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Swimming efficiency and the influence of morphology on swimming costs in fishes

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Abstract Swimming performance is considered a main character determining survival in many aquatic animals. Body morphology highly influences the energetic costs and efficiency of swimming and sets general limits on a species capacity to use habitats and foods. For two cyprinid fishes with different morphological characteristics, carp (*Cyprinus carpio* L.) and roach (*Rutilus rutilus* (L.)), optimum swimming speeds (U_{mc}) as well as total and net costs of transport (COT, NCOT) were determined to evaluate differences in their swimming efficiency. Costs of transport and optimum speeds proved to be allometric functions of fish mass. NCOT was higher but U_{mc} was lower in carp, indicating a lower swimming efficiency compared to roach. The differences in swimming costs are attributed to the different ecological demands of the species and could partly be explained by their morphological characteristics. Body fineness ratios were used to quantify the influence of body shape on activity costs. This factor proved to be significantly different between the species, indicating a better streamlining in roach with values closer to the optimum body form for efficient swimming. Net swimming costs were directly related to fish morphology.

Keywords Energetic costs · Fish · Morphology · Optimum speed · Swimming efficiency

Abbreviations AMR: Active metabolic rate (W) · COT: Total cost of transport when swimming at U_{mc} · COT×W: COT times body weight (N) · M: Fish mass (kg) · NCOT: Net cost of transport · SMR: Standard

metabolic rate (W) · U: Swimming speed ($m s^{-1}$) · U_{mc} : Swimming speed associated with minimum costs ($m s^{-1}$)

Introduction

Swimming performance is considered a main trait determining fitness in many aquatic animals (Plaut 2001). Swimming is the only alternative for most aquatic prey to escape from a predator and the swimming capacity is directly related to food capture, habitat shifts and reproduction (Webb 1994; Videler 1993). It is thus of high ecological importance and presumed to be subjected to selection pressures that enhance evolutionary fitness (Priede 1985). Energetic costs of swimming are influenced by a variety of environmental factors as well as swimming mode and physiological aspects (Lighthill 1969; Rome et al. 1988; Webb 1994; Hammer 1995).

Besides this, swimming costs also depend on the morphological characteristics of a species (Lighthill 1969; Weihs and Webb 1983). Morphology sets general limits on the capacity of an organism to use habitats and foods (Wainwright 1991; Matthews 1998; Wainwright 2002; Svanbäck and Eklöv 2004). Design features can be related to energy use or swimming activity by functional analyses and it has been shown that body shape is an important factor for energy-reducing strategies (Webb 1993; Pettersson and Hedenström 2000). Many aquatic animals have produced streamlined bodies for an efficient swimming performance, which is exemplary for a convergent evolution in design to minimize locomotion costs in water (Howell 1930). Streamlining reduces drag by delaying the point of boundary layer separation (Vogel 1981). In this study we focus on the morphological characteristics of carp (*Cyprinus carpio* L.) and roach (*Rutilus rutilus* (L.)) to explain differences in energetic costs of swimming.

The total energy used during steady swimming is commonly referred to as the active metabolic rate (AMR). It is composed of the standard metabolic rate

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(SMR) and the energy required for movements relative to the surrounding water (Videler 1993). The energy for movements relative to water is required to produce thrust to overcome drag. Energetic costs of swimming are positively correlated to speed and size, because drag increases with increasing speed and surface or frontal area (Webb 1975). Morphological adaptations thus aim at reducing hydrodynamic resistance, which determines the overall energy expenditure during locomotion (Webb 1975; Aleyev 1977). The relationship between AMR and swimming speed (U) is best described by a power function (Videler and Nolet 1990; Korsmeyer et al. 2002; Ohlberger et al. 2005). This allows computing the swimming velocity associated with minimum costs per unit distance (U_{mc}), i.e. optimum speed, and the cost of transport (COT), the amount of energy expenditure at this speed (Tucker 1970). COT and U_{mc} are generally accepted for comparison of energetic costs associated with locomotion (Videler 1993). Thus, we use these energetic variables to compare the swimming efficiency of carp and roach which are characterized by different body shapes and different ecological demands.

Carp and roach belong to the family of cyprinid fishes. The common carp is native to South-East-Europe but has been widely introduced and is now found almost worldwide. This species 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 freshwaters. It inhabits lakes, standing waters, rivers and the brackish waters of the Baltic Sea. Literature regarding the swimming energetics of these two cyprinids is rare. Studies of active metabolism of adults or larger juveniles at various swimming speeds have been provided for both carp (Beamish 1978) and roach (Hölker 2000), but no data on optimum speeds and costs of transport are available.

The main objectives of the study were to (1) calculate the COT and the optimum swimming speed as relevant swimming traits in relation to body mass and (2) compare the species with respect to their swimming efficiency in relation to ecological and particularly, morphological aspects.

