs Lt ; $U_{crit/rel}$ vs Fulton's condition factor (K) and $U_{crit/rel}$ vs Gonadosomatic index (GSI). In order to find possible intraspecific relations, linear regression was also performed between individuals of different sex for both species, using the following variables: $U_{crit/rel}$ vs Lt ; $U_{crit/abs}$ vs Lt ; $U_{crit/rel}$ vs K ; $U_{crit/abs}$ vs K ; $U_{crit/rel}$ vs GSI and $U_{crit/abs}$ vs GSI . These procedures were performed with the program Microsoft Office Excel (2007).

Analysis of covariance (ANCOVA) was used to compare linear slopes and intercepts of significant regressions. This analysis was performed to compare the relation between $U_{crit/rel}$ and Lt of both species and to compare males and females within each tested species. This statistical procedure was performed with the program BIOMstat for Windows (version 3.0).

Student t-test was used to compare K between *P. polylepis* of different gender. This statistic test was also used to compare the $U_{crit/rel}$ of *S. carolitertii* male and female individuals of the same dimensional classe (10-15cm). Mann-Whitney non parametric test were used to compare GSI between *P. polylepis* of different gender. Non-parametric

significance test was only applied when the assumptions of the parametric statistic were not verified. These statistical tests were performed with the program SPSS for Windows (version 15.0).

Significant differences were accepted at $P < 0.05$. Results are presented as means \pm S.D unless stated otherwise.

RESULTS

From a total of 80 *P. polylepis*, 79% ($N=63$) completed the U_{crit} test successfully (see Appendix III - tableIII.1. for individual data). For *S. carolitterii*, from a total of 72 individuals, 94% ($N=68$) completed the U_{crit} test successfully (see Appendix III - tableIII.2 for individual data). Descriptive statistic of the critical swimming speed, gonadosomatic index, Fulton's condition factor, total length and total weight values are presented in table 1, for both species. In table 2 and table 3 the same parameters are presented separately for each sex for *P. polylepis* and *S. carolitterii*, respectively.

Table 1 - Relative critical swimming speed ($U_{crit/rel}$ in bl/s), absolute critical swimming ($U_{crit/abs}$ in m/s), total length (Lt in cm) and total weight (Wt in g), gonadosomatic index (*GSI*), Fulton's condition factor (*K*), values for *P. polylepis* and *S. carolitterii* (mean; SD; maximum; minimum)

		Mean	S.D.	Max.	Min.
<i>P. polylepis</i>	$U_{crit/rel}$	3.74	0.93	6.80	2.17
	$U_{crit/abs}$	0.78	0.15	1.06	0.45
	<i>GSI</i>	4.22	3.26	13.57	0.48
	<i>K</i>	0.41	0.04	0.49	0.33
	Lt	21.92	5.43	31.20	11.70
	Wt	95.09	62.61	255.56	10.52
<i>S. carolitterii</i>	$U_{crit/rel}$	4.43	0.72	5.78	2.75
	$U_{crit/abs}$	0.54	0.10	0.73	0.28
	<i>GSI</i>	3.36	2.01	8.49	0.28
	<i>K</i>	0.47	0.05	0.65	0.32
	Lt	12.42	3.19	21.00	5.50
	Wt	22.69	18.54	99.84	1.74

The average $U_{crit/abs}$ observed for *P. polylepis* was 0.78 ± 0.15 m/s and for *S. carolitterii* the same parameter revealed a lower value, 0.54 ± 0.1 m/s (Tab. 1). The average $U_{crit/rel}$ found for *P. polylepis* was 3.74 ± 0.93 bl/s and for *S. carolitterii* the determined average $U_{crit/rel}$ value was higher, 4.43 ± 0.72 bl/s (Tab. 1). The regression analysis performed between $U_{crit/abs}$ and Lt and the regression between $U_{crit/rel}$ and Lt shows, within each species, that the $U_{crit/abs}$ increased with increasing fish size, and that the $U_{crit/rel}$ decrease with increasing fish size (Fig. 1 and 2). The results obtained for *P. polylepis* and *S. carolitterii* show a significant positive relation between absolute critical

swimming speed and size (Fig. 1). Between relative critical swimming speed and size the relation is even stronger, but negative (Fig. 2). The Ancova analysis conducted to compare the test relation between relative critical swimming speed and size of both species, revealed significant differences among adjusted intercepts but not among slopes of the linear regressions (intercepts $F = 10.94$, $P < 0.01$ and slopes $F = 1.54$, $P = 0.216$).

Table 2 - Relative critical swimming speed ($U_{crit/rel}$ in bl/s), absolute critical swimming speed ($U_{crit/abs}$ in m/s), total length (Lt in cm) and total weight (Wt in g), gonadosomatic index (GSI), Fulton's condition factor (K), values for males ($N=51$) and females ($N=26$) of *P. polylepis* (mean; SD; maximum; minimum)

		Mean	S.D.	Max.	Min.	
<i>P. polylepis</i>	Males	$U_{crit/rel}$	3.77	0.99	6.8	2.37
		$U_{crit/abs}$	0.78	0.15	1.06	0.45
		GSI	4.15	2.71	13.03	0.49
		K	0.41	0.04	0.49	0.33
		Lt	21.84	5.86	31.20	11.80
		Wt	97.25	68.38	255.60	11.75
	Females	$U_{crit/rel}$	3.66	0.77	5.69	2.17
		$U_{crit/abs}$	0.79	0.15	1.02	0.48
		GSI	4.41	4.39	13.60	0.52
		K	0.41	0.03	0.48	0.37
		Lt	22.1	4.31	29.60	11.70
		Wt	89.7	46.40	186.80	10.52

P. polylepis presented an average GSI of 4.226 ± 3.265 g while *S. carolitertii* presented a lower value 3.369 ± 2.013 g (Tab.1). For Fulton's condition factor *S. carolitertii*, exhibited a value of 0.5 ± 0.04 which is higher than 0.4 ± 0.04 , the value achieved for *P. polylepis* (Tab.1). Regression analyses were performed for both species to examine relationships between the following variables: K and Lt; $U_{crit/rel}$ and K ; $U_{crit/rel}$ and GSI . For *P. polylepis* a significant relation was only observed in the regression performed between $U_{crit/rel}$ and K while for *S. carolitertii*, significant relation was identified in the linear regression performed between $U_{crit/rel}$ and GSI (Tab.4).

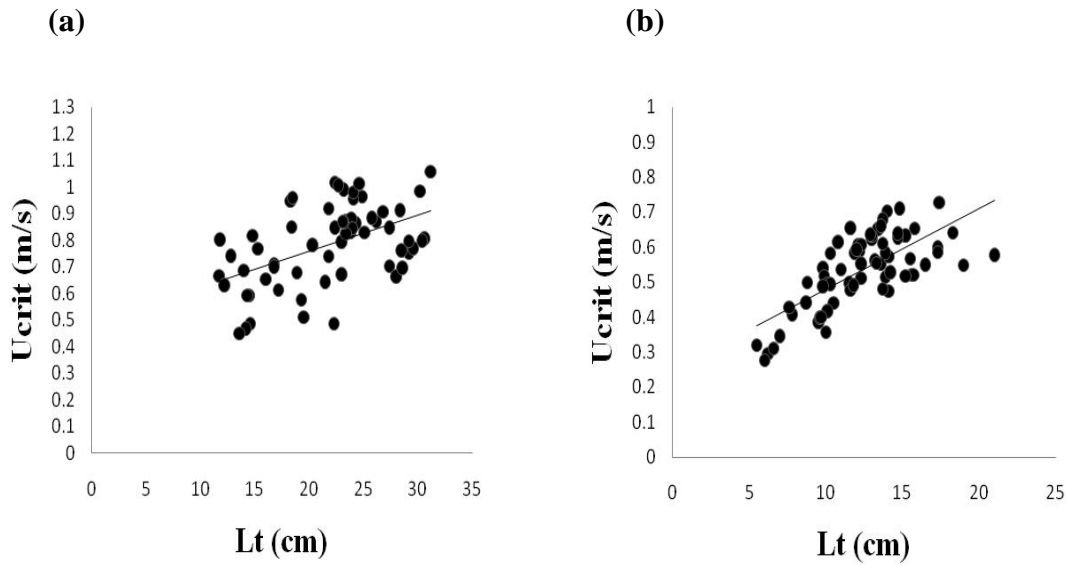


Figure 1. Relationship between the total length (Lt) and absolute critical swimming speed ($U_{crit/abs}$) expressed in m/s, for **(a)** *P. polylepis* (Linear regression parameters: $y = 0.0146x + 0.487$; $r^2 = 0.246$; $d.f. = 61$; $F = 19.87$; $P < 0.001$); and for **(b)** *S. carolitertii* (Linear regression parameters: $y = 0.023x + 0.248$; $r^2 = 0.50$; $d.f. = 66$; $F = 66.14$; $P < 0.001$).

