

Modelling Energetic Costs of Fish Swimming

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ABSTRACT The oxygen consumption rates of two cyprinid fishes, carp (*Cyprinus carpio* L.) and roach (*Rutilus rutilus* (L.)), were analysed for a wide range of body mass and swimming speed by computerized intermittent-flow respirometry. Bioenergetic models were derived, based on fish mass (M) and swimming speed (U), to predict the minimal speed and mass-specific active metabolic rate (AMR) in these fishes ($AMR = aM^bU^c$). Mass and speed together explained more than 90% of the variance in total swimming costs in both cases. The derived models show that carp consume far more oxygen at a specific speed and body mass, thus being less efficient in energy use during swimming than roach. It was further found that in carp ($AMR = 0.02M^{0.8}U^{0.95}$) the metabolic increment during swimming is more strongly effected by speed, whereas in roach ($AMR = 0.02M^{0.93}U^{0.6}$) it is more strongly effected by body mass. The different swimming traits of carp and roach are suitable for their respective lifestyles and ecological demands. *J. Exp. Zool.* 303A:657-664, 2005. © 2005 Wiley-Liss, Inc.

The energetic costs of locomotion constitute a large proportion of the energy budget of a fish. Up to 40% of the total energy expenditure is used for swimming (Jobling, '94; Hölker and Breckling, 2002). Swimming costs thus represent an important variable when studying energy balances in fish. The swimming performance of a fish responds to a variety of environmental factors, including temperature, salinity, diet, photoperiod, pH, oxygen tension and various pollutants (Fry, '71; Webb '75; Videler, '93; Hammer, '95). Beyond this, the swimming performance depends on the species swimming mode (Hertel, '66; Sfakiotakis et al., '99) and its physiological (Rome et al., '88) and morphological (Lindsey, '78; Webb, '78) attributes. When differences in swimming costs are discussed, lifestyles and habitat preferences thus represent a link to the swimming performance of a certain species. Energetic models that relate the energy use during swimming to fish-specific or environmental factors can predict fish swimming costs. Some studies have already provided empirical energetic models of fish swimming (Tang and Boisclair, '95; Tang et al., 2000), and it has been suggested that fish body mass and swimming speed are the most important factors influencing the energy turnover during forced swimming (Boisclair and Tang, '93).

Estimations of fish swimming costs play a major role in ecological studies that evaluate the energy

turnover of a certain ecosystem. Two important species in temperate freshwater habitats are the carp, *Cyprinus carpio* L., and the roach, *Rutilus rutilus* (L.), which belong to the family of cyprinid fishes. The common carp is native to Southeast Europe, but has been widely introduced and is now found almost worldwide. It inhabits lakes or slow-moving waters and is found in a wide range of environments. Roach is one of the most abundant fish species in European fresh waters. This species inhabits lakes, stagnant waters, rivers and the brackish water of the Baltic Sea. Studies on the active metabolic rates (AMRs) related to swimming speed and body mass in carp or roach are scarce, and detailed models of speed- and mass-specific swimming costs in these species are lacking. This is particularly surprising in the case of carp because it is one of the most commonly studied fish species in the world.

The main objectives of the study were (1) to derive detailed bioenergetic models based on swimming speed and body mass to predict swimming costs in carp and roach and (2) to compare

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these cyprinids in view of their ecological demands.

MATERIALS AND METHODS

Roach were caught from Lake Müggelsee in Berlin, Germany ($52^{\circ}27'N$; $13^{\circ}40'E$). After capture, the fish were immediately transferred to the laboratory aquaria, where they were acclimated to experimental conditions for several weeks. The fish were kept without any medical treatment under experimental temperature for at least 2 weeks before removal for an experiment (Beamish, '64; Jobling, '94). Carp were obtained from the Wageningen University, Netherlands. All individuals were cloned from one strain, thus being genetically identical. Before experiments, fish were kept under laboratory conditions for several months. Both carp and roach were held in glass aquaria with constantly aerated water at a temperature of $20.0 \pm 0.5^{\circ}C$ under a 12:12 hr photoperiod cycle. Feeding was interrupted for at least 48 hr before removal of a fish for an experiment to ensure that the fish were in a post-absorptive state without elevated metabolic rates and heat increment due to specific dynamic action (Beamish and Trippel, '90; Herrmann and Enders, 2000). Specimens of roach, 21–33 cm in total length weighing 115–339 g, and carp, 19–30 cm in total length weighing 113–564 g, were used in this study.