Materials and methods

Roach were caught from Lake Müggelsee in Berlin, Germany (52°27'N; 13°40'E). After capture the fish were immediately transferred to the laboratory aquaria, where they were acclimated to experimental conditions for several weeks. Carp were obtained from the Wageningen University, The Netherlands. All individuals were cloned from one strain, being thus genetically identical. Before experiments started they were already kept under laboratory conditions for several months. Both carp and roach were held in glass aquaria with constantly aerated water at a temperature of $20 \pm 0.5^\circ\text{C}$

under a 12 h:12 h photoperiod cycle. Feeding was interrupted for at least 48 h prior to an experiment to ensure that the fish under consideration were in a post-absorptive state without elevated metabolic rates and heat increment due to specific dynamic action (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 tunnel respirometer designed after Hölker (2003). An automated and computerized intermittent flow system allowed short-interval measurements of the rate of oxygen consumption (Steffensen et al. 1984).

The respirometer consisted of a measuring recirculation system (25 l) with a swimming chamber of 15 cm in diameter, and an external ventilation recirculation system (125 l) for the exchange of aerated water. Water flow during the measuring cycle was driven by a paddlewheel pump (Jesco, BN100-65-125), 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. 1994).

The whole respirometer was temperature-controlled to a preset value of $20 \pm 0.2^\circ\text{C}$. Temperature and oxygen concentration 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 and ventilation status were recorded every 6 s by a computer.

Experimental protocol

The oxygen content of the water decreased during a measuring phase until a fixed lower threshold was reached. The ventilation circuit was opened and aerated fresh water entered the measuring circuit until an upper threshold was re-established. The upper and lower thresholds were fixed in such a manner to run all measuring periods for roughly the same time (10–15 min) and to ensure short mixing periods (3–5 min). The lower limit ranged from 80 to 86% oxygen saturation. Above these values carp (Takeda and Itazawa 1979) and roach (Kaufmann and Wieser 1992) are not oxygen-limited. A flow velocity of 0.5 bl s^{-1} (body length per second) 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 h

each. After removal of the fish a blank value was determined. Bacterial respiration accounted for up to 30% of the total respiration, a value also found by Dalla Via (1983).

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 changes in water pressure, i.e. solid blocking effects, speed adjustments were performed for all individuals showing cross-sectional areas >10% of the whole cross-sectional area of the swimming chamber according to Bell and Terhune (1970). The cross-sectional area of the fish, which was assumed to be an ellipse based on maximal depth and width measurements, was used as the reference area to calculate the magnitude of solid blocking.

Data analysis

For each phase of closed respirometry a linear regression of the decrease in oxygen saturation against time was fitted to compute the acute oxygen consumption rate of the fish as described in Hölker (2003). Oxygen consumption rates were high at the beginning of each experiment as a result of stress during transfer to the chamber (adaptation phase). As the fish became progressively calmer, oxygen consumption rates stabilized at a distinctly lower level (routine phase) after a period of up to 60 h. Only data from the routine phases were used for further analyses.

To distinguish between adaptation and routine phases of respirometry, the procedure after Herrmann and Enders (2000) was used: (1) the median of last 30 oxygen consumption values was calculated and used as a first approximation of routine metabolism; (2) 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%; (3) then the median over all values in the routine phase was computed and used as a second approximation of the routine metabolism; (4) 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} .

Subsequently, minimum AMRs (min. AMR, $\text{mgO}_2 \text{ h}^{-1}$) were determined from the lowest 10% of the oxygen consumption rates of the routine phase of swimming (Herrmann and Enders 2000). The power function constantly resulted in higher regression coeffi-

cients than the exponential function and was therefore used as a model to describe the AMR-to-speed relationship (Videler and Nolet 1990; Korsmeyer et al. 2002; Ohlberger et al. 2005):

$$\text{AMR} = U^c \times d + e,$$

where c , d and e are constants; e is the estimated SMR, i.e. the metabolic rate at zero speed, and c is the speed exponent. Subsequently, the power function was used to determine the swimming speed associated with minimum costs (U_{mc}) and the total or gross COT as AMR at U_{mc} divided by body weight (Tucker 1970). The SMR was subtracted from the AMR at optimum speed to obtain the net costs of transport (NCOT), which represents the energetic costs for activity only. Moreover, COT was multiplied by weight (W) to compute the total energy needed by a fish per unit distance ($\text{COT} \times W$). An oxy-caloric value of $14.2 \text{ J mgO}_2^{-1}$ was used to convert oxygen consumption rates into energy units (Hepher 1988).

Fish morphology

To determine the influence of shape on the drag of a moving body in water, engineers and biologists use the fineness ratio of an elliptical body of revolution, which is the ratio of major to minor body axis (Landweber 1961; Webb 1975; Blake 1983). As a fish is not a body of revolution, the length of the minor axis can be found as the geometric mean of maximum body depth and maximum body breadth (cf Walker 2004). We calculated the fineness ratios for each individual by dividing the maximum body length by the square root of maximum depth \times maximum breadth.

Statistics

$P=0.05$ was defined as general significance level for all analyses. T -test was performed for a significance analysis of the mean speed exponents. To compare the regression equations of the swimming characteristics, F -statistics were performed to evaluate whether the regressions of both species differed significantly. To this end the pooled residuals of both discrete regressions were compared to the total regression residuals of the combined data set (Zar 1999).