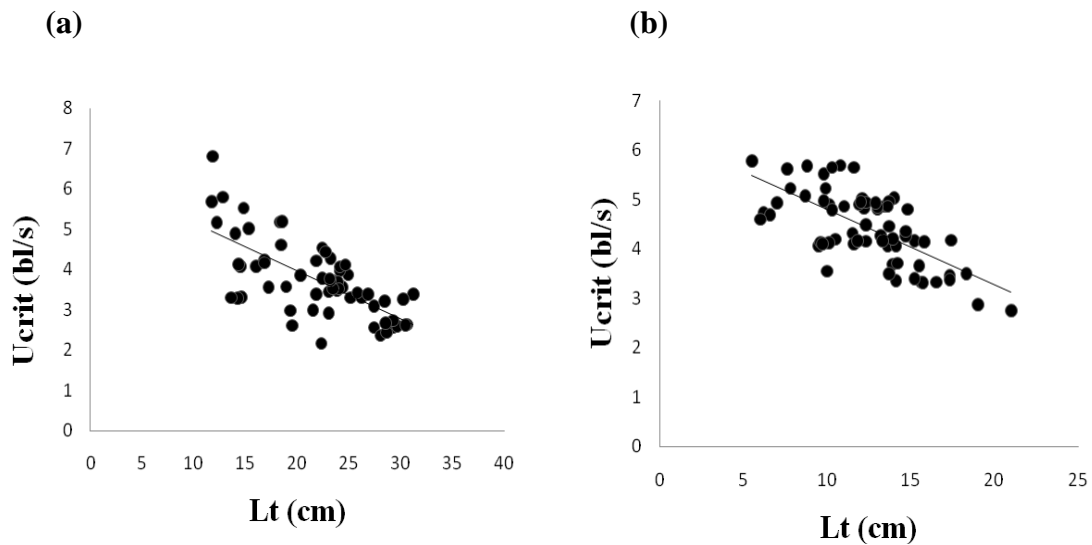


Figure 2. Relationship between the total length (Lt) and the relative critical swimming speed ($U_{crit/rel}$) expressed in bl/s, for **(a)** *P. polylepis* (Linear regression parameters: $y = 0.119x + 6.340$; $r^2 = 0.48$; $d.f. = 61$; $F = 56.09$; $P < 0.001$) and for **(b)** *S. carolitertii* (Linear regression parameters: $y = 0.153x + 6.329$; $r^2 = 0.45$; $d.f. = 66$; $F = 54.67$; $P < 0.001$).

A similar set of analysis were performed for each sex separately, in an attempt to identify possible intraspecific relations. Male and female individuals of *P. polylepis* presented very similar U_{crit} values (Tab. 2), and both have shown a significant positive relation between $U_{crit/abs}$ and Lt (see figure 3 and table 5). Between $U_{crit/rel}$ and Lt a significant relation was also observed, but negative (see figure 4 and table 5). *S. carolitertii* also presented similar U_{crit} values between males and females (Tab. 3), and have also shown a significant positive relation between $U_{crit/abs}$ and Lt (see figure 3 and table 6). The regression between $U_{crit/rel}$ and Lt showed, a significant and negative relation, for each sex, as well (see figure 4 and table 6). An Ancova analysis was performed between sexes, to compare the relation between $U_{crit/rel}$ and Lt (cm), for both species. The Ancova between *S. carolitertii*, males and females revealed significant differences in slopes but not in intercepts of the linear regression (intercepts $F = 0.23$, $P = 0.634$ and slopes $F = 4.54$, $P < 0.05$). No difference between the $U_{crit/rel}$ of male and female *P. polylepis*, was detected (intercepts $F = 0.14$, $P = 0.707$, and slopes $F = 0.13$, $P = 0.722$). The student t-test conducted according to sex revealed no significant differences between $U_{crit/rel}$ of *S. carolitertii* males and females of the same dimensional class (10-15cm) ($t = 0.499$, $d.f. = 33$, $P = 0.621$).

Table 3 - Relative critical swimming speed ($U_{crit/rel}$ in bl/s), absolute critical swimming speed ($U_{crit/abs}$ in m/s), total length (Lt in cm) and total weight (Wt in g), gonadosomatic index (*GSI*), Fulton's condition factor (*K*), values for males ($N=29$) and females ($N=39$) of *S. carolitertii* (mean; SD; maximum; minimum)

		Mean	S.D.	Max.	Min.	
<i>S. carolitertii</i>	Males	$U_{crit/rel}$	4.64	0.59	5.78	3.32
		$U_{crit/abs}$	0.52	0.11	0.7	0.31
		<i>GSI</i>	1.45	0.91	4.19	0.28
		<i>K</i>	0.5	0.04	0.6	0.4
		Lt	11.40	2.62	15.7	5.5
		Wt	16.54	10.63	39.99	1.74
	Females	$U_{crit/rel}$	4.29	0.79	5.69	2.75
		$U_{crit/abs}$	0.57	0.072	0.73	0.38
		<i>GSI</i>	4.68	1.42	8.49	1.44
		<i>K</i>	0.5	0.04	0.6	0.3
		Lt	13.65	2.91	21	8.7
		Wt	28.94	20.94	99.84	5.98

The regression analysis performed for males *P. polylepis* individuals, has shown a significant relation between $U_{crit/rel}$ and K , and also a significant relation between $U_{crit/abs}$ and GSI (Tab. 5). For females no significant differences were observed besides the regression between U_{crit} and size (Tab. 5). The student t-test conducted according to sex revealed no significant differences in Fulton's condition factor between males and females ($t = 0.21$, $d.f.= 61$, $P = 0.83$) in *P. polylepis*. For this species Mann-Whitney non-parametric test conducted according to sex revealed no significant differences in GSI between males and females ($U = 339$, $d.f.= 60$, $P = 0.53$). The same set of analysis performed for *S. carolitertii* male and female individuals separately, did not reveal any significant relations between U_{crit} and K or GSI (Tab. 6).

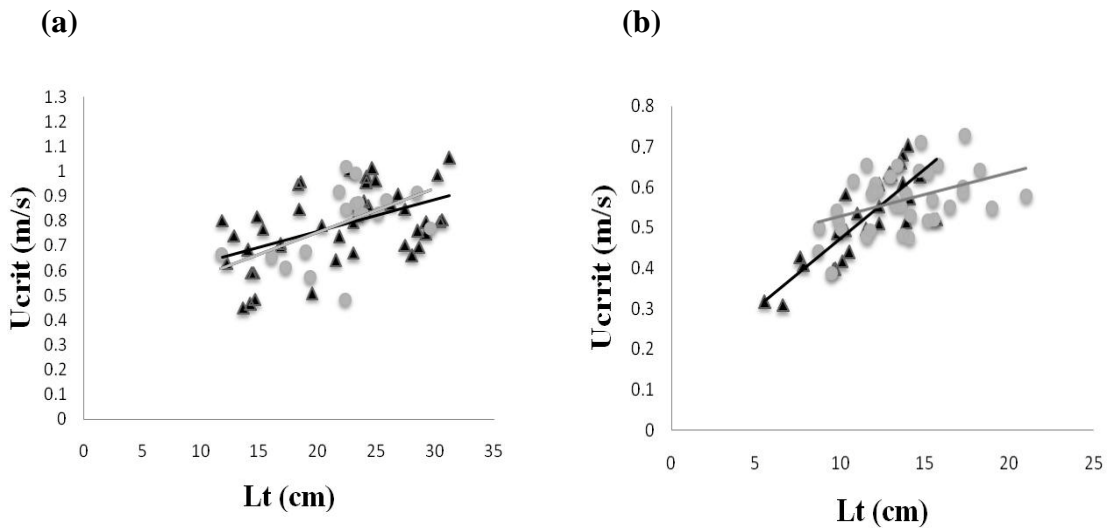


Figure 3. Relationship between the total length (Lt) and absolute critical swimming speed ($U_{crit/abs}$) expressed in m/s, for **(a)** *P. polylepis* male (\blacktriangle) and female (\bullet) (Linear regression parameters for males: $y = 0.127x + 0.504$; $r^2 = 0.24$; $d.f. = 43$; $F = 13.91$; $P < 0.001$; and for females: $y = 0.018x + 0.400$; $r^2 = 0.27$; $d.f. = 16$; $F = 5.77$; $P < 0.05$) and for **(b)** *S. carolitertii* male (\blacktriangle) and female (\bullet) individuals (Linear regression parameters for males: $y = 0.034x + 0.127$; $r^2 = 0.68$; $d.f. = 24$; $F = 52.63$; $P < 0.001$; and for females: $y = 0.011x + 0.420$; $r^2 = 0.68$; $F = 8.29$; $d.f. = 36$; $P < 0.01$).

