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ORIGINAL PAPER

Effects of temperature, swimming speed and body mass on standard and active metabolic rate in vendace (*Coregonus albula*)

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Abstract This study gives an integrated analysis of the effects of temperature, swimming speed and body mass on standard metabolism and aerobic swimming performance in vendace (*Coregonus albula* (L.)). The metabolic rate was investigated at 4, 8 and 15°C using one flow-through respirometer and two intermittent-flow swim tunnels. We found that the standard metabolic rate (SMR), which increased significantly with temperature, accounted for up to 2/3 of the total swimming costs at optimum speed (U_{opt}), although mean U_{opt} was high, ranging from 2.0 to 2.8 body lengths per second. Net swimming costs increased with swimming speed, but showed no clear trend with temperature. The influence of body mass on the metabolic rate varied with temperature and activity level resulting in scaling exponents (b) of 0.71–0.94. A multivariate regression analysis was performed to integrate the effects of temperature, speed and mass ($AMR = 0.82 M^{0.93} \exp(0.07T) + 0.43M^{0.93}U^{2.03}$). The regression analysis showed that temperature affects standard but not net active metabolic costs in this species. Further, we conclude that a low speed exponent, high optimum speeds and high ratios of standard to activity costs suggest a remarkably efficient swimming performance in vendace.

Keywords *Coregonus spp.* · Energetic costs · Metabolic rate · Swimming performance · Temperature

Abbreviations

AMR	Active metabolic rate (J s^{-1})
BL	Body length (m)
COT	Cost of transport when swimming at U_{opt} (J m^{-1})
M	Fish mass (kg)
net	Refers to metabolic rate excluding SMR (–)
SMR	Standard metabolic rate (J s^{-1})
T	Temperature (°C)
U	Swimming speed (m s^{-1})
U_{opt}	U associated with minimum costs (m s^{-1})

Introduction

The capacity for movement in fish is directly related to food capture, habitat shift and reproduction, and it is considered a main trait determining ecological fitness (Videler 1993; Plaut 2001). The swimming performance of fishes responds to a variety of environmental factors such as diet, photoperiod, season, oxygen tension and temperature (Fry 1971; Webb 1975). Multi-factor analyses of the energetic costs during swimming are fundamental to understand the effects of extrinsic as well as intrinsic factors on the swimming capacity. It has been suggested that fish mass and swimming speed are the most important and significant factors influencing the energy turnover during swimming (Boisclair and Tang 1993), and temperature is known to be

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the most important environmental factor when the standard metabolism is considered.

The influence of temperature on the metabolic rate is of particular relevance for freshwater fishes in the temperate zone that are subjected to severe seasonal temperature changes. The temperature dependence of the standard or routine metabolic rate in animals is generally described by an exponential relationship. The corresponding temperature coefficient rages from 0.05 to 0.10 in vertebrates (White et al. 2006). The argument whether this coefficient is universal, like suggested by Gillooly et al. (2001), continues up to date (Clarke 2006; Gillooly et al. 2006). On the other hand, the influence of temperature on the active metabolic rate, especially the net activity costs, remains unclear. Different metabolic rates or swimming behaviours might be affected differently by temperature due to their different physiological bases. Various studies indicated that environmental temperature affects the swimming performance in fish (Tang et al. 2000; Lee et al. 2003; Day and Butler 2005; Claireaux et al. 2006), but nevertheless, its impact remains poorly understood due to the diversity of interacting physiological, biochemical and behavioural processes that are involved (Taylor et al. 1997). Furthermore, the few studies that have investigated the effect of thermal acclimatisation upon net activity costs described a lack of thermal effect (Beamish 1990; Claireaux et al. 2006). However, there are some examples in the literature where net swimming cost was shown to be influenced by water temperature (Johnston and Temple 2002; Dickson et al. 2002).

The energy expenditure during locomotion is further influenced by the swimming velocity of a fish. With increasing velocity, the energy expenditure for propulsion becomes more important with respect to the total energetic costs while the influence of other factors diminishes. Webb (1975) suggested that swimming cost is a power function of speed with an exponent of 2.5 under laminar flow conditions, but other authors computed distinctly lower exponents (e.g. Beamish 1978). A comparison of coefficients reported in the fish physiology literature, either determined by single- or multi-factor analyses, is difficult due to the variety of regression methods used, which include linear, semi-logarithmic or logarithmic relationships (Webb 1975; Beamish 1978; Videler and Nolet 1990; Wieser 1991; Boisclair and Tang 1993; Ohlberger et al. 2005).

The other important intrinsic parameter affecting the energy consumption of an animal is its body mass. The metabolic rate, like many other physiological processes, is related to body mass by an allometric relationship (Winberg 1961; Schmidt-Nielsen 1972). It has been assumed that the scaling exponent of this relationship is 0.75 for all animals and plants, derived from the physics of distribution networks (West et al. 1997; Brown et al. 2004). However, broad literature reviews revealed significant allometric exponent heterogeneity between various animal groups (White et al. 2006; Glazier 2005). Moreover, ectotherms seem to have higher exponents compared to endotherms (McNab 2002) and values found in the fish physiology literature vary considerably.

An integrated analysis of the effects of temperature, swimming speed and body mass on standard and net activity costs in vendace (*Coregonus albula* (L.)) is provided in this study by means of a multivariate non-linear regression analysis. Moreover, the swimming speed associated with minimum costs per unit distance (U_{opt}) and the energy expenditure when swimming at this speed (COT), representing two ecologically important measures of the swimming performance, were computed for this species.