Results

Minimum AMR (min. AMR, $\text{mgO}_2 \text{ h}^{-1}$) during swimming increased with increasing speed in all individuals of both species. The lowest minimum rates occurred at 0.5 bl s^{-1} and the highest at 1.5 bl s^{-1} . The relationship between minimum AMR and swimming speed (U) is best described by the power function ($\text{AMR} = U^c d + e$), which resulted in regression coefficients of determination > 0.99

in all cases (Fig. 1, Table 1). AMR was found to be higher in carp than in roach when individuals of the same size were compared at any speed. The speed exponent (c) of the power fit showed no mass dependency. The mean speed exponents were $2.53 (\pm 0.29)$ and $2.23 (\pm 0.31)$ for carp and roach, respectively (Table 1). The difference in speed exponents between the species was significant ($t = 2.19$; $N = 19$; $P = 0.044$).

Optimum swimming speed

In both species, the optimum speed allometrically correlated with body mass. Relative optimum speed (bl s^{-1}) decreased but absolute optimum speed (m s^{-1}) increased with increasing mass (Fig. 2; Table 2). Optimum speeds were significantly higher in roach (Fig. 2; Table 3). This difference becomes clearer as fish mass increases. Thus, roach optimally swim faster than carp of the same size to cover a certain distance under minimal energetic costs.

Cost of transport

In both species, COT, $\text{COT} \times W$ and NCOT showed allometric correlations with body mass. COT and NCOT decreased but $\text{COT} \times W$ increased with increasing mass of the animals (Fig. 3; Table 2). In roach, however, the relationship of COT and NCOT with mass was not significant on the basis of a 5% error probability. Mass exponents were computed as -0.17 and -0.23 for the COT and -0.17 and -0.18 for the NCOT in carp and roach, respectively. The mass exponents of the energetic costs for a fish per unit distance ($\text{COT} \times W$) were 0.77 for carp and 0.79 for roach. Swimming costs were significantly higher in carp (Table 3). The differences between the regressions for COT, $\text{COT} \times W$ and NCOT between the species were all significant ($P < 0.001$, Table 3).

Fineness ratio

Fineness ratios decreased with increasing mass of the animals. For carp the ratios ranged from 1.3 to 3.3, whereas for roach it ranged from 2.9 to 4.4 (Fig. 4; Table 4). The difference between carp and roach was significant ($F_{2,14} = 38.51$; $P < 0.001$; Table 3). The fineness ratio directly correlated with NCOT in both species. This correlation proved to be significant in carp ($r^2_{\text{carp}} = 0.764$, $N = 10$) but in roach ($r^2_{\text{roach}} = 0.531$, $N = 9$) it only describes a trend. The difference between the regressions of the species was significant ($F_{2,14} = 31.88$; $P < 0.001$).

Discussion

Speed exponents in fishes are generally assumed to be somewhere between 2 and 3 (Wieser 1991). Videler and Nolet (1990) reviewed several studies of swimming costs and presented speed exponents of 1.1–3.0 for fishes. The mean values computed for carp (2.53) and roach (2.23) are within these ranges. Based on hydrodynamic considerations, a value of 2.5 has been suggested for the metabolic increment with swimming speed under laminar flow conditions (Webb 1975). The empirically derived values in this study represent a good validation of this theoretical value. Moreover, the speed exponent of the power fit contains information on the efficiency of aerobic swimming (Webb 1993; Wardle et al. 1996). It has been shown that high-drag morphs have higher speed exponents, which result in steeper power curves and thus lower swimming efficiencies compared to low-drag fishes (Pettersson and Hedenström 2000). Speed exponents were significantly smaller in roach, indicating a higher swimming efficiency compared to carp.

The optimum swimming speed is an important parameter of a species swimming performance with high ecological relevance, because like other aquatic animals

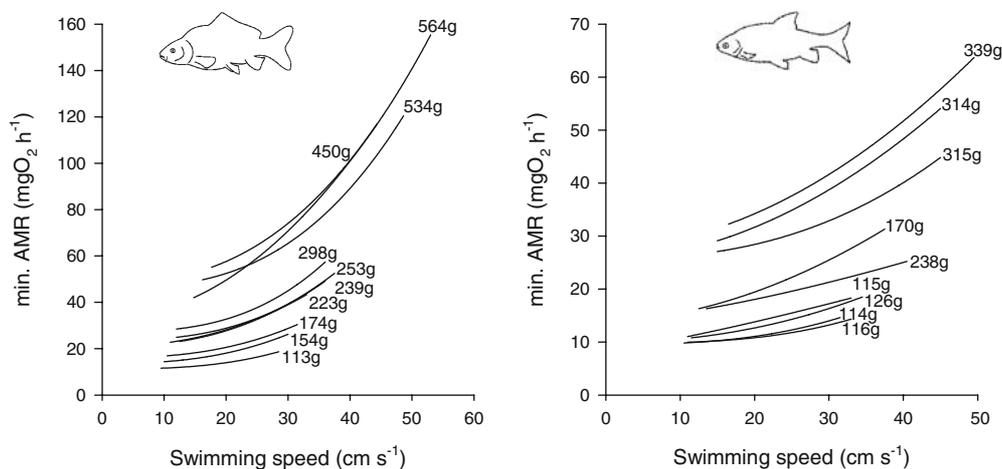


Fig. 1 Relationship between minimal active metabolic rates (AMR) and swimming speed of all carp (left) and roach (right). Small fish generally show lower AMR than larger fish. The increase of AMR with speed is stronger in carp compared to roach