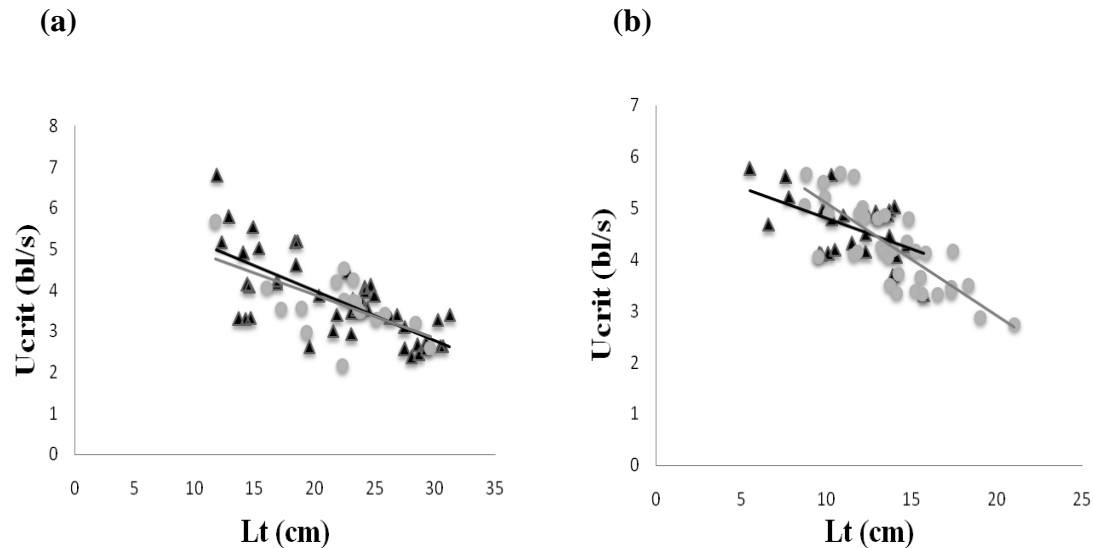


Figure 4. Relationship between the total length (L_t) and the relative critical swimming speed ($U_{crit/rel}$) expressed in bl/s, for (a) *P. polylepis* male (\blacktriangle) and female (\bullet) (Linear regression parameters for males: $y = -0.121x + 6.414$; $r^2 = 0.51$; $d.f. = 43$; $F = 44.53$; $P < 0.001$; and for females: $y = -0.106x + 6.012$; $r^2 = 0.36$; $d.f. = 16$; $F = 8.80$; $P < 0.01$) and for (b) *S. carolitertii* male (\blacktriangle) and female (\bullet) (Linear regression parameters for males: $y = -0.119x + 5.988$; $r^2 = 0.27$; $d.f. = 24$; $F = 9.02$; $P < 0.01$; and for females: $y = -0.219x + 7.281$; $r^2 = 0.64$; $d.f. = 66$; $F = 64.52$; $P < 0.001$).

Table 4 - Linear regression estimation parameters and statistics of *P. polylepis* and *S. carolitertii* for the following relations: K vs L_t , $U_{crit/rel}$ vs K and $U_{crit/rel}$ vs GSI

		Slope	Intercept	r^2	d.f.	F	Significance
<i>P. polylepis</i>	K vs L_t	-3.0E-03	0.41	0.002	61	0.11	ns
	$U_{crit/rel}$ vs K	7.73	0.545	0.105	61	7.15	$P < 0.01$
	$U_{crit/rel}$ vs GSI	0.052	3.525	0.032	58	1.94	ns
<i>S. carolitertii</i>	K vs L_t	3.3E-04	0.466	0.001	66	0.04	ns
	$U_{crit/rel}$ vs K	-0.392	4.617	0.001	66	0.04	ns
	$U_{crit/rel}$ vs GSI	-0.106	4.789	0.085	62	5.75	$P < 0.05$

K - Fulton's condition factor; L_t - total length; GSI - Gonodassomatic index; ns- non significant.

Table 5 - Linear regression estimation parameters and statistics for males and females of *P. polylepis* for the following relations: $U_{crit/rel}$ vs Lt, K Vs Lt, $U_{crit/rel}$ vs K , $U_{crit/rel}$ vs GSI , $U_{crit/abs}$ vs Lt and $U_{crit/abs}$ vs GSI

		Slopes	Intercepts	r ²	d.f.	F	Significance	
<i>Pseudochondrostoma polylepis</i>	Males	$U_{crit/rel}$ vs Lt	-0.121	6.414	0.509	43	44.53	P < 0.001
		K vs Lt	1.6E-	0.410	0.001	43	0.02	ns
		$U_{crit/rel}$ vs K	8.440	0.277	0.125	43	6.15	P < 0.05
		$U_{crit/rel}$ vs GSI	0.082	3.440	0.048	40	1.99	ns
		$U_{crit/abs}$ vs Lt	0.013	0.504	0.244	43	13.91	P < 0.001
		$U_{crit/abs}$ vs GSI	0.016	0.735	0.106	40	4.74	P < 0.05
	Females	$U_{crit/rel}$ vs Lt	-0.106	6.010	0.355	16	8.80	P < 0.01
		K vs Lt	-0.002	0.467	0.113	16	2.03	ns
		$U_{crit/rel}$ vs K	4.510	1.803	0.036	16	0.60	ns
		$U_{crit/rel}$ vs GSI	0.026	3.547	0.022	16	0.36	ns
$U_{crit/abs}$ vs Lt		0.018	0.400	0.265	16	5.77	P < 0.05	
	$U_{crit/abs}$ vs GSI	0.001	0.788	0.001	16	0.01	ns	

K- Fulton's condition factor; Lt- total length; GSI - Gonodassomatic index; ns- non significant.

Table 6 - Linear regression estimation parameters and statistics for males and females of *S. carolitertii* for the following relations: $U_{crit/rel}$ vs Lt, K Vs Lt, $U_{crit/rel}$ vs K , $U_{crit/rel}$ vs GSI , $U_{crit/abs}$ vs Lt and $U_{crit/abs}$ vs GSI

		Slopes	Intercepts	r ²	d.f.	F	Significance	
<i>Squalius carolitertii</i>	Males	$U_{crit/rel}$ vs Lt	-0.119	5.988	0.273	24	9.03	P < 0.01
		K vs Lt	-0.001	0.492	0.005	24	0.11	ns
		$U_{crit/rel}$ vs K	2.838	3.276	0.047	24	1.18	ns
		$U_{crit/rel}$ vs GSI	-0.162	4.872	0.061	24	1.57	ns
		$U_{crit/abs}$ vs Lt	0.034	0.127	0.687	24	52.63	P < 0.001
		$U_{crit/abs}$ vs GSI	-0.014	0.542	0.014	24	0.35	ns
	Females	$U_{crit/rel}$ vs Lt	-0.219	7.281	0.642	36	64.53	P < 0.001
		K vs Lt	9.7E-04	0.455	0.004	36	0.15	ns
		$U_{crit/rel}$ vs K	-4.181	6.249	0.053	36	2.02	ns
		$U_{crit/rel}$ vs GSI	-0.089	4.708	0.025	36	0.94	ns
$U_{crit/abs}$ vs Lt		0.011	0.420	0.187	36	8.29	P < 0.01	
	$U_{crit/abs}$ vs GSI	0.006	0.540	0.013	36	0.47	ns	

K- Fulton's condition factor; Lt: total length; GSI - Gonodassomatic index; ns- non significant.