Vendace is a typically lacustrine coregonid that mainly occurs in northern and Baltic Europe. It is the dominant pelagic fish species in the dimictic, oligotrophic Lake Stechlin, Germany (Mehner and Schulz 2002). Vendace prefers high concentrations of dissolved oxygen and low water temperatures (see Helland et al. 2007). Mean environmental temperature at the population depth for vendace in Lake Stechlin ranges year-round from 3.3 to 7.3°C, but the fish encounter higher water temperatures during food capture since they perform diel vertical migration to lower water depths (Helland et al. 2007). It can be assumed that vendace feature an efficient swimming performance due to its streamlined body form. In this study, we present the first ever published data of active metabolic costs in this species.

Materials and methods

Fish hatching and maintenance

Autumn/winter spawning vendace (*Coregonus albula)* were caught in late December by gill netting (15 mm mesh size) from Lake Stechlin (53°10′N, 13°02′E), Germany. Ripe adults were striped and propagated artificially. Larvae were hatched at 4°C, subsequently raised in circular basins (80 l) and fed with brine shrimp (*Artemia salina*), rotifers (*Brachionus* spp.) and commercially available dry food. At a size of approximately 10 cm, fish were transferred to 500–1,000 l basins and fed with salmon dry food only. The study was conducted in consideration of the seasonal temperatures in the lake, i.e. experiments were carried out in winter, autumn or spring and summer for the 4, 8 and 15°C, respectively. The fish were held at the respective experimental temperatures for at least one week before experiments started. Feeding was interrupted 48 h prior to the experiments to avoid elevated oxygen consumption

rates due to specific dynamic action. Vendace used in this study had a length of 10–22 cm and a body mass of 10–75 g.

Experimental design

The experiments were conducted with three different respirometers. One had a simple flow-through design, where fish were placed in small measuring chambers with a minimized water flow to determine the standard metabolic rate. The other two were Brett-type tunnel respirometers (Brett 1964) with an automated and computerised intermittent-flow system to measure the active metabolic rates during swimming. All respirometers were placed in a climatic chamber and equipped with a chilling unit for fine-tuning of the temperature.

SMR measurements

The standard oxygen consumption of the fish was measured with a flow-through respirometer (Ludolph, Bremerhaven, Germany). It consisted of six Plexiglas chambers surrounding a central cone with the oxygen sensor (type 1000-200) connected to an oxymeter (M200, both Eschweiler, Kiel, Germany). Each measuring unit (680 ml) was supplied by aerated fresh water from the reservoir tank surrounding the six chambers. Oxygen rates were measured alternately by switching the direction of the central cone. A tubing pump (Ismatec, Wertheim-Mondfeld, Germany) generated a water flow through the chamber into the central cone where the oxygen electrode was installed to measure the partial oxygen pressure of the outflow. Flow velocity was 53 ml min^{-1} avoiding a potential drop of the oxygen concentration beneath 80% saturation. Oxygen saturation of the inflow was set to 100% as the reservoir was aerated and circulated though an UV sterilizer constantly.

Individual fish were introduced into fife of the respirometer chambers at least 24 h prior to measurements to allow adaptation to the experimental conditions. The sixth chamber was used to measure a blank value, which accounted for up to 15% of the oxygen depletion. Oxygen consumption of a single fish was recorded continuously for a period of approximately 1 h with a sampling interval of 0.5 s. Data were analysed using Chart v. 4.0.1 (PowerLab, ADInstruments, Oxfordshire, UK). Oxygen consumption rates (MO_2, mgO_2 h^{-1}) were calculated using the equation:

$$MO_2 = \Delta PO_2 \beta M V_{fl}, \quad (1)$$

where ΔPO_2 is the difference in oxygen content between in- and outflow (Pa), β is the oxygen capacity of the water (mol l^{-1} Pa^{-1}), M is the molar mass of the oxygen (mg mol^{-1}) and V_{fl} is the flow rate though the chamber (l h^{-1}). Only data from the lowest 10% of the calculated oxygen consumption rates were used for the SMR analysis.

Moreover, data from fish that showed permanent spontaneous activity even within the small chambers used for this analysis were excluded from further SMR calculations. The scaling relationship of the SMR data of all individuals (N = 56) was described by the commonly used allometric function:

$$SMR = aM^b, \quad (2)$$

where SMR is the metabolic rate at complete rest, M is body mass and b is the mass exponent. The regression of the direct SMR data at 15°C was compared to the regression of the extrapolated SMR values from the swim tunnel experiments at this temperature. Since the extrapolation to zero speed proved to be a reliable method for estimating the SMR, further analyses were conducted with the estimates from the swim tunnel measurements.

AMR measurements

Active metabolic rates were determined using two different automated intermittent-flow systems, one for smaller fish of 10–25 g and the other for fish larger than 25 g body mass. Due to the relatively small fish sizes used in both respirometers, a correction for solid blocking effects was not necessary in either of the swim tunnels, because fish cross-sectional area did never exceed 10% of the area of the whole swimming chamber (Bell and Terhune 1970). Only relatively small fish were used for the experiments since larger fish were not able to turn easily within the swimming section and hence got stuck at the grid at the end of the section when occasionally attempting to turn at higher speeds.