Table 1 Statistical results for the power fit of all carp ($N=10$) and roach ($N=9$). The constants c , d and e are estimates of the power function $AMR = U^c \times d + e$, where c is the speed exponent and e is the standard metabolic rate (SMR) estimated by extrapolation to zero speed. Regression coefficients (r^2) and standard errors (SE) of all estimates are given for every single fish

Carp										
Mass (g)	113	154	174	223	239	253	298	450	534	564
r^2	0.998	0.995	0.999	0.999	0.999	0.998	0.999	0.994	0.999	0.998
c	2.86	2.41	2.55	2.22	2.25	2.70	2.90	2.09	2.81	2.47
SE (c)	0.26	0.44	0.07	0.20	0.13	0.28	0.24	0.41	0.03	0.25
d	2.33	3.26	5.10	9.00	12.39	8.55	9.29	29.68	17.25	26.16
SE (d)	0.29	0.68	0.18	0.96	0.85	1.20	1.05	7.93	0.26	4.36
e	11.25	14.81	16.06	20.89	20.39	23.60	27.25	33.59	46.36	48.03
SE (e)	0.23	0.54	0.14	0.78	0.69	0.96	0.83	6.83	0.23	4.02
Roach										
Mass (g)	114	115	116	126	170	238	314	315	339	
R^2	0.999	0.997	0.999	0.997	0.999	0.997	0.999	0.993	0.999	0.999
c	2.67	2.3	2.27	2.11	1.85	2.63	1.91	2.43	1.91	
SE (c)	0.14	0.28	0.06	0.31	0.12	0.38	0.11	0.47	0.11	
d	1.71	3.16	1.36	3.63	8.19	1.67	13.11	7.11	16.51	
SE (d)	0.12	0.48	0.04	0.63	0.61	0.29	0.84	1.75	1.02	
e	9.56	10.94	9.56	9.96	14.02	19.24	25.63	25.77	27.87	
SE (e)	0.1	0.39	0.03	0.52	0.51	0.23	0.71	1.41	0.86	

Fig. 2 Optimum swimming speeds of carp ($N=10$) and roach ($N=9$) in relation to body mass. Species-specific regressions for relative and absolute swimming speed differ significantly (Table 3). Note: double-logarithmic plots

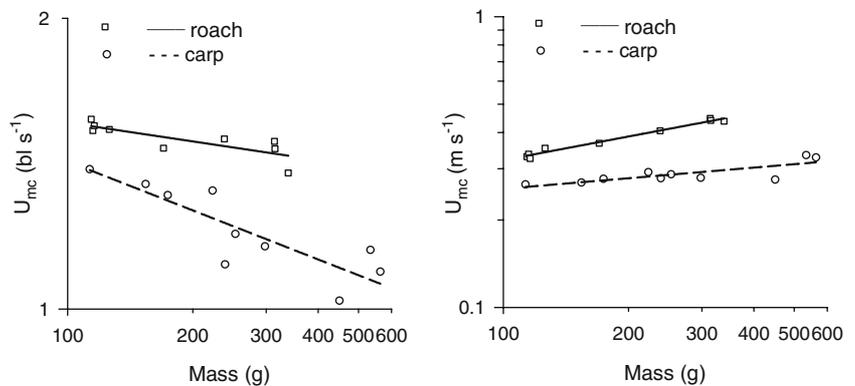


Table 2 Regression coefficients (r^2) and slopes (b) of the mass dependencies according to the allometric function $a \times M^b$ for carp ($N=10$) and roach ($N=9$)

Regression	rel. U_{mc}	abs. U_{mc}	COT	COT \times W	NCOT
<i>Carp</i>					
r^2	0.74	0.62	0.70	0.96	0.60
b	-0.17	0.12	-0.17	0.77	-0.17
SE (b)	0.03	0.03	0.04	0.06	0.05
P (b)	0.001	0.007	0.003	<0.001	0.010
<i>Roach</i>					
R^2	0.69	0.98	0.34	0.85	0.39
b	-0.06	0.27	-0.23	0.79	-0.18
SE (b)	0.02	0.02	0.12	0.14	0.09
P (b)	0.008	<0.001	0.104	<0.001	0.077

Relative U_{mc} (bl s^{-1}), absolute U_{mc} (m s^{-1}), COT, NCOT and COT \times W (N). Standard errors (SE) and P -values of the estimated slopes are given

(Fish 1998) fish generally swim close to optimum speed (Videler 1993). Optimum speeds were found to be higher in roach. This again suggests that roach experience a higher swimming efficiency than carp. According to Videler's (1993) empirically derived equation, a 100 g fish would swim optimally at 1.52 bl s^{-1} , which is intermediate to the values of 1.42 and 1.56 bl s^{-1} predicted for carp and roach, respectively. This means that carp

optimally swim slower and roach optimally swim faster than the average of several other species from various fish groups. Based on theoretical considerations, Weihs (1973) predicted optimum swimming speeds for fishes of about $1\text{--}2 \text{ bl s}^{-1}$. All single U_{mc} values for carp and roach are within this scope.