DISCUSSION

Arguably prolonged swimming is the best studied form of fish locomotion, as the water velocities necessary to exercise the fish are reproducible in the laboratory with a swimming chamber and because fatigue (the inability of the fish to continue swimming) is a discrete, identifiable endpoint (Kolok, 1999). The critical swimming speed measurements give at least a rough estimate of the maximal aerobic swimming velocity in fishes, and generally assumed to reflect maximum oxygen consumption capability. Thus a reduction in critical swimming speed demonstrates reduction in general aerobic capacity (Plaut, 2001). In order to prevent anaerobic fatigue, even during moderate exercise, the oxygen carrying capacity of the blood must exceed the aerobic demands of locomotion (Bannon, 2006).

The results of this study present the critical swimming speed of two different Iberian cyprinid species. As found, *P. polylepis* shows a better aerobic swimming capacity than *S. carolitertii*, since it presents the higher absolute U_{crit} values (expressed in meters *per* second). The expression of the data in an absolute form is valuable, as it gives an estimate of the maximum velocity at which the fish can swim aerobically (Kolok, 1999). According to Santos *et al.* (2004) one of the main differences between both cyprinids were that *S. carolitertii* appeared to use slower velocities than *P. polylepis*, suggesting that water velocity may have been the primary parameter influencing microhabitat use by these species. However when comparing the relative U_{crit} mean values (expressed in body length *per* second) of both species, *S. carolitertii* presented a higher value than the *P. polylepis*. Expression of the data in relative terms can also be valuable particularly when the fish vary substantially in body size and when the ultimate goal of the study is to emphasize swimming efficiency (Kolok, 1999).

It is well-known that the absolute swimming speed of fishes increase with size, and the relative speed however decrease as size increase, as does the velocity or speed critical to the fish (Beamish, 1978; Hammer, 1995). The importance of body size as a trait that can influence the locomotor performance of animals has been recognized for almost as long as the measurements have been made (Kolok, 1999). In the present study, the regression of $U_{crit/abs}$ and the relative $U_{crit/rel}$ against total length, as shown a highly significant relationship for both species. The same analysis was performed

between males and females of both species and we have found a similar and strong significant relationship. These results are consistent with the assumption that swimming speed is dependent on length (Hammer, 1995). Therefore if a group of fish species from a wide amplitude of size range are examined, $U_{\text{crit/abs}}$ generally scales positively with body size, as well as $U_{\text{crit/rel}}$ often scales negatively with the same parameter, meaning that smaller individuals swim more efficiently than do larger ones (Kolok, 1999). In order to resist a given current speed, a small fish must swim relatively much faster than a larger fish. Moreover, assuming that predatory fish are significantly larger than prey, to avoid predation, the prey must swim or maneuver much faster and better than the predator (Plaut, 2000). While smaller individuals exhibit a superior swimming efficiency, the larger ones can reach higher swimming velocities. As reported by Santos *et al.* (2004) larger nase occurred in microhabitats with significant higher water velocities than did small conspecifics, and larger Iberian chub also occupied significantly fast-flowing areas than smaller individuals. Mateus *et al.* (2008) achieved similar results for the critical swimming speed measurement of the Iberian barbel, *Barbus bocagei* (Steindachner, 1865).

The swimming performance was compared between both Iberian cyprinids, using the relation between $U_{\text{crit/rel}}$ and size. Through this analysis we verified that the relation shifted indistinguishably between both species (i.e. similar slopes) with increasing body length. This means that the Iberian chub are, proportionally to their size, better swimmers than the Iberian nase, but the relation between swimming performance and total length of the fish is identical for both species because the $U_{\text{crit/rel}}$ decreases with increasing size.

Absolute and relative U_{crit} are both frequently measured prolonged performances, and it is likely that traits correlating with absolute U_{crit} may be different from traits that correlate with relative U_{crit} (Kolok, 1999). No significant differences between the swimming performance of male and female Iberian nase were detected, but for the Iberian chub significant differences were found between genders. However, in the case of the Iberian chub, by observing the length distribution of males and females separately we can presume that this hypothesis might be related with the differences of length revealed by individuals of different gender. The mean Lt of male individuals is 11.4 cm while for females the mean Lt is 13.6 cm. The differences found among slopes in both performances are related to the distribution of Lt between males and females.

This assumption was corroborated by the student t-test analysis performed subsequently to compare the $U_{crit/rel}$ of male and female of similar size, meaning that these individuals of different gender have indistinguishable swimming performances. According to Brett (1965) differences in the performance of sockeye salmon (*Oncorhynchus nerka* Walbaum, 1972) influenced by sex are minimal. Reidy *et al.*, (2000) concluded that there were no effect of sex on the U_{crit} when studying individual variations on the performance of Atlantic cod *Gadus morhua* L.. Mateus *et al.* (2008) have achieved the same conclusion when studying the swimming performance of another cyprinid endemic to the Iberian Peninsula the *Barbus bocagei*.

The regression conducted to test the influence of condition factor (K) on the relative U_{crit} , suggested for *P. polylepis* that fitter fish have better swimming performances, because a significant positive relation has been achieved between relative U_{crit} and K . Conversely, for the *S. carolitertii*, the same result was not found. As reported by Reidy *et al.* (2000) condition factor was also not related to the swimming performance of the cod. However Kolok (1992a) found a significant positive correlation between K and the aerobic swimming performance of winter - acclimated largemouth bass (*Micropterus salmoides*, Lacepède 1802). It appears that variation in K is only correlated to variation in swimming performance when K is very low (Reidy *et al.*, 2000).

Analogous results were attained for the regression conducted to test the influence of gonadosomatic index (GSI) on the relative U_{crit} . For the chubs a significant and negative relation was detected however for the nases the same relation was not significant. The hypotheses that fish with higher gonadosomatic index, could achieve higher U_{crit} values was then analyzed. Williams & Brett (1987) stated that in general, gravid fish were stronger swimmers than spawning fish which in turn were stronger swimmers than fish that were spawned out. Conversely Plaut (2002) reported that an increase in body mass and cross-section area at the widest part along the body of *Gambusia affinis* (Baird & Girard, 1853) resulted in a decrease in the U_{crit} to about 80% of that of non-pregnant females.

Differences in the swimming performance related to K and GSI between individuals of different sex, were examined and two significant relations were detected only in *P. polylepis* male individuals. The relation between K and $U_{crit/rel}$, as well as the relation between GSI and $U_{crit/abs}$ showed a positive significant relation for males. Thus,

these results were not corroborated with the t-student test analysis performed subsequently to compare K of different gender, and with the Mann Whitney non parametric analysis used to compare GSI of *P. polylepis* individuals of different gender.

Critical swimming speed is probably the best ecophysiological measure to estimate swimming performance capability, especially for riverine fishes that migrate upstream or fishes that hold their positions against currents (Plaut, 2001). Nelson *et al.*, (2002) stated that as employed by most investigators, critical swimming speed test causes the fish to use variant swimming modes at different times during the exercise. Thus, two conspecific fish may have identical U_{crit} values but may have used quite different physiologies and may have swum quite differently in arriving at U_{crit} . In other words, individual fish of a species show the variation in exercise physiology we have come to expect as routine from humans. According to Hammer (1995) and Plaut (2001), critical swimming speed obtained in the laboratory is not a measurement that can be extrapolated directly to populations swimming in the wild but it does give an indication of the swimming capacities of the species tested. In confined spaces such as swimming tunnels, fish alter their behavior and show very different maximum sustained speeds compared with fish in the wild. Nevertheless factors associated with Darwinian fitness have shown to be positively correlated with U_{crit} (Kolok, 1999).

