

Effect of body mass and water temperature on the standard metabolic rate of juvenile yellow perch, *Perca flavescens* (Mitchill)

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Abstract Fish respiration rates that are presumed to represent standard metabolic rates (SMR) may sometimes include an unspecified energy expenditure associated with activity and digestion. This situation may introduce a bias in bioenergetics models because standard metabolism, digestion, and activity may not be affected by the same environmental conditions. The aim of this study was to (1) develop a SMR model for juvenile yellow perch, *Perca flavescens* (Mitchill), that represent the minimum energy expenditure required to maintain life and (2) compare the results of this study with published perch metabolic rates and bioenergetics models. SMR was

estimated for yellow perch over a range of body mass (4.4–24.7 g) and water temperature (12–20°C). The intercept of the relationship between fish respiration and swimming velocity obtained during forced swimming experiments was used to determine SMR. SMR estimated by the present study were comparable to values presented by two published studies on Eurasian perch, *Perca fluviatilis* L. However, estimated SMR were 4.1–20.9 times lower than values of a third respirometry study and predictions of bioenergetics models for perch. The present study suggests that published SMR models may sometimes include a significant fraction of energy expenditures (39.2–75.9%) associated with digestion and activity. This may complicate the implementation and the interpretation of fish bioenergetics models. The present study indicates that the intercept of respiration-velocity relationships and long-term respiration rates during starvation experiments may provide similar and reliable SMR values.

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Introduction

Bioenergetics models are equations that partition the energy consumed by fish into physiological

compartments such as growth, metabolism, and waste (Winberg 1956). These models have been used to predict fish consumption, growth, and activity costs under specified environmental conditions (Kitchell et al. 1977; Stewart et al. 1983; Rice and Cochran 1984; Brandt et al. 1992; Boisclair and Rasmussen 1996). The predictive power of bioenergetics model strongly depends on the accuracy of the parameters used to represent the different physiological components (Ney 1993; Bajer et al. 2003). Metabolic costs, especially the metabolic costs related to fish activity, are the least understood compartment in the fish energy budget. This may explain why, with few exceptions (Boisclair 2001), standard metabolic rate (SMR) and activity costs are rarely defined as independent variables. Instead, in bioenergetics models, activity costs are often estimated as multiples (i.e. activity multiplier) of SMR (Hewett and Johnson 1992; Hanson et al. 1997). This strategy, while practical, is conceptually questionable because SMR and activity costs may not be influenced by the same environmental variables. For example, an increase of water temperature may increase SMR but not the activity costs (Boisclair and Tang 1993). Conversely, an increase in prey density may affect activity costs (Ware 1975, 1978; Boisclair and Sirois 1993) but not SMR. Yet, the value that represents activity costs automatically increases each time SMR increases in most bioenergetics models using activity multipliers.

A number of values and models of metabolic rates have been published for perch. Solomon and Brafield (1972) estimated metabolic rates of Eurasian perch, *Perca fluviatilis* L., allowed to feed and to swim in a respirometer. Karås (1990) performed starvation experiments with Eurasian perch of 2 g held at 10°C. This author estimated SMR from the loss rate of fish body mass. Huuskonen and Karjalainen (1997) conducted short-term respirometry experiments with Eurasian perch of 2 g swimming in small respirometers held at 12°C. Kitchell et al. (1977), Karås and Thoreson (1992), and Hanson et al. (1997) used the data produced by Solomon and Brafield (1972) to develop perch metabolic rate models. Despite the number of studies performed on the metabolic rate of perch, a model that represents

the effect of body mass and water temperature on fish respiration independently from digestion and activity costs, is still lacking for this species. However, the development of adequate SMR models is an obligatory prerequisite to the development and the testing of models on activity costs. The aim of this study was therefore to (1) develop a SMR model for juvenile yellow perch, *Perca flavescens* Mitchill, and (2) compare the results of this study with published perch metabolic rates and bioenergetics models.

Materials and methods

Fish and holding conditions

Wild yellow perch were collected using a beach seine from the littoral zone of Lake Hertel (near Montréal, Québec, Canada). Fish body mass ranged from 4.4 to 24.7 g wet weight and total body length ranged from 7.2 to 13.0 cm (Table 1). Fish were maintained in three 700 l tanks containing de-chlorinated freshwater at the targeted water temperature of 12, 16, and 20°C, respectively, for at least 1 month before experiments were performed. Light intensity (40 lux) and photoperiod (12L:12D) were held constant during the entire study period. Water quality was tested regularly throughout the study. Ammonia (NH_3 ; $\mu\text{g l}^{-1}$), nitrites (NO_2 ; mg l^{-1}), and water hardness (mg l^{-1} of CaCO_3) were estimated using standard procedures (APHA 1989) and kept within the tolerance limits for aquaculture (MAPAQ 1990). Water hardness and alkalinity were adjusted to $65 \text{ mg l}^{-1} \text{ CaCO}_3$ by adding calcium chloride (CaCl_2) and sodium bicarbonate (Na_2HCO_3). Fish were fed once a day *ad libitum* with equal parts of commercial trout pellets and Tetramin flakes.