Experimental design

Experiments were conducted in a modified Brett-type (Brett, '64) tunnel respirometer (Fig. 1). An automated and computerized intermittent-flow system allowed short interval measurements of the oxygen consumption rates (Forstner, '83; Steffensen et al., '84; Kaufmann et al., '89; Hölker, 2003). The respirometer consisted of a measuring circuit (25l), which contained a swimming chamber of 15 cm diameter, and a ventilation circuit (125l) controlled by an electronic measurement system for the exchange of aerated fresh water. Water flow within the measuring circuit was driven by a paddlewheel pump (Jesco, BN 100-65-125) that was controlled by a frequency changer (NORDAC vector mc). A flow transmitter (+GF+ Signet 8550-1) on the pressure side allowed sensitive velocity adjustments. Flow velocity was calibrated using a field version of the three-dimensional acoustic Doppler velocity meter (ADV, Nortek AS, Norway), which uses acoustic sensing techniques to measure all three components of the velocity vector in a remote sampling volume (Kraus et al., '94). The respirometer was temperature controlled to a preset value of $20 \pm 0.2^{\circ}C$. Oxygen concentration and temperature were measured with a fixed TriOxmatic 701 sensor (WTW) coupled to an oximeter (WTW, Oxi 171) that allowed automated flushing and measuring periods. The output signals for oxygen concentration, temperature

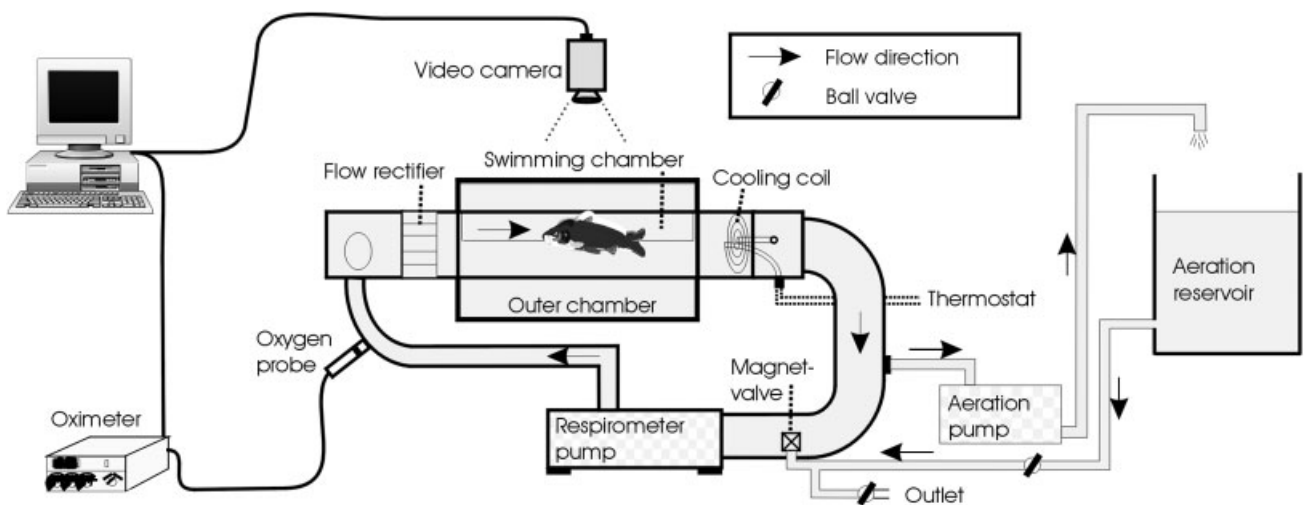


Fig. 1. Schematic diagram of an intermittent-flow respirometer. A fish is forced to swim against a water current of a given velocity. During swimming the oxygen content in the water is measured continuously with a fixed oxygen probe and recorded by a PC. The oximeter allows automated flushing and measuring periods by opening and closing the aeration circuit via a magnet valve.

and ventilation status were recorded every 6 sec by a computer.