Data on swim performance of salmonids are abundant, and they are excellent swimmers. This is not surprising as they are typical long distance migratory species (Tudorache *et al.*, 2008). However data for Iberian cyprinids was found to be scarce, and more research dedicated to filling these information gaps and validating the applicability of forced swimming performance protocols to fish passage situations in the field are needed (Peake, 2008). Mateus *et al.* (2008) mentions an U_{crit} value for *B. bocagei* of 0.81 ± 0.11 m/s or 3.1 ± 0.86 bl/s, which is close to the value achieved by *P. polylepis* (0.78 ± 0.15 m/s or 3.74 ± 0.93) but much higher than the absolute U_{crit} value of *S. carolitertti* (0.54 ± 0.1 m/s or 4.43 ± 0.72 bl/s) (see figure 5). Tudorache *et al.* (2008) compared the swimming capacity of seven European freshwater fish species and three were cyprinids. For *Cyprinus carpio* L. these authors found an average absolute U_{crit} that ranged from 0.87 m/s to 0.43 m/s, when average Lt varied from 22.8 cm to 4.9 cm. For *Rutilus rutilus* L. the same authors found that U_{crit} ranged from 1.1 m/s to 0.45 m/s as the Lt varied from 15.7 cm to 4.6 cm, and for *Gobio gobio* L. the U_{crit} ranged from 0.6 m/s to 0.54 m/s as the Lt varied from 12.3 cm to 10 cm. *Carassius auratus* with average Lt = 6 cm presented an U_{crit} value of 0.42 m/s or 7.0 bl/s, when tested with

an endurance procedure, according to Bainbridge (1960). Myrick & Cech (2000) studied the swimming performances of North American stream fishes, given the temperature effects on the U_{crit} , and three of this species were cyprinids. When tested at 20° C, *Mylopharodon conocephalus* (Baird & Girard 1853) presented an U_{crit} value of 0.51 m/s, *Lavinia exilicauda* (Baird & Girard 1853) presented an U_{crit} value of 0.57 m/s and *Ptychocheilus grandis* (Ayres 1854) presented an U_{crit} of 0.50 m/s. According to these authors temperature did not affect significantly the U_{crit} , however swimming performances tended to be lowest at 10° C, higher at 15° C and then decreased or remained the same at 20° C.

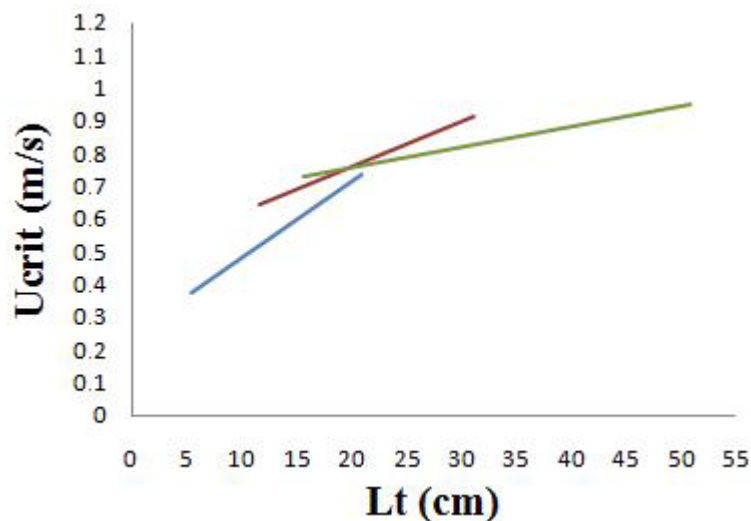


Figure 5. Relationship between the absolute critical swimming speed ($U_{crit/abs}$) and total length (Lt) of *S. carolitertii* (—) *P. polylepis* (—) and *B. bocagei* (—).

According to Hammer (1995) critical swimming speed should provide a sensitive measure for the effects of environmental or physiological stressors. The effects of environmental factors on exercise in fish were explored by Randall & Brauner (1991), and they stated that maximum aerobic swimming performance can be seen as a series of compromises between conflicting functions. Environment factors, water pH, temperature, salinity affect exercise performance in fish.

Globally, the migratory pathways are becoming increasingly degraded by anthropogenic impacts including chemical, thermal and nutrient pollution, canalization, abstraction, loss of riparian shading, construction of physical barriers, and global

climate change. Proximate consequences include eutrophication and hypoxia, loss of habitat complexity, alterations to water flow, and elevated temperatures. Migratory fishes, therefore, run a gauntlet of diverse stressors to reach adult or reproductive habitats (Bannon, 2006). The study of migratory capability of fish to pass obstacles such as fishways is crucial to migratory fish. As swimming performance and energetics are different with distinct fish species all fish species should be considered when evaluating possible effects of barriers. Man made obstacles on the pathways of migrating fish species can be one of the factors that may lead to fragmentation of populations and finally extinction of threatened fish species (Tudorache *et al.*, 2008). *P. polylepis* and *S. carolitertii*, were used in this study, because besides their intrinsic conservation value, they are emblematic species of the genera *Pseudochondrostoma* and *Squalius*. They can also be considered environmental sentinels because they present a wide distribution in northern and central Portuguese rivers where most hydroelectric infrastructures are/were implemented.

Critical swimming speed separates the sustained and prolonged performance envelopes, and it was therefore considered the best available metric for establishing water velocity criteria in culverts and fishways (Peake, 2008). One of the considerations in the construction and operation of a fishway is to provide flows at the entrance which will attract the desired species (Beamish, 1978). In general, research on passage efficiency of fish in existing culverts and fishways indicate that most problems are associated with high water velocities and turbulence at the entrance (Peake, 2008).

To evaluate swimming performance of fish with regard to the physical clearance of obstructions on migration paths, absolute values of critical swimming speed seem appropriate, because water velocities in culverts and fish ladders are absolute values (Tudorache *et al.*, 2008). The same authors argue that the U_{crit} data cannot be used to estimate maximum allowable speeds in culverts and fishways but based on the obtain data from forced swimming tests estimation could be made for maximum acceptable velocities in fish passes. Unfortunately, many problems with fishways have been identified, but very few studies have been conducted to solve these problems and/or quantitatively assess their relative importance. Water velocity appears to be the primary issue associated with culverts and fishways, although very little focused research has been conducted on fish passage through these structures, despite their number and potential to block migratory routes (Peake, 2008).

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Appendixes

Appendix I – General overview

I.1 – Measurement of the swimming performance of fish

The vast majority of information relating to swimming capacity and exercise physiology of fish has been generated by studying individuals forced to perform in swim tunnel respirometers (Hammer, 1995).

There are several methods of measuring swimming capability of fishes (Plaut, 2001). The main three methods are: critical swimming speed (Brett, 1964), endurance (Beamish, 1978) and gait transition speed (Drucker, 1996).

The endurance method, measures the time fish can swim continually against a prescribed constant water velocity. During this measurement many fish should be examined individually at different speeds, and thus, this measurement is highly time consuming, and not favorable (Plaut, 2001).

In the method of gait transition speed, a fish is placed in a water tunnel and swims against incrementally increased speed. Some species swim over low speeds by pectoral fin propulsion and with increasing speed they supplement paired fin movements with caudal fin oscillations. By observing the fish in its performance, the investigator can determine the swimming speed at which the fish shifts from one gait to another, called pectoral-caudal gait transition speed (Drucker, 1996; Plaut, 2001).

The majority of fish locomotion studies have employed a graded water velocity increment test first developed by Brett (1964), which was designated to evaluate the relative ability of salmonid fishes to ascend lotic waters to natal streams (Nelson *et al.*, 2002). Ever since Brett's work, the most common way to measure swimming performance of fishes has been by the procedure of critical swimming speed. For the measurement, a fish is placed in a water tunnel or flume and forced to swim against water current at different velocities. Fishes usually tend to hold their position against the current due to "opto-motor" response (Plaut, 2001). In some studies an electrified downstream screen is used to force the fish to swim against the current (Beamish, 1978).

According to the commonly used experimental protocol, prior to the measurement the fish is introduced into the swimming chamber and left there at water velocity of 0.5-1.0 body length (bl/s) to recover from handling stress before test begins. Recovery duration is variable, the recommended is 8-12 h because metabolic rate measurements show that this is the period required for the fish to recover from handling stress. However, recent studies showed no significant difference in U_{crit} between fish left to recover overnight and fish to recover 1-2 h (Plaut, 2001). After the recovery period, the water velocity is increased at a prescribed increment (usually 0.5-1.0 bl/s) for a prescribed duration (usually 10-60 min) and at the end of this time interval water velocity is increased again in the prescribed increment for the next interval. According to Hammer (1995) intervals shorter than 15-20 min will have a marked effect on U_{crit} . The time increments of less than 20 min may be too short, however there is no particular reason why intervals of 60 min should be used if U_{crit} alone is required.

After several intervals and increments the fish is fatigued and is swept downstream to a net screen located at downstream end of the water tunnel that prevents the fish from being carried out of the working section of the water tunnel. At this stage the measurement and critical swimming speed can be calculated (Brett, 1964; 1967).

The application of critical swimming speed is exclusive to laboratory studies, where the use of swim chambers provides a controlled environment for experimental studies of fish swimming abilities (Beamish, 1978; Drucker, 1996). The environment that the fish experiences in a water tunnel under the common experimental protocol of measuring critical swimming speed is rarely, if ever, experienced by fishes in their natural habitat. However critical swimming speed is the easiest available method of measuring swimming performance that can be measured in laboratory conditions, and gives at least a rough estimate of maximal aerobic swimming velocity in fish (Plaut, 2001).