Respirometry system and experimental protocol

The respirometers used in this study were Blazka-type swim tunnels ($3.37 \pm 0.03 \text{ l}$), similar to those described by Beamish et al. (1989). The respirometers were submerged into a temperature-controlled water tank ($\pm 0.5^\circ\text{C}$) and were

Table 1 Number of respirometry experiments of yellow perch at corresponding water temperature of given body mass, body length, and estimated standard metabolic rate (SMR)

<i>n</i>	Temperature (°C)	Body mass (g)	Body length (cm)	SMR (mg O ₂ h ⁻¹)
9	12	9.6–21.9	10.1–12.6	0.28–1.28
13	16	5.3–23.8	7.9–13.0	0.53–2.76
19	20	4.4–19.8	7.2–11.9	0.71–3.72

connected to a continuous-flow system, through which oxygenated water flowed at a rate ranging from 20 to 80 ml min⁻¹ depending on the water temperature. Flow velocities (15–35 cm s⁻¹) were adjusted by varying the voltage of the submersible pump that created the water current inside each respirometer. The relationship between pump voltage and flow velocity was calibrated using a miniature velocimeter (Ott, C2; Kempton, Germany; Blade number 2–3). A mildly electrified (0–5 V) metallic grid installed at the end of the swim tunnel was used to motivate the fish to swim against the water flow. Water flowed continuously through all respirometers at a stable rate.

Six respirometers were connected simultaneously to the respirometry system. A single fish was placed in each respirometer. The oxygen concentration of the water entering and leaving each chamber was estimated once every hour by directing the water flow with solenoid valves to sub-sampling chambers containing the probe of an oxygen meter (YSI Incorporated, model 54). A 15 min delay between oxygen measurements was allowed to insure a complete water change in the probe chamber. The oxygen meters were calibrated daily using air-saturated water maintained at the experimental temperature, and their accuracy was verified weekly using the Winkler titration method modified for small volumes (APHA 1989). The water flow rate through each respirometer was measured twice daily. Estimated oxygen consumption rates (mg O₂ h⁻¹) were corrected for the biological oxygen demand occurring in empty respirometers and for the time lag associated with continuous-flow respirometry systems according to Niimi (1978).

Two days prior to experiments, individual fish were isolated and starved in a tank. The day before

starting an experiment, fish were individually placed in a respirometer, in which the flow velocity U was set at 15 cm s⁻¹. After starting an experiment, the oxygen consumption rate of the fish was recorded while gradually increasing the flow velocity U every 2 h, by intervals of 5 cm s⁻¹, from 15 to 35 cm s⁻¹, or until the fish were unable to maintain a stable position inside the respirometer. Only data from individuals that swam consistently for at least three flow velocities and for 2 h at each flow velocity were kept for further analysis. After the experiment, fish were removed from the respirometer and weighed to the nearest 0.1 g.

Data analysis

For each fish, the relationship between metabolic rate and flow velocity was described using the equation (Beamish 1978):

$$\log V_{O_2} = \alpha + \beta \cdot U \quad (1)$$

where V_{O_2} is the oxygen consumption rate in mg O₂ h⁻¹, the intercept α corresponds to log transformed standard metabolic rate SMR ($SMR = 10^\alpha$), β represents a coefficient, and U is the swimming speed of the fish which corresponds to flow velocity in cm s⁻¹. A two-way ANOVA was used to test the effect of body mass and water temperature on the SMR of yellow perch.

The effect of body mass on the SMR at given water temperature was described by the following allometric relationship (Winberg 1956):

$$SMR = a \cdot M^b \quad (2)$$

where SMR is the standard metabolic rate in mg O₂ h⁻¹, a the intercept, M the fish body mass in g and b is a scaling exponent in the relation between SMR and body mass, which is generally referred to as body mass exponent. The coefficients a and b of the formula were estimated using linear regression analysis with the log transformed data of SMR and M .

The effect of body mass and water temperature on the SMR was modeled using the following equation (Ware 1978; Stewart et al. 1983):

$$SMR = a \cdot M^b \cdot e^{c \cdot T} \quad (3)$$

where SMR is the standard metabolic rate in $\text{mg O}_2 \text{ h}^{-1}$, M the fish body mass in g and T the water temperature in $^{\circ}\text{C}$. The coefficients a , b , and c were estimated using the multiple regression analysis with the log transformed data.