Experimental protocol

The oxygen content of the water decreased during a measuring phase until a lower threshold value was reached, at which the ventilation connection was opened and aerated fresh water entered the measuring circuit. Ventilation of the measuring circuit stopped when the upper threshold value was reached again. The upper and lower thresholds were fixed so that all measuring periods were roughly of the same length (10–15 min) and all mixing periods were relatively short (3–5 min). The lower limit ranged from 80% to 86% oxygen saturation, so that the fish were not exposed to hypoxia. Above these values, carp and roach (Takeda and Itazawa, '79; Wedemeyer, '96) are not oxygen limited. After introducing the fish into the respirometer, a flow velocity of 0.5 bl s^{-1} was run for 2 days to acclimate the fish to experimental conditions. Subsequently, flow velocities of 0.75, 1.0, 1.25 and 1.5 bl s^{-1} were run for approximately 24 hr each. Thus, all fish were tested under equal conditions at the same relative swimming speeds. After removal of the fish a blank value was determined. Bacterial respiration remained constant after the adaptation phase of respirometry (see below) and accounted for up to 30% of the total respiration in some fish, a value also found by Dalla Via ('83).

Speed corrections

Water flow velocity in a flume increases in the presence of a fish creating a different pressure regime in the vicinity of the animal. To correct for these solid blocking effects, speed adjustments were performed for all fish showing cross-sectional areas $>10\%$ of the whole cross-sectional area of the swimming chamber (Bell and Terhune, '70):

$$U_F = U_T(1 + \varepsilon_S),$$

where U_F is the corrected flow velocity, U_T is the velocity in the swimming chamber without a fish and ε_S is the fractional error due to solid blocking (dimensionless). ε_S is defined by

$$\varepsilon_S = \tau \lambda (A_0 A_T^{-1})^{1.5},$$

where τ is a dimensionless factor depending on flume cross-sectional area, λ is the shape factor of the test fish (dimensionless), A_0 is the cross-sectional area of the test fish (cm^2) and A_T is the cross-sectional area of the swim tunnel (cm^2). We

can assume $\tau = 0.8$ for any sectional shape and $\lambda = 0.5l/t$ for any streamlined body, where l is body length and t is body thickness (Bell and Terhune, '70; Webb, '75). Body thickness was calculated as the average of the fish depth and width, and the cross-sectional area of the fish was assumed to be an approximated ellipse based on maximal depth and width measurements (Korsmeyer et al., 2002). The fractional cross-sectional area of the swimming section occupied by the fish ($A_0 A_T^{-1}$) ranged from 5% to 25%.

Data analysis

For each phase of closed respirometry, a linear regression of the decrease in oxygen saturation against time was fitted. From this slope, which gives the total respiration (R_T , $\% \text{ min}^{-1}$) of the measuring cycle, the oxygen consumption rate for a fish ($\text{mg O}_2 \text{ hr}^{-1}$) was determined using the following formula (Hölker, 2003):

$$\dot{M}_{\text{O}_2} = (R_T - R_B) \times (V_{\text{MC}} - V_F) \times 60 \times 100^{-1} \times C,$$

where \dot{M}_{O_2} is the acute oxygen consumption rate ($\text{mg O}_2 \text{ hr}^{-1}$), R_T is the total respiration ($\% \text{ min}^{-1}$), R_B is the bacterial respiration ($\% \text{ min}^{-1}$), V_{MC} is the volume of the measuring circuit (l), V_F is the volume of the fish (l), 60 is a conversion factor from min to hr, 100 is a conversion factor from mg O_2 at 100% to mg O_2 at 1% and C is the equilibrium oxygen concentration at non-standard pressure ($\text{mg O}_2 \text{ l}^{-1}$). C was computed each day to consider fluctuations of air pressure during the experiments.