I.2 – Physiology of fish swimming

The aerobic swimming performance in fish is affected by muscle contractibility and and/or the rate of gas transfer. Fish increase gas transfer during exercise by increasing water and blood flow, as well by increasing diffusing capacity and oxygen extraction in tissues (Randall & Brauner, 1991). Fatigue is reported in the scientific literature to result from the accumulation of waste products in particular large quantities of lactate and metabolic protons, which result in intracellular acidosis (Bannon, 2006). A reduction in blood pH results in a decrease in the haemoglobin oxygen capacity and when this capacity is reduced, a reduction in swimming performance might be anticipated (Randall & Brauner, 1991).

There are many locomotor strategies which allow fish to survive in various ecological niches. Many factors such as predator - prey interactions, reproductive behaviour and habitat distributions are of profound ecological importance and depend heavily on fish's capacity for movement (Kieffer, 2000). Swimming activity in fish is normally categorized as either aerobic or anaerobic (Beamish, 1978).

Fish locomotion can be classified within three categories: sustained, prolonged and burst swimming (Beamish, 1978). The sustained swimming performance depends on many extrinsic and intrinsic variables (Hammer, 1995), especially those that affect oxygen uptake and delivery to aerobic musculature (Bannon, 2006). During sustained exercise, muscle metabolism is largely aerobic (Beamish, 1978). In contrast to burst swimming, metabolic demand matches the supply, while waste production is balanced by disposal, thus can be maintained for long periods without resulting in muscle fatigue (Bannon, 2006). This category of swimming is primarily fuelled by fatty acid oxidation and is supported by red, slow-twitch, lateral muscle fibers and steady, undulatory locomotory gait. However sustained swimming is also supported by anaerobic capacity of the white muscle mass, with the aerobic capacity appearing to be around 25 – 35 % that of the red muscle (Bannon, 2006).

Prolonged swimming is an intermediate mode utilizing both oxidative muscles fibers and white glycolytic muscle, and depending on swimming speed, is terminated by exhaustion of white muscles (Bannon, 2006). Prolonged swimming is very difficult to separate from sustained swimming speed in the natural habitat, because rarely, if ever, can fatigue be assessed in the field. Conversely, prolonged swimming speeds are most

accurately measured in the laboratory in a swimming tunnel (Beamish, 1978), because fatigue is easy to determine (Plaut, 2001).

While much of the swimming activity in fish is aerobic in nature (Beamish, 1978), periods when the capacity for this type of swimming is exceeded exist. During these events (e.g. predator-prey interactions and spawning migrations, Beamish, 1978), burst-type exercise is largely supported by anaerobic glycolysis within the white muscle (Kieffer, 2000). Unlike aerobic-type swimming, burst swimming can be maintained for only short periods and ends in fatigue (Beamish, 1978).

Over the past decades the major research areas of fish physiologists where related to describing the physiological response to exhaustive exercise. More recently, researchers focused on inter-species and intraspecific differences, as well as the variations in the physiological response to exhaustive exercise. In particular, the role of body size, temperature, training, diet/nutrition, and water quality have been shown to limit both the exercise performance and recovery from exhaustive exercise (Kieffer, 2000).

To evaluate the effects of different environmental conditions or pollutants on fish fitness or survival in an ecological system, reliable ecologically relevant measurement of swimming capability is required. Critical swimming speed is frequently used to evaluate the effects of different factors on fish swimming ability, usually in order to predict their ecological effects on fishes and their habitats (Plaut, 2001).

I.3 - Bioecology of *Pseudochondrostoma polylepis*

The Iberian nase (Fig. I.1), *Pseudochondrostoma polylepis* (Steindachner, 1865), is an endemic cyprinid from the Iberian Peninsula (Almaça, 1995). It is distinguished by its straight mouth with a horny layer on the lower lip thick (Torralva & Oliva-Paterna, 1997). Its diet consists of vegetation (encrusting algae), detritus and occasionally invertebrates (Doadrio, 2001).



Figure I.1. The Iberian nase (*P. polylepis*)

Like other European cyprinids, females tend to grow more in length than males (Cervia & Elvira, 1981). The *P. polylepis* can attain a maximum length of 33 cm (Ribeiro, 2007) and a maximum weight of 500 g (Fig. I.2).

The life span of this species is around 10 years and they reach sexual maturity at 2/3 years (Cervia & Elvira, 1981). No clear sexual dimorphism has been found in this species, but there are some slight differences in fin size, head size and other biometrics characters (Torralva & Oliva-Paterna, 1997). However males develop small and numerous nuptial tubercles, during breeding season (Ribeiro, 2007). When the reproductive period occurs, usually between March and June, this species perform upstream migrations over great distances during breeding season, to perform posture,

which occurs in gravel substrates (Cervia & Elvira, 1981; Doadrio, 2001; Santos *et al.*, 2005).

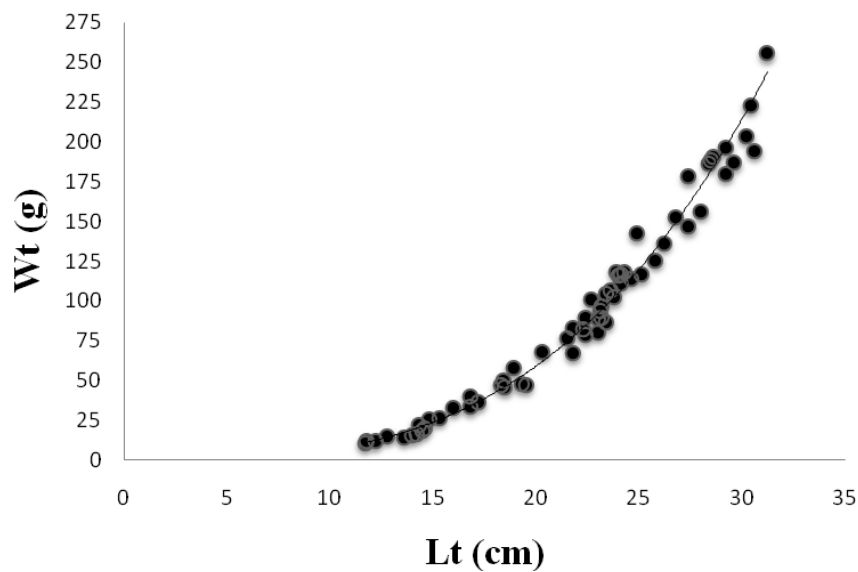


Figure I.2. Relationship between total length (Lt) and total weight (Wt) for *P. polylepis* (Linear regression estimation parameters: $y = 0.004x^{3.194}$; $r^2 = 0.988$; $d.f. = 61$; $F = 812.76$; $P < 0.001$).

Evidence of agonistic behavior has been observed in *P. polylepis*, the highest levels were observed in summer when fishes are forced to congregate in pools, and where alga growth may quickly become a scarce resource. This behavior may be linked to the defense of areas rich in algae growth on objects like large rocks that may provide some shelter against currents (Robalo *et al.*, 2004).

P. polylepis presents a great adaptability to different aquatic systems, but prefers lotic environments, with moderate or fast water flow, however this species are also well abundant in dams reservoirs (Oliveira, 2007). One of the main threats to the survival of this species in the river basins where it occurs is the apparent population isolation as a result of habitat fragmentation caused by dams and reservoirs. The construction of dams and the constant increase of hydraulic infrastructures have led to habitat reduction, through blocking and delaying the upstream fish migrations and thus contribute to the decline of the species (Cabral *et al.*, 2005).

I.3 - Bioecology of *Squalius carolitertii*

The Iberian chub (Fig. I.3), *Squalius carolitertii* (Doadrio, 1988) is an endemic cyprinid from the Iberian Peninsula (Santos *et al.*, 2005). This species can attain a maximum length of 25 cm and a maximum weight of 350 g (Carmona & Doadrio, 2000) (Fig. I.4). It is omnivorous during juvenile state, feeding on arthropods and other animals when they are adults (Carmona & Doadrio, 2000).



Figure I.3. The Iberian chub (*S. carolitertii*)

The life span of this species is around 9 years and like most cyprinids females grow faster, and became sexually mature later than males. According to Maia *et al.*, (2006) sexual maturity was reached by males at smaller size (6.6 cm for the males and 8.1 cm for the females).