Large swim tunnel

The design of the respirometer and its data analysis is described in detail in Ohlberger et al. (2005). The swim tunnel for the larger fish was a modified Brett-type tunnel respirometer designed after Hölker (2003). It consisted of a measuring recirculation system (25 l) with a swimming section of 15 cm in diameter and 40 cm in length. A black screen darkening the first part of the swimming section motivated the fish to swim in an upstream position. Water flow was driven by a paddle-wheel pump (BN100-65-125, Jesco, Wedemark, Germany), which was controlled by a frequency changer (NORDAC vector mc, Getriebebau Nord, Bargteheide, Germany). A flow transmitter (+GF+Signet 8550-1, Signet Scientific Company, El Monte, CA, USA) was installed on the pressure side for sensitive velocity adjustments. Flow velocity was calibrated using a

field version of the three-dimensional acoustic Doppler velocity meter (ADV, Nortek AS, Norway). Oxygen concentration was measured with a fixed TriOxmatic 701 oxygen sensor (WTW, Weilheim, Germany) coupled to an oximeter (WTW Oxi 171) that allowed automated measuring and flushing periods via a magnet valve. The respirometer was temperature-controlled to the desired value ±0.2°C. The oxygen content of the water decreased during the measuring phase until a lower threshold was reached. The ventilation connection was opened and aerated fresh water from an external ventilation system (125 l) entered the measuring circuit until the upper threshold was re-established. The upper and lower thresholds were fixed depending on fish mass and swimming speed to have a constant drop of approximately 5% in oxygen saturation during each measuring phase. Minimum lower threshold was 80% oxygen saturation. Oximeter output, including oxygen saturation, temperature and ventilation status, was recorded every 6 s by a computer.

Small swim tunnel

The smaller swim tunnel for intermittent-flow respirometry was a Swim5 acquired from Loligo (Loligo Systems ApS, Hobro, Denmark). The respirometer consisted of a recirculation loop (5 l) with flow generated by a propeller and an ambient tank (20 l) for fresh water supply. Another reservoir with cooled fresh water (60 l) was installed beside the respirometer for a sensitive temperature control of the system. The recirculation loop consisted of deflectors and a honeycomb serving as flow rectifier on the upstream side of the swimming section (10 × 10 × 30 cm). A black screen darkening the first part of the swimming section motivated the fish to swim in an upstream position. The propeller was connected to the motor outside of the respirometer via a submersed coupling. A submersible flush pump in the ambient tank was used for fresh water supply of the measuring section. The oxygen content in the swimming chamber was measured by a dissolved oxygen probe (MINI-DO, Loligo Systems ApS). The whole system was run by the LDAQ instrument from Loligo, connected to a computer via USB port. The instrument (LDAQ) recorded oxygen saturation and temperature in the swimming section and controlled the ambient tank pump for automated flushing as well as a pump for the temperature control that delivered cooled water from the reservoir into the ambient tank. The software LoliResp allowed automated measuring, wait and flush periods, a sensitive temperature control and velocity adjustments of the motor. Water velocity was calibrated to the voltage output of the motor using a three-dimensional acoustic Doppler velocity meter (ADV, Nortek AS, Norway). Measuring phases were set at 500–1,500 s depending on fish mass and swimming speed to ensure that the oxygen content in the measuring section never dropped below 80% saturation. Flush period was set to 80 s and wait period to 30 s. Temperature was set to the desired value with a hysteresis of ±0.1°C.

Experimental protocol

Experiments were conducted from May 2005 to September 2006. At each of the three temperatures (4, 8 and 15°C), 14 vendace were used for the swim tunnel experiments. Fish length was measured prior to the tests. Individuals of 10–15 cm were introduced into the small and those of 15–22 cm into the large swim tunnel. To allow adaptation to experimental conditions, a velocity of 0.5 BL s^{-1} (body length per second) was run for at least 24 h. Subsequently, velocities of 0.75, 1.0, 1.5 and 2.0 BL s^{-1} were run for 8–16 h each, day and overnight. After 5 days of swimming trail, fish were removed from the respirometer and weighted immediately. This was done afterwards to reduce handling stress prior to the experiment. Subsequently, a blank value was determined. Microbial respiration accounted for up to 15 and 35% of the total respiration in the small and large respirometer, respectively (for comparison see Dalla Via 1983).

Data analysis

For the small swim tunnel, the LoliResp software delivered the regression values of the acute oxygen consumption in the respirometer during each measuring period ($mgO_2\ kg^{-1}\ h^{-1}$). For the large respirometer the acute oxygen consumption rate of the fish was computed by fitting a linear regression to the decrease in oxygen saturation against time for each phase of closed respirometry. All oxygen consumption values were corrected for bacterial respiration.

To distinguish between adaptation and routine phase of swimming, the procedure after Hermann and Enders (2000) was applied to the 0.5 BL s^{-1} data. Adaptation phases in vendace lasted for up to 12 h. Data from the adaptation phase were excluded from further calculation. The active metabolic rate for every single swimming velocity was computed from the lowest 10% of all values. This was done to determine the minimum active metabolic rate without any spontaneous activity or stress phases the fish might have experienced during the experiment.

A power function was used to describe the AMR to speed relationship (Videler and Nolet 1990; Korsmeyer et al. 2002):

$$\mathrm{AMR} = a + bU^{c}, \tag{3}$$

where a, b and c are constants and U is swimming speed (BL s^{-1}). Constant a represents the estimated SMR, i.e.

metabolic rate at zero speed, and c is the speed exponent. The estimated SMR values (a) were plotted against body mass for all three temperatures and mass exponents (b) were calculated according to the allometric function (Eq. 2). Further, to evaluate the effect of temperature on the active metabolism, AMR values were corrected for body mass using the mass exponents derived for the relationship between standard rate and body mass. Subtracting the SMR from these values delivered the mass-corrected net active metabolic rate (net AMR).