As a result of handling stress during transfer from the aquaria into the respirometer, the fish showed very high oxygen consumption rates at the beginning of each experiment, the "adaptation phase". After some hours they became calmer and the oxygen consumption rate stabilized at a lower level, the "routine phase" of swimming. To distinguish between adaptation and routine phases, the following procedure after Herrmann and Enders (2000) was used: (i) The median of the last 30 oxygen consumption values was calculated and used as a first approximation of the routine metabolism. (ii) The moving average over ten oxygen consumption rates was calculated from the start of the experiment. The beginning of the routine phase was set where the first three of these consecutive moving averages were less than the first approximation of the routine metabolic rate increased by 10%. (iii) Then the median over all values in the routine phase was computed and

used as a second approximation of the routine metabolism. (iv) Thereafter, the moving average over ten oxygen consumption rates was calculated again from the start of the experiment. The final routine phase was set where the first three consecutive moving averages were less than the second approximation of the routine metabolic rate increased by 10%. This procedure was conducted for each single fish at the initial swimming velocity of 0.5 bl s^{-1} .

The minimal AMRs at a given speed were determined from the lowest 10% of the oxygen consumption rates of the routine phase of swimming. This is the oxygen needed only for movements relative to the water without thrusts of spontaneous activity within the respirometer. It was done for ten carp and nine roach at five different speeds giving 50 and 45 data points of minimal AMRs, respectively. These AMR data were pooled for each species to derive bioenergetic models of the minimal speed- and mass-specific AMR during swimming at different speeds.

AMR is the total metabolic rate of a swimming fish and thus includes the standard metabolic rate (e.g., $\text{SMR} = 0.227M^{0.73}$ for roach, Hölker, 2003). It can be converted into energy units by multiplying the oxygen consumption rate by an oxy-caloric value, which was approximated by $14.2 \text{ J mg O}_2^{-1}$ (Hepper, '88). Total swimming costs, which are represented by the AMR, are therefore composed of the SMR plus the energy required for movements relative to the surrounding water. Net swimming costs, on the other hand, refer to the measured total costs less the SMR.

Bioenergetic models

Energetic models of the swimming costs depending on body mass and swimming speed were derived from the empirical data by multivariate non-linear regression (SPSS Inc., Chicago, IL). The relationship between mass and metabolic rate is generally described by an allometric function (Peters, '83), whereas the relationship between swimming speed and metabolic rate has been described by linear, exponential or power functions (Webb, '93). However, these models are based on two-dimensional relationships. In our three-dimensional analysis, we combined the different terms of mass and speed dependency to derive the best bioenergetic model of swimming costs. These models include energy costs, fish mass and speed as independent variables of a multivariate regression. The following criteria were

tested for each model: (a) an overall regression coefficient of $r^2 > 0.5$, (b) a mean standard error (SE in %) of all estimated parameters $< 25\%$ and (c) a significance level for each estimated parameter of $P < 0.05$ of the t -value. Moreover, to test overparameterization of a model the asymptotic correlation matrix, giving all correlations between each pair of parameters, was computed. In case of high inter-parametric dependencies, a simpler model was designed leaving out one of the former parameters. Thus, several non-linear models were derived to obtain a significant correlation that described the fitted data as precise as possible without losing particular significance of the estimated parameters. The model that met these conditions best was the following multivariate function:

$$\text{AMR} = aM^bU^c,$$

where AMR is active metabolic rate ($\text{mg O}_2 \text{ hr}^{-1}$), a is a constant, M is body mass (g) and U is absolute swimming speed (cm s^{-1}). The exponents b and c are slopes of the logarithmic regression of the metabolic increment as a function of mass and speed, respectively. To test for an overall significant difference between the models, F -statistics were performed. Therefore, the residuals of both discrete models were pooled and compared with the total regression residuals of the combined data set (Zar, '99).