The *S. carolitertii* is particularly common in medium sized reaches although it can be found in a wide variety of habitats both upstream and downstream (Carmona & Doadrio, 2000). This species often adopt a pool-dwelling behavior, particularly in summer periods when flows reach their minima (Santos *et al.*, 2005). During summer

drought the chubs are well-adapted to live in marginal pools with low levels of dissolved oxygen (Carmona & Doadrio, 2000).

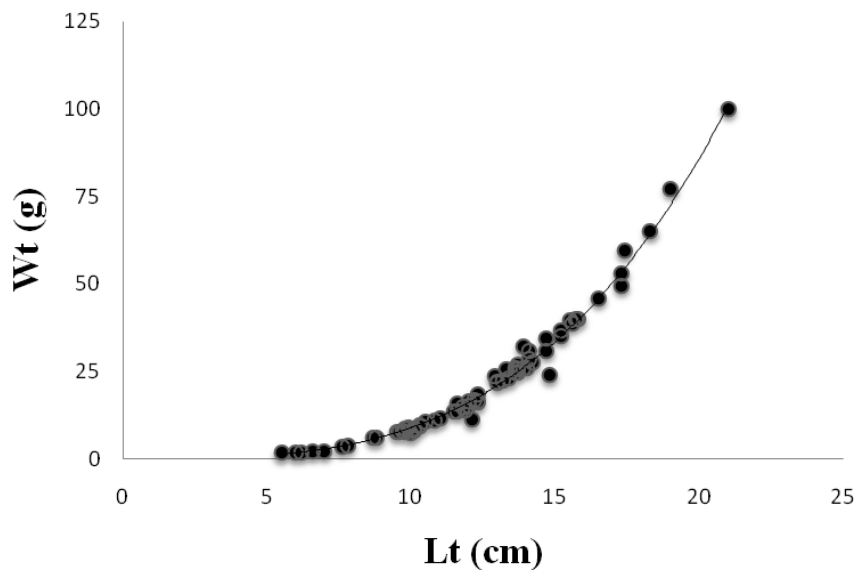


Figure I.4. Relationship between total length (Lt) and total weight (Wt) for *S. carolitertii* (Linear regression estimation parameters: $y = 0.005x^{3.277}$; $r^2 = 0.988$; d.f. = 66; $F = 402.90$; $P < 0.001$).

According to Santos *et al.*, (2005) the shift observed towards to finer substrates in spring might be related to the reproductive period which usually takes place from April to June on gravel bottoms. Water temperature is apparently the major factor associated with the fish movements (Maia *et al.*, 2005).

Principal threats affecting the Iberian chub are those related to habitat alterations due to uncontrolled agriculture development, especially water intakes, stream canalization and dams. It is extremely important to correct the impacts derived from the hydraulic infrastructures, including the construction and optimization of the fishways (Ribeiro, 2007).

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Appendix II – Swimming tunnel

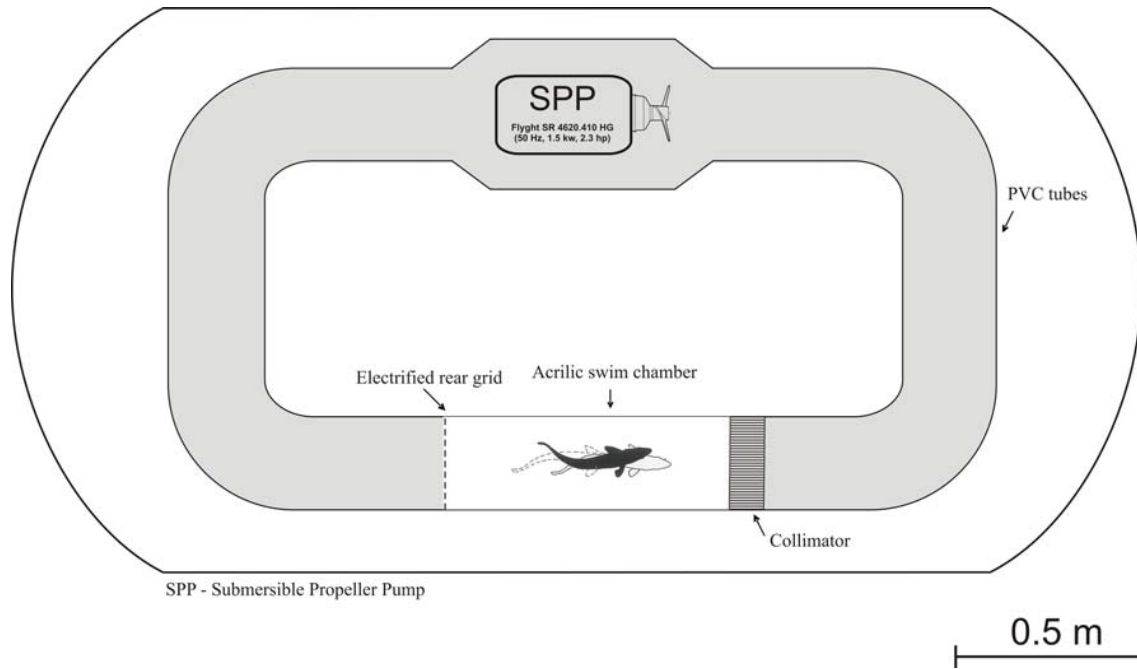


Figure II.1 – Top view of the swimming tunnel.

Table II.1 - Linear regression estimation parameters and statistics

Location	r^2	F	d.f.	Regression	P
Anterior	0.99	58517.52	48	$y = 0.0297x - 0.0125$	< 0.001
Medium	0.99	66082.35	48	$y = 0.0294x - 0.0113$	< 0.001
Posterior	0.99	53159.88	48	$y = 0.0278x - 0.0066$	< 0.001

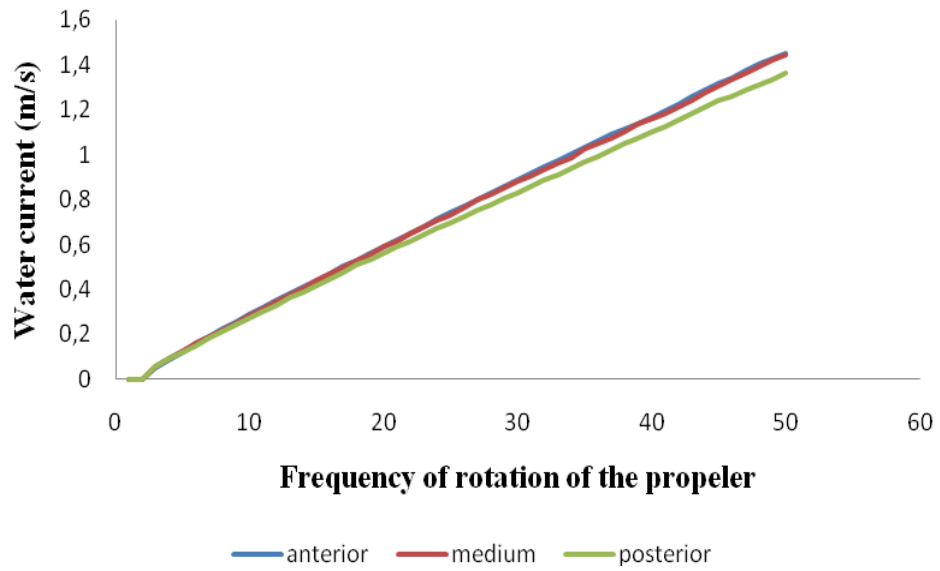


Figure II.2 - Relationships between water current (m/s) and frequency of rotation of the propeller in three different positions, anterior, medium and posterior.