Differentiation of Eq. 3 with respect to U and zero-setting gives the swimming speed associated with minimum energetic costs per unit distance, which is also referred to as optimum speed (U_{opt}). It is thus the speed where the ratio of the active metabolic rate to swimming speed reaches a minimum (Tucker 1970):

$$U_{opt} = [a/b(c-1)]^{1/c}, \quad (4)$$

The energy expenditure when swimming at U_{opt} is called the cost of transport (Videler and Nolet 1990). It is the minimum energy needed by a fish to swim one unit distance (J m^{-1}):

$$COT = AMR_{opt}/U_{opt}, \quad (5)$$

where AMR_{opt} (J s^{-1}) is active metabolic rate at U_{opt} (m s^{-1}). Subtracting the SMR from the AMR_{opt} value in this equation delivers the net cost of transport (net COT). All data of the oxygen consumption rates were converted into energy units using an oxycaloric value of 14.2 mg O_2^{-1} (Hepher 1988).

Regression analysis and model selection criteria

To evaluate the integrative effects of temperature, body mass and swimming speed on the metabolic rate, a multivariate non-linear regression analysis was performed. The formula to describe the empirical data was designed according to the following considerations. The mass to metabolic rate relationship is generally assumed to have an allometric form and was thus modelled using a power fit (M^b). Temperature is generally described by an exponential relationship to metabolic rate and was hence modelled by an exponential function with a temperature coefficient (e^{dT}). The relationship between swimming speed and metabolic rate was again described by a power fit (U^c), since this method produced better fits than the exponential function when the individual data were analysed. Other parameters were added to the model as normalisation constants.

All computed non-linear regression models were tested for significance of the single parameter estimates. Only models with parameter estimates that were significantly different from zero were included into the subsequent test procedure.

Two information criteria based methods were used to determine the model that best described the experimental data. Since the range of possible formulas to describe the data set includes models with different numbers of parameters, a simple coefficient of determination-based method is not sufficient. More accurate indicators for a discrimination of regression models are the Akaike information criterion (Akaike 1974) and the Schwarz/Bayesian information criterion (Schwarz 1978). Both the Akaike (AIC) and the Schwarz/Bayesian (S/BIC) information criterion were originally based on the maximized likelihood (L) of a model with a given number of parameters (k). Under the assumption that the model errors are normally distributed, L can be replaced with the residual sum of squares (RSS) divided by the number of observations (n):

$$AIC = 2k + n\ln(RSS/n) \quad (6)$$

$$S/BIC = k\ln(n) + n\ln(RSS/n) \quad (7)$$

The model associated with the smallest values of AIC and S/BIC is the most appropriate, with S/BIC being a more restrictive criterion on increasing parameter numbers.

The multivariate non-linear regression analysis was performed using a data set (n) of 210 AMR values. This number was achieved by testing 14 fish at each of the three temperatures at five different swimming speeds, respectively.

Statistics

The significance level for all statistical tests was $P < 0.05$. All calculated mean values were tested for significance using t-tests. Linear regressions of the allometric functions for standard metabolic rate and cost of transport as well as the power fits of the AMR to speed relationship were tested for overall significance of the data sets using F-statistics (Zar 1996). The F-test was performed by comparing a global model where slope is shared among the data sets with a model where each dataset gets its own slope, i.e. by comparing the pooled residuals of both discrete regressions to the regression residuals of the combined data set. Additionally, analysis of variation in the fitted slopes and intercepts across temperatures were computed in SPSS by using analysis of covariance (ANCOVA).

Results

The standard metabolic rate was directly measured in vendace at rest for 15°C. These values were compared to the extrapolated values from the swimming experiments at

this temperature. The two allometric regressions (Eq. 2, Fig. 1) were not significantly different (F-test: $F = 1.53$; $P = 0.22$). They showed similar intercepts, 0.0014 and 0.0017 (ANCOVA: $F = 0.79$; $P = 0.38$), and similar slopes, 0.77 and 0.71 (ANCOVA type III SS: $F = 0.70$; $P = 0.41$), for the direct and the estimated SMR values, respectively. It was therefore sufficient for further evaluations to use the estimates from the indirect method to compare the SMR at different temperatures. SMR increased with temperature (Fig. 3, Table 1) showing a significant difference between the regressions for 4, 8 and 15°C ($P < 0.01$ for all F-tests). The scaling exponents for these fits decreased with increasing temperature ($b_{SMR(4°C)} = 0.94$, $b_{SMR(8°C)} = 0.84$, $b_{SMR(15°C)} = 0.71$), showing significantly different slopes between 4 and 8°C (ANCOVA type III SS: $F = 6.34$; $P = 0.02$) and 8 and 15°C (ANCOVA type III SS: $F = 6.80$; $P = 0.02$).

For a comparison of the active metabolic rate at all speeds, the data of all individual fish were corrected for size with the respective temperature specific mass exponents from the SMR regressions. AMR and net AMR data are presented in Fig. 2 for all temperatures. While AMR increased significantly with temperature ($P < 0.01$ for all F-tests), net AMR did not differ significantly between 4 and 8°C ($F = 0.89$, $P = 0.45$). The individual speed exponents (c) of the AMR showed no clear trend with temperature, varying between 1.7 and 3.7 for all temperatures and body masses (Eq. 3). The AMR of every single speed at 15°C was further tested against the SMR from the direct measurements. No significant difference was found between the regressions for the SMR and the active metabolic rate at 0.5 ($P = 0.77$), 0.75 ($P = 0.34$) and 1.0 BL s^{-1} ($P = 0.25$). Only the swimming metabolism at 1.5 ($P < 0.01$) and 2.0 BL s^{-1} ($P < 0.001$) was significantly higher compared to the standard rate. A similar test for the other two temperatures was not possible because of the lack of independent SMR measurements.