Total and net energetic costs of transport decreased with body mass due to the more favourable ratio of body volume to body surface in larger animals (Webb 1975). It has been shown before in a comparison of high-drag to low-drag fishes that SMR adjustments can compensate for hydrodynamical disadvantage by reducing the standard metabolism (Pettersson and Brönmark 1997). The estimated SMRs, however, were slightly higher in carp than in roach when fishes of the same size were compared (Table 1). Therefore and because of significantly higher net costs of swimming in carp, possible SMR adjustments cannot compensate for hydrodynamical disadvantages of the carp. Although care should be taken when using the power fit to estimate SMRs due to potential overestimation, the power fit still represents the most appropriate model of fish swimming costs (Korsmeyer et al. 2002).

Total and net COT, computed as energetic costs at U_{mc} , are significantly lower in roach, although optimum speeds are higher (Figs. 2, 3). Thus, if we compare both species at the same swimming speed the difference in

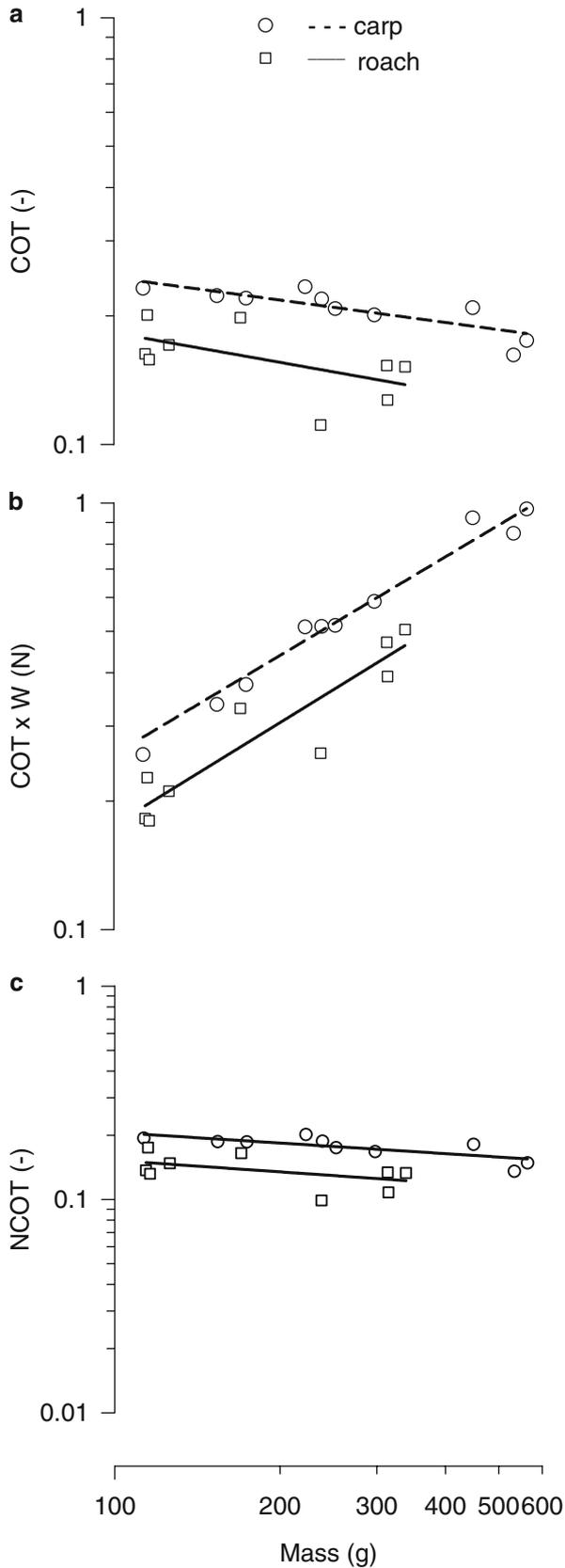


Fig. 3 Comparison of swimming costs in relation to mass between carp ($N=10$) and roach ($N=9$). Linear regressions on double-logarithmic plots are given for the total and net energetic costs per unit mass and distance (COT, *a*; NCOT, *c*) and the total energy needed by a fish per unit distance (COT \times W, *b*). All regressions differ significantly between the two species (Table 2)

locomotion costs is remarkable. Moreover, when calculating the swimming costs for speeds that distinctly deviate from the optimum velocity the difference between the species becomes even clearer. In their work