A sensitivity analysis was carried out to vary model input parameters over a reasonable range (range of uncertainty in values of model parameters) and observe the relative change in model response. For this the value of each parameter was changed by its standard error (SE). For model validation three criteria were used (Mayer and Butler, '93): (1) visual techniques by plots of both simulated and observed data, (2) dimensionless modelling efficiency factor (EF) and (3) coefficient (r^2) of the linear regression between observed and predicted values.

RESULTS

The rate of oxygen consumption increased with fish mass and swimming speed in both species. Fish mass and swimming speed together explained 97% and 93% of the variance in total swimming costs in carp ($F_{2,47} = 249.59$; $P < 0.001$; $r^2 = 0.97$) and roach ($F_{2,42} = 202.06$; $P < 0.001$; $r^2 = 0.93$), respectively. In general, energetic costs were higher in carp than in roach (Fig. 2). The

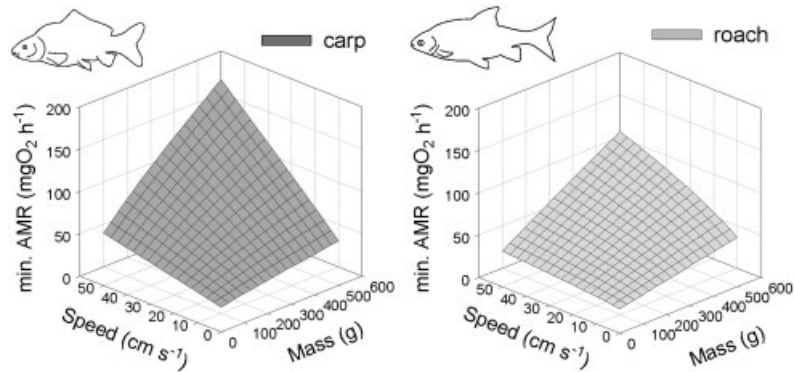


Fig. 2. Models of active metabolic rates (AMRs) in carp ($F_{2,47} = 249.59$; $P < 0.001$; $r^2 = 0.97$; left) and roach ($F_{2,42} = 202.06$; $P < 0.001$; $r^2 = 0.93$; right) predicted by a model of the form $AMR = aM^bU^c$. AMRs are predicted for the same ranges in mass (100–600 g) and speed (10–60 cm s^{-1}). The models are plotted on the same scales for a good comparability of the data. The increase of AMR with mass is slightly higher in roach ($b = 0.93$) than carp ($b = 0.80$), whereas the increase with speed is much higher in carp ($c = 0.95$) than in roach ($c = 0.60$). The models differ significantly ($F_{89,92} = 36.21$; $P < 0.001$).