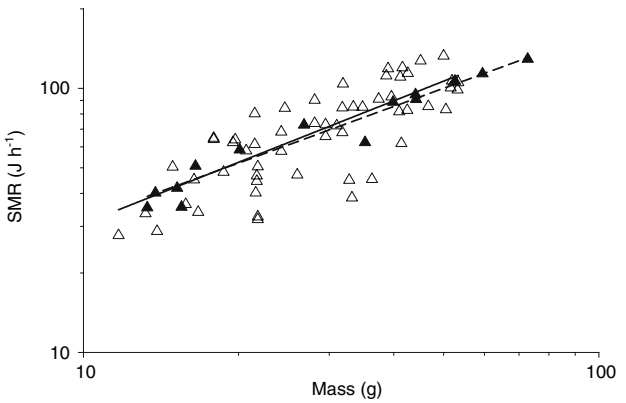

Fig. 1 Relationship between standard metabolic rate and body mass at 15°C. *Open triangles* represent the direct SMR measurements (regression indicated by *solid line*: 5.19 $M^{0.77}$) and *filled triangles* represent the extrapolated SMR values from the swim-tunnel tests (regression indicated by *dashed line*: 6.17 $M^{0.71}$). Regression lines were fitted by least-squares regression according to SMR = aM^b (Eq. 2). Note: double-logarithmic plot

The ratio of standard metabolism to total swimming costs at optimum speed was calculated for each temperature. Mean percentages were 46.4 ± 4.5, 68.6 ± 3.9 and 53.8 ± 5.9% at 4, 8 and 15°C, respectively. The differences were significant ($P < 0.01$ for all t-tests), but no trend with temperature was observed.

The swimming velocity associated with minimum energetic costs per unit distance, i.e. optimum speed (U_{opt}), showed no trend with temperature and only increased slightly with body mass at 4 and 8°C but not at 15°C. Mean relative optimum speeds were 2.4 ± 0.4, 2.0 ± 0.2 and 2.8 ± 0.9 BL s^{-1} at 4, 8 and 15°C, respectively. The minimum amount of energy needed by a fish to swim a unit distance (COT) increased with temperature and body mass (Fig. 3, Table 1). The regressions differ significantly between 4, 8 and 15°C ($P < 0.01$ for all F-tests). The slope of the relationship decreased with increasing temperature ($b_{COT(4°C)} = 0.81$, $b_{COT(8°C)} = 0.80$, $b_{COT(15°C)} = 0.70$), but the difference was only significant between 4 and 15°C (ANCOVA type III SS: $F = 8.10$; $P = 0.01$). The energy

Table 1 Regression analysis results for the allometric relationships (Eq. 2) for SMR, COT and net COT at all three temperatures

T (°C)	Constant	Estimate	SE	P	r^2
SMR (J h^{-1})					
4	a	1.125	0.246	<0.001	0.992
	b	0.944	0.056	<0.001	
8	a	2.285	0.855	0.020	0.975
	b	0.843	0.103	<0.001	
15	a	6.175	1.081	<0.001	0.994
	b	0.712	0.046	<0.001	
net COT (J m^{-1})					
4	a	0.002	0.000	0.004	0.985
	b	0.831	0.072	<0.001	
8	a	0.001	0.000	0.007	0.982
	b	0.784	0.086	<0.001	
15	a	0.006	0.001	<0.001	0.991
	b	0.565	0.054	<0.001	
COT (J m^{-1})					
4	a	0.003	0.001	0.002	0.987
	b	0.810	0.065	<0.001	
8	a	0.004	0.001	0.011	0.980
	b	0.797	0.092	<0.001	
15	A	0.008	0.003	0.011	0.980
	B	0.689	0.087	<0.001	

Estimate, standard error (SE) and P-value are given for each parameter

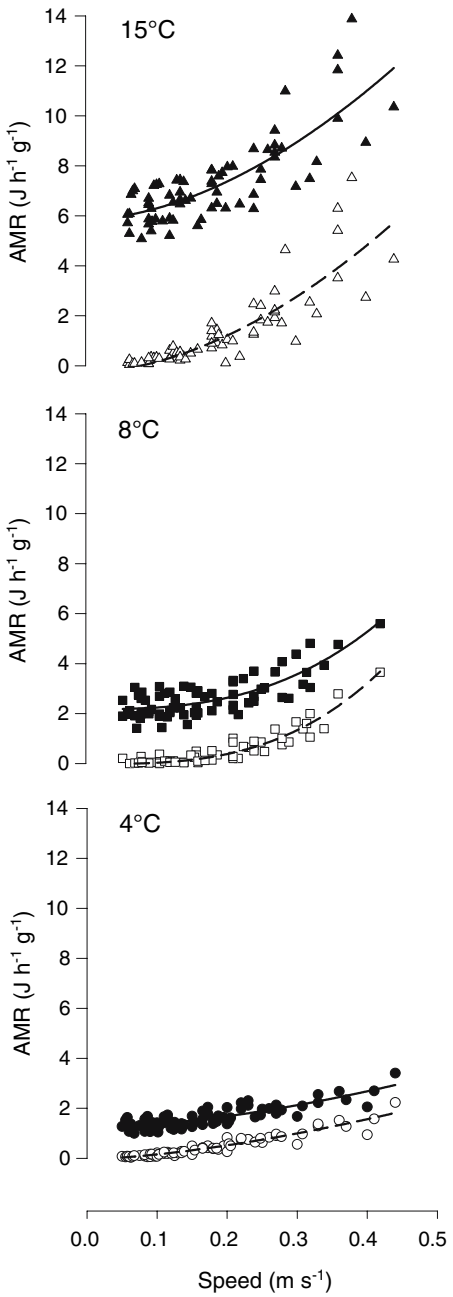

Fig. 2 Relationship between mass-corrected active metabolic rates and absolute swimming speed at 4, 8 and 15°C shown at the same scales. *Filled symbols* (*solid lines*) represent the total swimming costs (AMR) and *open symbols* (*dashed lines*) the net costs (net AMR). Regression lines were fitted by least-squares regression according to AMR = $a + bU^c$ (Eq. 3)