Appendix III – U_{crit} individual data

Table III.1 - Individual critical swimming speed of *P. polylepis* tested

ID	Lt (cm)	Wt (g)	sex	T°C	$U_{crit/rel}$ (bl/s)	$U_{crit/abs}$ (m/s)
1*	25.2	129.59	M	16	-	-
2	22.4	89.64	F	16	3.781	0.847
3	21.5	76.63	M	16	2.994	0.644
4	19.3	47.54	F	16	2.98	0.575
5	19.5	47.07	M	17	2.618	0.51
6*	21.5	73.74	F	17.5	-	-
7	22.3	82.42	F	17.5	2.174	0.485
8	23.6	106.48	F	18	3.525	0.832
9*	22.1	69.89	M	18	-	-
10	23.4	86.7	F	17.5	3.727	0.872
11*	20.1	50.25	F	18	-	-
12*	22.4	76.34	F	17	-	-
13	22.4	78.73	F	17	4.544	1.018
14*	21.5	69.54	F	16	-	-
15*	14	21.82	M	16	-	-
16*	22	75.02	F	16	-	-
17	21.8	67.11	M	16	3.388	0.739
18	21.8	82.92	F	16	4.221	0.92
19	23	80.37	M	17	3.453	0.794
20*	30.4	237.14	M	17	-	-
21	20.3	68.12	M	17	3.858	0.783
22	24.9	142.28	M	17	3.876	0.965
23	18.4	49.67	M	17	4.614	0.849
24	27.4	178.14	M	17	3.095	0.848
25	27.4	146.53	M	18	2.564	0.703
26	29.2	196.37	M	18	2.574	0.751
27	24.1	116.63	M	18	3.971	0.957
28	23.2	96.36	F	18	4.275	0.991
29	24.3	118.02	M	18	3.558	0.864
30	23.8	102.1	F	19	3.482	0.829
31	23.9	118.21	M	19	3.682	0.88
32	24.1	110.91	M	19	4.069	0.981
33	24	116.11	M	18	3.526	0.846
34	23.4	104.31	M	18	3.523	0.824
35	23.2	89.61	F	18	3.742	0.868
36	23.1	93.49	M	18	3.769	0.871
37	22.7	101.03	M	18	4.436	1.007
38	24.6	114.01	M	18	4.122	1.014
39	31.2	255.56	M	18	3.391	1.058
40	18.3	47.17	M	18	5.176	0.947

Continues

Table III.1- Cont.

ID	Lt (cm)	Wt (g)	sex	T°C	$U_{crit/rel}$ (bl/s)	$U_{crit/abs}$ (m/s)
41	29.6	186.75	F	18	2.601	0.77
42*	32.2	255.38	M	18	-	-
43	30.6	194.33	M	18	2.636	0.806
44*	11.7	11.64	M	18	-	-
45	18.5	45.54	M	18	5.19	0.96
46	30.2	203.6	M	18	3.265	0.986
47*	29.7	187.63	F	18	-	-
48	16.8	33.34	M	18	4.229	0.71
49*	29.6	189.92	M	18	-	-
50	25.1	116.38	F	18	3.304	0.829
51	29.2	179.79	M	18	2.731	0.797
52*	32.3	251.77	F	18	-	-
53	30.4	222.94	M	18	2.629	0.799
54	26.2	136.3	M	18	3.321	0.87
55*	28.1	172.84	M	18	-	-
56	28	156.37	M	18	2.369	0.663
57	28.4	186.29	F	18	3.217	0.914
58	28.6	190.15	M	18	2.433	0.696
59	17.2	36.2	F	18	3.561	0.612
60	28.5	188	M	18	2.672	0.761
61	25.8	125.44	F	18	3.431	0.885
62*	30.6	263.4	M	18	-	-
63	26.8	152.56	M	18	3.387	0.908
64	23	88.62	M	18	2.921	0.672
65	14.6	20.17	M	18	3.321	0.485
66	11.7	10.52	F	18	5.691	0.665
67	14.5	18.26	Un	18	4.079	0.591
68*	19.6	56.21	F	18	-	-
69	14.2	16.24	Un	18	3.291	0.467
70	14	15.28	M	18	4.903	0.686
71	13.6	14.2	Un	18	3.303	0.449
72	12.2	11.75	M	18	5.166	0.63
73	14.8	25.29	M	17	5.527	0.818
74	16	32.72	F	18	4.086	0.654
75	14.3	22.15	M	18	4.136	0.591
76	12.8	15.19	M	18	5.793	0.741
77	11.8	11.78	M	18	6.804	0.803
78	18.9	57.78	F	18	3.58	0.677
79	15.3	26.55	M	18	5.02	0.768
80	16.8	40.07	M	18	4.168	0.7

ID: animal identification; Lt: total length; Wt: total weight; T°C: water temperature; U_{crit} : critical swimming speed. Un: undetermined sex*: fish that did not perform well in the swimming chamber.

Table III.2 - Individual critical swimming speed of *S. carolitertii* tested

ID	Lt (cm)	Wt (g)	sex	T°C	$U_{crit/rel}$ (bl/s)	$U_{crit/abs}$ (m/s)
1	11.5	13.71	M	18	4.323	0.497
2	9.8	8.75	F	18	5.517	0.541
3	9.9	9.11	F	18	5.227	0.517
4	17.3	49.51	F	18.5	3.466	0.599
5	12	16.38	F	18.5	4.906	0.589
6	12.2	16.72	F	20	4.836	0.589
7	11.9	14.06	F	20	4.903	0.583
8*	12.1	15.47	M	20	-	-
9	10.8	10.82	F	20	5.688	0.614
10	10.1	7.92	F	20	4.902	0.495
11	11.6	13.54	F	20	5.644	0.655
12	12.1	11.34	F	20	5.022	0.608
13	10.3	9.41	M	20	5.65	0.582
14	14.8	23.97	F	20	4.803	0.711
15	8.8	6.04	F	19	5.674	0.499
16	11.6	15.79	F	19	4.108	0.477
17	12.3	16.04	M	19	4.153	0.511
18	11	11.56	M	19.5	4.865	0.535
19	10.3	9.58	M	19.5	4.794	0.494
20	11.8	14.94	F	19.5	4.164	0.491
21	10.5	10.48	M	20	4.195	0.44
22	10.1	8.8	M	20	4.128	0.417
23*	11.8	14.58	M	20	-	-
24	9.5	7.61	F	20	4.062	0.386
25	9.6	7.64	M	20	4.139	0.397
26*	10	8.81	M	21	-	-
27*	10	8.79	F	21	-	-
28	18.3	64.98	F	16	3.508	0.642
29	21	99.84	F	16.6	2.754	0.578
30	19	77.12	F	16.5	2.884	0.548
31	13.6	24.63	F	18	4.066	0.553
32	15.6	38.81	F	18	3.334	0.52
33	17.3	52.99	F	18	3.386	0.586
34	16.5	45.89	F	18	3.336	0.55
35	15.2	36.8	F	18	4.172	0.634
36	15.7	39.99	M	18	3.319	0.521
37	13.9	26.04	M	18	3.697	0.513
38	14.1	28.52	F	18	3.363	0.474
39	15.5	39.62	F	18	3.662	0.568
40	17.4	59.45	F	18	4.182	0.728
41	14.1	30.85	M	18	4.071	0.574
42	14.7	34.4	M	18	4.269	0.628
43	13.9	31.99	F	18	4.203	0.584
44	13.7	24.76	F	18	3.509	0.481
45	15.2	35.2	F	18	3.402	0.517

Continues

Table III.2-Cont.

ID	Lt (cm)	Wt (g)	sex	T°C	$U_{crit/rel}$ (bl/s)	$U_{crit/abs}$ (m/s)
46	13.7	27	M	18	4.456	0.61
47	15.8	39.84	F	18	4.143	0.655
48	13.4	22.92	F	18	4.864	0.651
49	13.2	22.41	F	18	4.264	0.563
50	14.7	30.92	F	17.5	4.356	0.64
51	14	25.86	M	17.5	5.03	0.704
52	13	21.96	F	18	4.801	0.624
53	13.3	25.73	F	18	4.165	0.554
54	13.7	25.55	M	18	4.965	0.68
55	14.2	27.6	F	18	3.718	0.528
56	13.6	25.86	M	18	4.861	0.661
57	13	21.79	M	19	4.856	0.631
58	12.3	18.37	M	19	4.493	0.553
59	12.3	16.64	M	19.5	4.939	0.608
60	12.9	23.57	M	20	4.933	0.636
61	7.8	3.87	M	19.5	5.22	0.407
62	6.2	1.84	Un	20	4.736	0.294
63	7.6	3.57	M	20	5.617	0.427
64	6.6	2.2	M	20	4.686	0.309
65	9.7	7.92	M	19	4.11	0.399
66	7	2.3	Un	20	4.9279	0.345
67	8.7	5.98	F	20	5.074	0.441
68	9.8	7.58	M	20	4.976	0.488
69	6	1.8	Un	21	4.599	0.276
70	10	7.24	Un	21	3.553	0.355
71	5.5	1.74	M	22	5.782	0.318
72	12	15.27	F	22	4.949	0.593

ID: animal identification; Lt: total length; Wt: total weight; T°C: water temperature; U_{crit} : critical swimming speed. Un: undetermined sex*: fish that did not perform well in the swimming chamber.