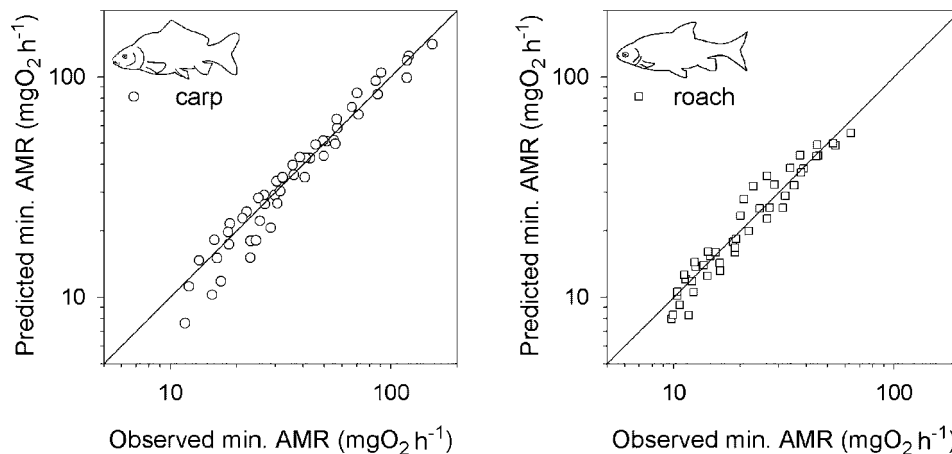


Fig. 3. Relationship between predicted and observed minimal active metabolic rates in carp (left) and roach (right). Note: double-logarithmic plot.

difference between the models for carp and roach proved to be significant ($F_{89,92} = 36.21$; $P < 0.001$).

In carp the increase of the minimal AMR was much more influenced by swimming speed than body mass, showing exponents of 0.95 (SE = 0.06; $t = 17.76$; $P < 0.001$) and 0.8 (SE = 0.06; $t = 16.30$; $P < 0.001$), respectively. The speed exponent did not differ significantly from unity. Thus, swimming costs in carp are an allometric function of fish mass but a linear function of speed. In contrast, the metabolic increment in roach was much more influenced by body mass than speed, showing exponents of 0.93 (SE = 0.07; $t = 14.45$; $P < 0.001$) and 0.6 (SE = 0.09; $t = 10.06$; $P < 0.001$), respectively. Here, the mass exponent did not differ significantly from unity. Thus, swimming costs in roach are an allometric function of speed but a linear function of body mass.

According to the sensitivity analysis the estimates of AMR were extremely sensitive to changes (\pm SE) in constant a (carp: 29%; roach: 33%), the mass exponent b (carp: 24–32%; roach: 29–41%) and the swimming exponent c (carp: 16–19%; roach: 17–21%). However, the deviation between the actually observed minimum AMR values and those predicted by the derived models was small (Fig. 3). Both EF (carp: 0.97; roach: 0.93) and r^2 (carp: 0.97; roach: 0.93) were quite good.

DISCUSSION

All swimming speeds investigated in this study were within the aerobic scope of the animals, so that anaerobic swimming, that is, recruitment of white muscle fibres, did not contribute to the energy consumption of the fish. Electromyogram

studies in carp showed that white muscle fibres are not recruited until speeds of 2.0–2.5 bls⁻¹ (Johnston et al., '77) and 2.3–2.9 bls⁻¹ (Rome et al., '84). Moreover, lactate levels remained unchanged in carp swimming at 2.0 bls⁻¹, also indicating a solely aerobic performance at this speed (van Dijk et al., '93). Since roach show much higher critical swimming speeds than carp (Heap and Goldspink, '86; Zerrath, '96), it is likely that white muscles are not recruited at speeds below 2.0 bls⁻¹ in either species.

The models presented here imply weaknesses only to a minor degree due to asymmetry and heterogeneity of the observed data. This can be assumed, because experimental conditions such as temperature, oxygen tension, diet and photoperiod were constant over the whole data set. Although all parameters respond extremely sensitively to changes in model input parameter, model validation revealed that the derived empirical models represent an accurate description of the minimal speed- and mass-specific swimming costs in these species. The bioenergetic models, based on swimming speed and fish mass, derived in this study explained 97% and 93% of the variance in total swimming costs (Table 1). In an earlier study, where the same model was used, mass and speed explained about 80% of the variance in net swimming costs, although experimental conditions for the analysed data on ten fish species differed markedly (Boisclair and Tang, '93). These results indicate that swimming speed and fish mass together are appropriate variables for modelling energetic costs of swimming. This, however, can only be assumed for forced swimming, but remains controversial with respect to spontaneous or routine swimming costs in fishes (Boisclair and

Tang, '93; Tang et al., 2000). Boisclair and Tang ('93) used the same multivariate function to estimate speed exponents and found a value of 1.21 ± 0.09 for forced swimming in fishes of various groups. This is much higher than those found for carp (0.95 ± 0.05) and roach (0.6 ± 0.06). Thus, the metabolic increment with swimming speed is slightly lower in carp but distinctly lower in roach when compared with other species. The mass exponent of 0.8 estimated by Boisclair and Tang ('93) is similar to that found in this study for carp, but is markedly lower than the exponent estimated for roach (0.93). However, the mass dependencies found here are generally consistent with allometric relationships reported for many physiological processes in animals showing exponents of 0.6–0.9 (Peters, '83).