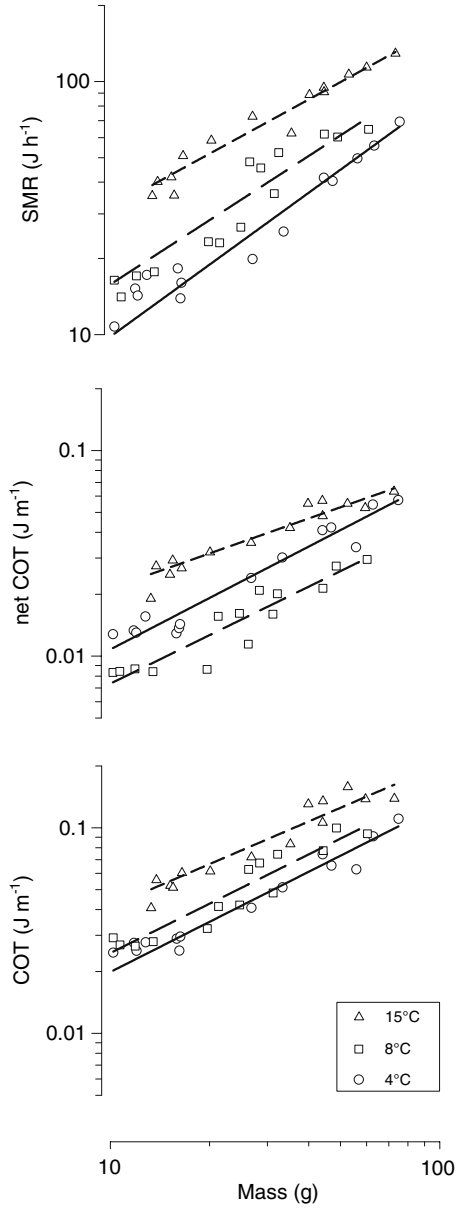

Fig. 3 Allometric relationships (Eq. 2) for the standard metabolic rate and the total and net minimum energetic costs per unit distance (COT, net COT) at 4, 8 and 15°C. *Triangles* (*short-dashed lines*) represent the 15°C, *squares* (*long-dashed lines*) the 8°C and *circles* (*solid lines*) the 4°C data. The regressions differ significantly between the temperatures for all three metabolic characteristics. The respective values for *a* and *b* are given in Table 1. Note: double-logarithmic plots

needed for locomotion only without the standard metabolism (net COT), showed a slightly different variation with temperature (Fig. 3, Table 1). The net COT was significantly lower in 8°C compared to 4°C and highest at 15°C ($P < 0.01$ for all *F*-tests).

The following energetic model was designed by multivariate non-linear regression analysis to predict active metabolic rates in vendace based on the presented selection criteria (Table 2):

$$\mathrm{AMR} = aM^b \exp(\mathrm{d}T) + eM^b U^c, \quad (8)$$

where AMR is the active metabolic rate (J h^{-1}), *M* is body mass (g), *T* is temperature (°C) and *U* is swimming speed

Table 2 Non-linear regression models for the active metabolic rate, ordered by the number of parameters included into the model (k) and the corresponding degrees of freedom (df)

Model	k	Df	r^2	RSS	AIC	S/BIC	NS
AMR = $aM^bU^c \exp(dT)$	4	206	0.903	38794	1104.0	1117.4	–
AMR = $aM^b \exp(dT) + eM^bU^c$	**5**	205	**0.916**	**33772**	**1076.9**	**1093.6**	**–**
AMR = $aM^b \exp(dT) + eM^bU^c \exp(dT)$	5	205	0.914	34440	1081.0	1097.7	–
AMR = $aM^b \exp(dT) + eM^fU^c$	6	204	0.932	27318	1034.3	1054.4	e
AMR = $aM^b \exp(dT) + eM^fU^c \exp(gT)$	7	203	0.932	27307	1036.2	1059.7	e, g

Given further are the coefficient of determination (r^2), residual sum of squares (RSS), Akaike information criterion (AIC), Schwarz/Bayesian information criterion (S/BIC) and non-significant parameter estimates (NS). A model was rejected if any of the estimated parameters was not significant. Out of the remaining models the one associated with the lowest AIC and S/BIC values was selected (bold)

(BL s^{-1}). Estimates of the constants a, b, c, d and e are given in Table 3. Insertion of the parameter estimates delivers the following formula ($r^2 = 0.92$):

$$\mathrm{AMR} = 0.82M^{0.93}\exp(0.07T) + 0.43M^{0.93}U^{2.03}, \qquad (9)$$

All other models either produced non-significant estimates of one of the parameters or showed higher AIC and SBIC values. The proposed formula represents the sum of standard plus net activity costs, where temperature is only related to the standard metabolism. Adding another temperature dependency to the activity term resulted in non-significant parameter estimates. Mass influenced standard and activity costs, but the mass exponent is the same for both since two exponents apart also resulted in non-significant parameter estimates (Table 2).