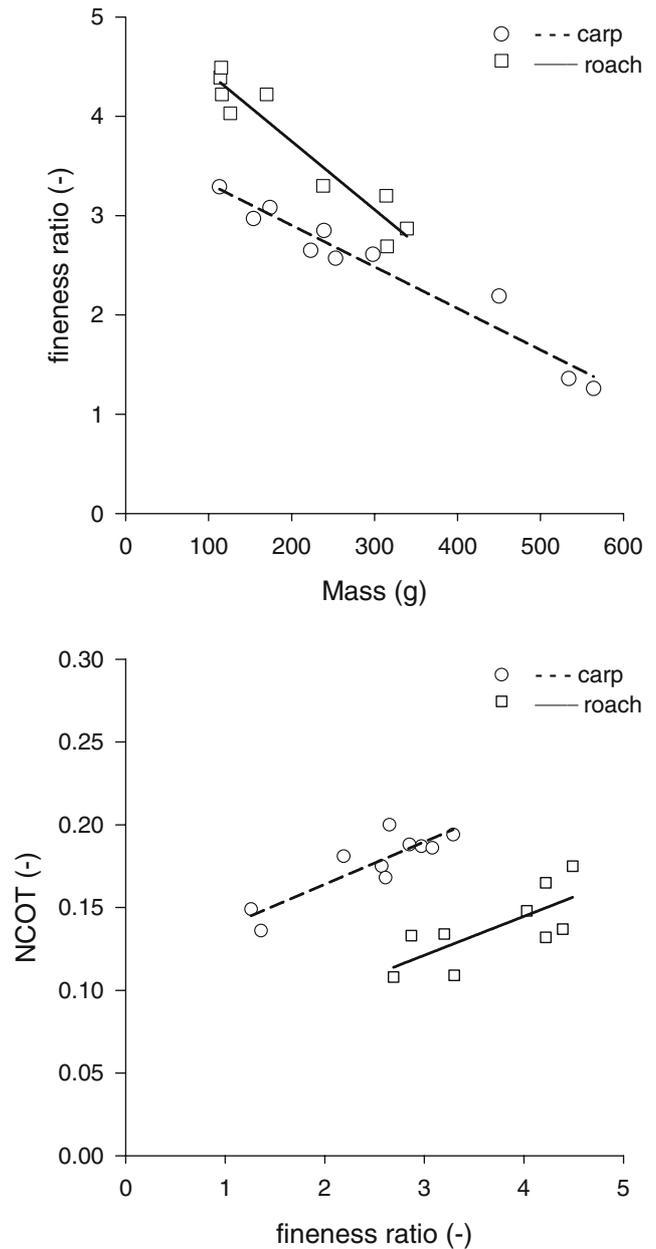


Fig. 4 Linear relationships of fitness ratio vs fish mass ($r^2_{\text{roach}}=0.92$; $r^2_{\text{carp}}=0.95$) and NCOT vs fitness ratio ($r^2_{\text{roach}}=0.53$; $r^2_{\text{carp}}=0.76$). For both plots, fitness ratio vs mass ($F_{2,14}=38.51$; $P<0.001$) and NCOT vs fitness ratio ($F_{2,14}=31.88$; $P<0.001$), the difference between the regressions for carp ($N=10$) and roach ($N=9$) is significant (Table 3)

Table 3 *F*-statistics for the comparison of optimum speed, energetic characteristics and fineness ratios of carp and roach (from Table 2)

Regression	rel. U_{mc}	abs. U_{mc}	COT	COT× <i>W</i>	NCOT	Fineness ratio
<i>F</i> -value	39.97	193.13	19.88	42.34	13.22	38.51
<i>P</i> -value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Significance	*	*	*	*	*	*

Relative U_{mc} (bl s^{-1}), absolute U_{mc} (m s^{-1}), COT, NCOT, COT×*W* (*N*) and fineness ratio. All regressions proved to be significantly different between the two species

on crucian carp, Pettersson and Hedenström (2000) showed that low-drag fishes can use a broader range of swimming velocities without substantial increase in swimming costs, whereas in high-drag fishes energetic costs increased markedly when deviating from the optimum speed. This also seems to be the case when comparing carp to roach. Carp might use a narrow range of swimming velocities due to strongly increasing energetic costs when deviating from U_{mc} . Roach, on the other hand, could use a wide range of speeds without much higher energy expenditure.

COT×body weight was correlated with fish mass with exponents of 0.77 and 0.79 in carp and roach, respectively (Fig. 3, Table 2). This can be explained by the increase in absolute U_{mc} and the increasing size of the animal, which raise the drag and hence the thrust required to overcome that drag. These values correspond to the classical value of 0.8 for the allometric relationship between body mass and metabolic rate in fishes (Clarke and Johnston 1999), but usually standard or basal metabolic rates are the subject of these studies. The allometric relationship between AMR and mass is more difficult to assess, because the activity level has to be normalized somehow. The COT provides the opportunity to compare energetic costs between species and even families or groups of animals by normalizing the activity level to the distance travelled under minimum energetic costs. Thus, the COT by definition represents the result of an optimizing process, which again correlates with mass with an exponent of nearly 0.8, namely 0.77 and 0.79 for carp and roach, respectively. It could be argued the other way round that this exponent is ubiquitous, just because it is the result of natural processes that optimize energy expenditures in animals.