Oxygen consumption rates of juvenile or adult roach during swimming have only been measured in a preliminary study by Hölker (2000), but the type of model used was different and therefore cannot serve for comparison here. The influence of swimming speed on the oxygen consumption in carp was calculated by Beamish ('78) for speeds up to 2.5 bls⁻¹. Unfortunately, neither a regression equation nor a mass range was provided, and information about spontaneous activity is also lacking. This makes it impossible to compare the data with those obtained in this study.

The mass and speed exponents estimated for carp and roach proved to be significantly different, but the intercepts, lying within each other's standard intervals, did not differ significantly (Table 1). The lower rate of AMR increase with speed in roach demonstrates a higher swimming efficiency of this species. In roach, energetic costs are influenced more strongly by body mass than

TABLE 1. Models of the minimum active metabolic rate (AMR) of carp and roach

Species	Model		R^2	N					
$AMR = aM^bU^c$									
Carp	$0.021M^{0.8}U^{0.95}$		0.97	10					
Roach	$0.024M^{0.93}U^{0.6}$		0.93	9					
Species	Estimate a (SE)	95% CI		Estimate b (SE)	95% CI		Estimate c (SE)	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Carp	0.021 (0.006)	0.009	0.032	0.800 (0.049)	0.701	0.899	0.948 (0.053)	0.840	1.055
Roach	0.024 (0.008)	0.007	0.041	0.930 (0.064)	0.800	1.060	0.600 (0.060)	0.480	0.720

Parameters are given with standard errors (SE) and confidence intervals (CI).

swimming speed. In carp, on the other hand, the increase in swimming costs is mainly influenced by speed, being directly proportional to it. A carp uses distinctly more energy than a roach of the same mass swimming at the same speed. Thus, roach are better adapted to a fast and cost-saving swimming performance than carp. The fact that carp grow faster and become larger (Barthelmes, '81), whereas roach show higher critical and maximum speeds (Heap and Goldspink, '86; Zerrath, '96), is consistent with these findings. This represents the different life strategies of these species. It should be mentioned that the "cultured" carp differs from the wild type in regard to its morphological characteristics (Balon, 2004). However, the common carp has been cultured in central Europe since the Middle Ages and has been released and spread into natural waters since then. It is the only carp in central European fresh waters, because the wild carp exists only in southeastern European habitats. Therefore, the cultured carp was used in the present study for a comparison with the endemic roach. The ecological demands of carp and roach are different. The carp can be characterized as a compact and deep-bodied fish, whereas the roach has a more streamlined body and a small head. In contrast to roach, carp are generally associated with slow-moving water profiles, because their reproduction area is located only in shallow and slow-moving waters (Zauner and Eberstaller, '99). Moreover, carp are bottom feeders, whereas roach are also oriented to planktic food. Fishes that forage in the open water for widely distributed prey should use higher search rates than those searching for more cryptic prey in the littoral zone, where manoeuvrability is more important (Andersson, '81; Webb, '84). This might be one reason why roach are more efficient in swimming at high speeds than carp. The habitat preferences are also represented by the partly different biogeographic river zones these species inhabit in Europe. Both species are found in the bream and barbel zones, but only roach inhabit the more upstream located, faster-flowing grayling zone of a river (Cowx and Welcomme, '98). In conclusion, the observed difference in swimming costs is consistent with the lifestyles and habitat preferences of the investigated species.

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