Discussion

The method of extrapolating to zero speed from activity measurements to estimate the SMR has been discussed controversially. The validity of this method has been questioned for reasons of potential overestimation (Videler and Nolet 1990; Dewar and Graham 1994) or underestimation (Forstner and Wieser 1990). However, there is also experimental validation for the method (Brill 1987). Moreover, two different fits have been used to describe the AMR to speed relationship, an exponential and a power function, which result in unequal estimates of the SMR (Pettersson and Hedenström 2000; Korsmeyer et al. 2002). In this study, the power fit constantly resulted in higher SMR values and showed higher correlation coefficients for the individual as well as the mass-specific AMR to speed data at all temperatures compared to the exponential fit. Moreover, the data presented here also support the accuracy of extrapolating to zero speed by applying the power fit, because the regressions of the direct SMR measurements and those from the swim tests showed no significant difference, suggesting that the power fit gives reliable estimates of the SMR. A comparison with data from a review by Clarke and Johnston (1999) shows that the calculated SMR for vendace are in good accordance with standard rates found in other salmonid species. The mean resting metabolic rate for a 50 g salmonid at 15°C is given by 0.231 mmol h^{-1} (Clarke and Johnston 1999, Table 1), which corresponds to an energy consumption of 104.9 J h^{-1} using the same oxycaloric value as in our study (14.2 mgO_2^{-1}, Hepher 1988). For a vendace of 50 g at this temperature, the regressions for the direct SMR and the extrapolated SMR measurements predict a metabolic rate of 106.5 J h^{-1} and 100.1 J h^{-1}, respectively.

The aerobic swimming performance of vendace is generally characterised by high ratios of standard to activity costs. The increase in metabolic costs when swimming at speeds of up to one length per second is not significant compared to the standard metabolism. These constant levels of activity costs might be attributed to the fact that the fish depend on compensatory movements by their pectoral and dorsal fins to keep balance when swimming at low speeds (Videler 1993; Hammer and Schwarz 1996). The phenomenon of constant metabolic rates at low swimming speeds has already been reported earlier (Forstner and Wieser 1990), but it is remarkable that the energetic costs remain relatively constant in vendace over such a wide range of swimming speeds. Even when swimming at optimum speed, standard costs account for up

Table 3 Statistical results of the non-linear regression according to the model AMR = $aM^b \exp(dT) + eM^bU^c$. Estimates and standard errors (SE) are given for each parameter

Estimate		SE
a	0.82	0.130
b	0.93	0.028
c	2.03	0.362
d	0.07	0.006
e	0.43	0.134

to 2/3 of the energy expenditure. This comparison shows that the SMR makes up a great proportion of the total swimming costs and points out the low energetic costs needed for propulsion. Claireaux et al. (2006) investigated sea bass and found similar ratios of standard to total metabolic costs at U_{opt} (55–60%) and similar optimum speeds (0.32 and 0.52 cm s^{-1} at 7 and 14°C, respectively) compared to vendace (0.28 and 0.41 cm s^{-1} at 8 and 15°C, respectively). Optimum speeds for various salmonids of different size classes at 12–15°C reviewed by Videler (1993) ranged from 0.8 BL s^{-1} in *Coregonus artedii* (Bernatchez and Dodson 1985), to 2.8 BL s^{-1} in sockeye salmon (Brett 1964). The calculated mean optimum speeds for vendace, 2.0 to 2.8 BL s^{-1}, lie at the upper end of this range, but other studies have calculated even higher optimum swimming speeds, for instance, Dabrowski et al. (1989) predicted U_{opt} of up to 4 BL s^{-1} for juvenile vendace.

Weihs (1973) predicts that a fish would swim at its optimum speed to maximize the distance covered per unit energy, when the energy needed for propulsion equals that for the standard metabolism, i.e. when SMR accounts for half of the total active costs, with corresponding optimum speeds of 1–2 BL s^{-1}. The 50% value is close to those found at 4 and 15°C in vendace, but the respective mean optimum speeds were distinctly higher (2.4 and 2.8 BL s^{-1}) then predicted by Weihs (1973). This suggests low net activity costs that enable the fish to swim at high speeds covering longer distances when doubling the standard energy expenditure per unit time.

The optimum swimming speed and the energetic costs at this speed have high ecological relevance, because free-ranging fish generally swim close to this speed during routine movements such as foraging (Ware 1978; Weihs and Webb 1983; Webb 1991; Videler 1993; Dewar and Graham 1994; Bejan and Marden 2006). It has been argued, that the optimum speed might be limited to long-distance migration and foraging (Steinhausen et al. 2005). Moreover, the optimum speed is influenced by the food concentration during foraging (Muir and Newcombe 1974), the direction of foraging (Tanaka et al. 2001) as well as the mode of swimming (Steinhausen et al. 2006). This implies that optimum speeds as calculated here are ecologically relevant only for long-term foraging under steady swimming conditions. However, long-term and steady foraging seems to be the most important swimming condition for the pelagic vendace in an oligotrophic lake under low food concentrations. For instance, Dabrowski et al. (1989) showed that juvenile vendace had to spend most of the time per day foraging, possibly above 20 h, to keep a high daily growth rate of 4% at very low food concentrations.

The cost of transport is especially useful for the ecological evaluation of the swimming characteristics as it determines the foraging or cruising efficiency of a species. The low net energetic costs during swimming (net COT) in vendace at 8°C might be attributed to the slightly lower optimum speeds found at this temperature. However, the power fits of the net AMR did not differ significantly between 4 and 8°C. This suggests that the energy needed for propulsion is similar at these temperatures, which roughly represent the year-round population depth of this species in its natural habitat (Helland et al. 2007).

The multivariate regression analysis of the metabolic rate in vendace explains 92% of the variance in total swimming costs. This indicates that body mass, temperature and swimming speed are adequate variables for modelling the energetic costs during swimming. Although it can be questioned if swimming tests from the laboratory are transferable to natural swimming conditions and ecological implications derived from these tests have to be made cautiously (Plaut 2001; Nelson et al. 2002), it is a reliable method in fish eco-physiology to describe the general effects of the investigated variables on the swimming performance and compare it to other laboratory-derived principles.