Fineness ratio, which is a dimensionless measure of body slenderness, gives information about the streamlining of a fish. Values from 2 to 6 result in reduced drag with an optimum ratio for efficient swimming at 4.5 (von Mises 1945; Blake 1983). The fineness ratios for carp and roach were all below 4.5. Roach, however, showed significantly higher fineness ratios within the range of optimum body form for efficient swimming. This comparison leads to the conclusion that roach experience lower swimming costs and higher optimum speeds due to the more favourable body shape. By directly relating NCOT to fineness ratio the influence of fish morphology on swimming efficiency becomes evident. Net swimming costs are directly related to body fineness, which proved to have a considerable effect on the energetic costs of swimming in these fishes.

The present findings correspond to the general ecological demands of the species under consideration. It has been shown that fineness ratio is related to microhabitat and flow (Scarnecchia 1988). The partly different biogeographical river zones inhabited by these fishes represent their habitat preferences. Both species are found in the bream and barbel zones of a river, but only roach inhabit the more upstream located, faster flowing grayling zone (Cowx and Welcomme 1998). Moreover, the reproduction area of carp is only located in shallow and slow moving water, which is not the case for roach (Zauner and Eberstaller 1999). Thus, carp are generally associated with slower moving water profiles. Our findings can also be related to the different life strategies of these cyprinids. Presumably, the deeper body of the carp enhances its manoeuvrability, which is important for feeding in littoral habitats with dense vegetation. The nearly streamlined roach, on the other hand, is more oriented to zooplankton as food, where fast and efficient swimming is essential. Svanbäck and Eklöv (2004) revealed that a functional trade-off exists between foraging performance and body form. Streamlined fish are thus more efficient at feeding in open water, while deeper-bodied individuals are efficient at using resources in the vegetation due to a higher manoeuvrability.

It should be mentioned that we investigated cultured and not wild carp, because the former are more abundant in European freshwaters nowadays. However, swimming traits in carp presumably have been influenced by its cultivation since many centuries. Steffens (1964) found that wild carp are lower and narrower than

Table 4 Fineness ratios and net costs of transport of all carp and roach

<i>Carp</i>										
Mass (g)	113	154	174	223	239	253	298	450	534	564
Fineness ratio	3.29	2.97	3.08	2.65	2.85	2.57	2.61	2.19	1.36	1.26
NCOT	0.194	0.187	0.186	0.200	0.188	0.175	0.168	0.181	0.136	0.149
<i>Roach</i>										
Mass (g)	114	115	116	126	170	238	314	315	339	
Fineness ratio	4.39	4.49	4.22	4.03	4.22	3.30	3.20	2.69	2.87	
NCOT	0.137	0.175	0.132	0.148	0.165	0.109	0.134	0.108	0.133	

domestic races. Aleyev (1977) compared the morphs of various fish species including wild carp and roach by computing a body thickness ratio of the animals, which was significantly higher in wild carp compared to roach. This leads to the assumption that energetic costs of swimming in wild carp would be intermediate to those of domestic carp and roach.

Taken together, the results show that roach optimally swim faster with lower costs of transport, thus being more efficient in swimming compared to carp. These differences in swimming efficiency can partly be explained by the morphological characteristics of the fishes. This is attributed to the general habitat preferences and different life strategies as a result of the species ecological demands.