The mean mass exponent (0.93), estimated for the standard and activity metabolism by the multivariate regression analysis, is significantly higher than the ¾-power or other fish specific relationships, although the mean scaling dependency of the SMR for all three temperatures (0.83) is within the range recorded for other fishes, most commonly 0.8 (Winberg 1961; Clarke and Johnston 1999) and 0.88 (White et al. 2006). In vendace, the activity metabolism thus tends to show higher exponents compared to the standard metabolism. This is in accordance with Brett and Glass (1973), who measured scaling relationships of 0.99 for AMR and 0.88 for SMR in Sockeye salmon. Two separate scaling relationships were not considered in the model, since the regression analysis then resulted in non-significant parameter estimates (see Table 2). However, all tested models where a specific mass exponent for the SMR and AMR were included, gave significantly higher values for the activity compared to the standard metabolic rate.

The deviation from the ¾-power might also be explained by the higher mass exponents generally found for ectothermic compared to endothermic animals. McNab (2002) revealed in his meta-analysis of scaling relationships for various vertebrate taxa that ectotherms have higher exponents (0.71–1.06) than endotherms (0.67–0.75). Moreover, pelagic animals seem to have generally steeper metabolic scaling relationships than non-pelagic species (Glazier 2005). For instance, pelagic fish that are active swimmers show steeper exponents for muscle-enzyme activities than benthic fish (Childress and Somero 1990; Somero and Childress 1990) and it has been suggested that

larval fish hatched from pelagic eggs exhibit higher exponents than those hatched from benthic eggs (Oikawa et al. 1991).

The different mass exponents found for the SMR at 4, 8 and 15°C suggest a temperature dependency of the scaling relationship itself. This is in accordance with many other experimental studies where temperature was the major extrinsic factor altering the exponent of scaling relationships (Glazier 2005). It can therefore be assumed that the influences of temperature and body mass are linked to each other and do not independently affect the metabolic rate. Regarding the observed mass dependencies for the standard metabolism and the cost of transport at optimum speed, we can further assume that the scaling relationship varies not only with temperature but also with activity level. This pattern has already been described in other fish studies (Brett 1965; Robinson et al. 1983; Herrmann and Enders 2000) and it is a common rule observed in many vertebrate groups (Nagy 2005). Such dependencies of the scaling exponent cannot be considered when using universal exponents like suggested for the "metabolic theory of ecology" (West et al. 1997; Brown et al. 2004).

Exponential temperature coefficients in fish typically range from 0.05 to 0.10 (Jobling 1994), corresponding to Q_{10} values of 1.65–2.70 ($Q_{10} = e^{(d*10)}$). Clarke and Johnston (1999) suggest a mean value of 2.35 for the resting metabolism in teleosts, but White et al. (2006) computed a mean Q_{10} of 1.65 for 82 fish species. Other species-specific Q_{10} include values from 2.1 for walleye (Beamish 1990) to 2.8 for bream (Hölker 2006). The temperature coefficient (0.07) for vendace corresponds to a Q_{10} of 2.11, which is thus an intermediate value for fishes. The regression analysis revealed that temperature did only significantly affect the standard but not the net active metabolic rate. This effect is also apparent when the net cost of transport is considered, which showed no clear trend with temperature. The same lack of a clear thermal effect on net COT has been observed in sea bass (Claireaux et al. 2006), however, examples from other species suggest that swimming costs might be influenced by water temperature (Johnston and Temple 2002). Besides this, swimming performance may be influenced by water temperature in other than a linear form, for instance by optimizing processes, like it has been proposed for maximum swimming speed (Myrick and Cech 2000; Lee et al. 2003). Which of the swimming characteristics are subject of optimizing processes remains unclear. Besides optimum or maximum swimming speed, the energy expenditure per unit distance (COT) might also be subjected to selection pressures, since COT determines the foraging or cruising efficiency of a species. Clearly, these assumptions remain speculative and overreach the scope of this paper. However, the link between swimming performance and its ecological function represents an interesting field of future research to better understand the ecological implications of swimming characteristics in fish.

Speed exponents in fishes are generally assumed to range from 2 to 3 (Videler and Nolet 1990; Wieser 1991). Based on hydrodynamical considerations, values of 2.5 and 2.8 have been suggested for fish swimming under laminar or turbulent flow conditions, respectively (Webb 1975; Alexander 2005). The speed exponent contains information on the efficiency of aerobic swimming (Webb 1993). Higher speed exponents result in steeper power fits and represent lower swimming efficiencies. It has been shown that high-drag morphs have higher values compared to low-drag fishes (Pettersson and Hedenström 2000) and that differences in swimming efficiency can be explained by morphological characteristics (Ohlberger et al. 2006). Among various teleost fishes a mean value of 2.3 has been computed (Beamish 1978). Other studies reported exponents of 2.44 for sea bass (Claireaux et al. 2006), 2.53 for carp and 2.23 for roach (Ohlberger et al. 2006). Although values smaller than 2.0 have also been measured (Videler 1989), the mean speed exponent calculated for vendace (2.03) is at the lower end of the reported range. This suggests a fairly good swimming efficiency of vendace compared to many other fish species. Foraging at high speeds under low energetic costs might be necessary for a sufficient food capture in this pelagic fish species that is subjected to low prey densities in its natural habitat (Schulz et al. 2003).

Taken together, this study shows that net activity costs in vendace are low and that aerobic swimming performance is mainly dominated by the standard metabolic rate, making it very efficient in foraging with high optimum swimming speeds. Our analysis shows that temperature, swimming speed and body mass are appropriate variables for modelling the energetic costs of swimming. It was found that temperature mainly affects the standard but not the activity metabolism in this species. Finally, it was argued that the heterogeneity of the mass dependencies and the integrative effects of temperature and body mass on the metabolic rate do not support a universal scaling relationship.

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