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References

- Aleyev YG (1977) Nekton. Junk, The Hague
- Beamish FWH (1978) Swimming capacity. In: Hoar WS, Randall DJ (eds) Fish physiology. Academic, New York, pp 101–189
- Bell WH, Terhune LDB (1970) Water tunnel design for fisheries research. Fish Res Board Can Tech Rep 195:1–69
- Blake RW (1983) Functional design and burst-and-coast swimming in fishes. Can J Zool 61:2491–2494
- Clarke A, Johnston M (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. J Anim Ecol 68:893–905
- Cowx IG, Welcomme RL (1998) Rehabilitation of rivers for fish. Fishing News Books for the Food and Agricultural Organisation of the United Nations, Oxford
- Dalla Via GJ (1983) Bacterial growth and antibiotics in animal respirometry. In: Gnaiger E, Forstner H (eds) Polarographic oxygen sensors. Springer, Berlin Heidelberg New York, pp 202–218
- Fish FE (1998) Comparative kinematics and hydrodynamics of odontocete cetaceans: morphological and ecological correlates with swimming performance. J Exp Biol 201:2867–2877
- Hammer C (1995) Fatigue and exercise tests with fish. Comp Biochem Physiol A 112:1–20
- Hepher B (1988) Nutrition of pond fishes. Cambridge University Press, Cambridge
- Herrmann J-P, Enders EC (2000) Effect of body size on the standard metabolism of horse mackerel. J Fish Biol 57:746–760
- Howell AB (1930) Aquatic mammals. Charles C Thomas, Springfield, IL
- Hölker F (2000) Bioenergetik dominanter Fischarten (*Abramis brama* (Linnaeus, 1758) und *Rutilus rutilus* (Linnaeus, 1758) in einem eutrophen See Schleswig-Holsteins—Ökophysiologie und individuenbasierte Modellierung. EcoSys (Suppl) 32:1–117
- Hölker F (2003) The metabolic rate of roach in relation to body size and temperature. J Fish Biol 62:565–579
- Kaufmann R, Wieser W (1992) Influence of temperature and ambient oxygen on the swimming energetics of cyprinid larvae and juveniles. Environ Biol Fishes 33:87–95
- Korsmeyer KE, Steffensen JF, Herskin J (2002) Energetics of median and paired fin swimming, body and caudal fin swimming, and gait transition in parrotfish (*Scarus schlegelii*) and triggerfish (*Rhinecanthus aculeatus*). J Exp Biol 205:1253–1263
- Kraus NC, Lohrmann A, Cabrera R (1994) New acoustic meter for measuring 3D laboratory flows. J Hydraul Eng 120:406–412
- Landweber L (1961) Motion of emmersed and floating bodies. In: Streeter VL (ed) Handbook of fluid dynamics. McGraw-Hill, New York
- Lighthill J (1969) Hydrodynamics of aquatic animal propulsion—a survey. Annu Rev Fluid Mech 1:413–446
- Matthews WJ (1998) Patterns in freshwater fish ecology. Kluwer Academic, New York
- von Mises R (1945) Theory of flight. Dover Books, New York
- Ohlberger J, Staaks G, van Dijk PLM, Hölker F (2005) Modelling energetic costs of fish swimming. J Exp Zool 303A:657–664
- Pettersson LB, Brönmark C (1997) Density-dependent costs of an inducible morphological defence in crucian carp. Ecology 78:1805–1815
- Pettersson LB, Hedenström A (2000) Energetics, cost reduction and functional consequences of fish morphology. Proc R Soc Lond B Biol Sci 267:759–764
- Plaut I (2001) Critical swimming speed: its ecological relevance. Comp Biochem Physiol A 131:41–50
- Priede IG (1985) Metabolic scope in fishes. In: Tytler P, Calow P (eds) Fish energetics: new perspectives. The John Hopkins University Press, Baltimore, MD, pp 33–64
- Rome LC, Funke RP, Alexander RM, Lutz G, Aldridge H, Scott F, Freadman M (1988) Why animals have different muscle fibre types. Nature 335:824–827
- Scarnecchia DL (1988) The importance of streamlining in influencing fish community structure in channelized and unchannelized reaches of a prairie stream. Reg Riv Res Manage 2:155–166
- Steffens W (1964) Vergleichende anatomisch-physiologische Untersuchungen an Wild- und Teichkarpfen (*Cyprinus carpio* L.). Ein Beitrag zur Beurteilung der Zuchtleistungen beim deutschen Teichkarpfen. Z f Fischerei, N F 12:725–800
- Steffensen JF, Johansen K, Bushnell PG (1984) An automated swimming respirometer. Comp Biochem Physiol A 79:437–440
- Svanbäck R, Eklöv P (2004) Morphology in perch affects habitat specific feeding efficiency. Funct Ecol 18:503–510
- Takeda T, Itazawa Y (1979) An estimation of the minimum level of dissolved oxygen in water required for normal life of fish. III. An experiment with carp avoiding carbon dioxide accumulation. Bull Jpn Soc Sci Fish 45:329–333
- Tucker VA (1970) Energetic cost of locomotion in animals. Comp Biochem Physiol A 34:841–846
- Videler JJ (1993) Fish swimming. Chapman and Hall, London
- Videler JJ, Nolet BA (1990) Cost of swimming measured at optimum speed: scaling effects, differences between swimming styles, taxonomic groups and submerged and surface swimming. Comp Biochem Physiol A 97:91–99
- Vogel S (1981) Life in moving fluids. Willard Grant Press, Boston, MA
- Wainwright PC (1991) Ecomorphology: experimental functional anatomy for ecological problems. Am Zool 31:635–645
- Wainwright PC (2002) Ecomorphology of locomotion in labrid fishes. Environ Biol Fishes 65:47–62
- Walker JA (2004) Dynamics of pectoral fin rowing in a fish with an extreme rowing stroke: the threespine stickleback (*Gasterosteus aculeatus*). J Exp Biol 207:1925–1939
- Wardle CS, Soofiani NM, O'Neill FG, Glass CW, Johnstone ADF (1996) Measurements of aerobic metabolism of a school of horse mackerel at different swimming speeds. J Fish Biol 49:854–862
- Webb PW (1975) Hydrodynamics and energetics of fish propulsion. Bull Fish Res Board Can 190F
- Webb PW (1993) Swimming. In: Evans DD (ed) The physiology of fishes. CRC Press, Boca Raton, FL, pp 47–73
- Webb PW (1994) Exercise performance of fish. In: Jones JH (ed) Comparative vertebrate exercise physiology: phyletic adaptations. Academic, San Diego, CA, pp 1–49
- Weihls D (1973) Optimal fish cruising speed. Nature 245:48–50

- Weihls D, Webb PW (1983) Optimization of locomotion. In: Webb PW, Weihls D (eds) Fish biomechanics. Praeger, New York, NY, pp 339–371
- Wieser W (1991) Physiological energetics and ecophysiology. In: Winfield IJ, Nelson JS (eds) Cyprinid fishes: systematics, biology and exploitation. Chapman and Hall, London, pp 427–455
- Zar JH (1999) Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ
- Zauner G, Eberstaller J (1999) Klassifizierungsschema der österreichischen Flußfischfauna in bezug auf deren Lebensraumansprüche. Österreichs Fischerei 52:198–205