The SMR model developed during this study was compared to published values of perch metabolic rates. Solomon and Brafield (1972) estimated metabolic rates of Eurasian perch by allowing them to feed and swim freely in a respirometer. Karås (1990) performed starvation experiments on Eurasian perch that were held in groups of 20. This author estimated what he defined as SMR from the body mass loss rate. However, energy expenditures related to spontaneous swimming and imputed to SMR have not been quantified. Huuskonen and Karjalainen (1997) conducted short-term respirometry experiments with starved individual Eurasian perch in small respirometers. The minimum oxygen consumption rate estimated over 15 min was defined as “near standard respiratory level”. Published values of perch metabolic rates were compared to the SMR predicted by the model developed during the present study by inputting it with fish body mass and water temperature employed by Solomon and Brafield (1972), Karås (1990), and Huuskonen and Karjalainen (1997) to perform their experiments. The SMR model developed during this study was also compared to three models intended to predict perch active metabolic rates (Kitchell et al. 1977; Karås and Thoresson 1992; Hanson et al. 1997). In the context of these three models, active metabolic rate (AMR) is not the physiologically maximum metabolic rate (Beamish 1978) but the sum of SMR and of the costs of swimming (A). The SMR model developed during the present study was compared to the three AMR models by implementing all models with body masses ranging from 4 to 25 g and water temperatures ranging from 12 to 20°C . In addition, AMR models were implemented with activity multipliers ($[\text{SMR} + A]/\text{SMR}$) having a value of 1. This activity multiplier was selected because it is expected to provide an active metabolic rate ($\text{SMR} + A$) closest to SMR (Kitchell et al. 1977).

Results

Standard metabolic rate estimates and models

SMR of yellow perch ranged from 0.28 to $3.72 \text{ mg O}_2 \text{ h}^{-1}$ (Table 1). Statistical analyses indicated that fish body mass (two-way ANOVA, $n = 41$, $P < 0.001$) and water temperature (two-way ANOVA, $n = 41$, $P < 0.001$) significantly affected SMR (Fig. 1). Linear regression analyses indicated that SMR increased significantly with body mass at 16°C and 20°C , however, at 12°C , no statistically significant relationship with body mass was observed (Table 2). Furthermore, the proportion of variation in SMR explained by body mass increased with water temperature, suggesting that the effect of body mass increase with temperature. Fish body mass contributed only to 0.9% of the variation in SMR while water temperature explained 70.9% of this variation (multiple regression analysis, $n = 41$, $P < 0.001$, $R^2 = 0.72$, Table 2).

Published metabolic rate estimates

Solomon and Brafield (1972) estimated that the metabolic rate (including unspecified digestion

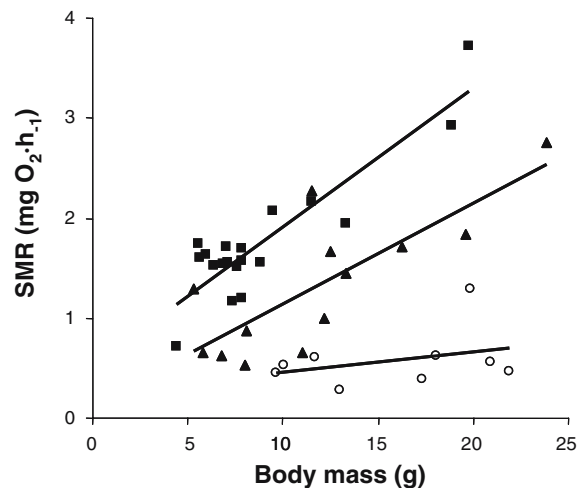


Fig. 1 Relationship between standard metabolic rate of yellow perch in relation to body mass at water temperatures of 12°C (open circle), 16°C (filled triangle) and 20°C (filled square). The linear regressions of SMR in relation to body mass are shown for the three different water temperatures

Table 2 Predictive models of standard metabolic rate (SMR, mg O₂ h⁻¹) of yellow perch using fish body mass (*M*, g) and water temperature (*T*, °C) as explicative variables

Model	Temperature (°C)	<i>a</i> ± SE	<i>b</i> ± SE	<i>c</i> ± SE	<i>R</i> ²	<i>P</i>
SMR = <i>a</i> · <i>M</i> ^{<i>b</i>}	12	0.17 ± 0.33	0.41 ± 0.46		0.10	0.40
SMR = <i>a</i> · <i>M</i> ^{<i>b</i>}	16	0.16 ± 0.19	0.84 ± 0.25		0.46	0.006
SMR = <i>a</i> · <i>M</i> ^{<i>b</i>}	20	0.37 ± 0.38	0.72 ± 0.12		0.68	< 0.001
SMR = <i>a</i> · <i>M</i> ^{<i>b</i>} · e ^{<i>c</i> · <i>T</i>}	all temperatures	0.01 ± 0.01	0.72 ± 0.13	0.19 ± 0.02	0.72	< 0.001

and activity metabolic expenditures) of 7.0–19.2 g Eurasian perch held at 14°C ranged from 1.22 to 3.55 mg O₂ h⁻¹ (Table 3). Karås (1990) estimated the metabolic rate of 2.0 g Eurasian perch at 10°C under two light regimes. Metabolic rates ranged from 0.12 mg O₂ h⁻¹ at a photoperiod of 8L:16D to 0.24 mg O₂ h⁻¹ at a photoperiod of 16L:8D (Table 3). Minimum oxygen consumption rate estimated for 2.0 g Eurasian perch during short-term respirometry experiments performed at 12°C was 0.20 mg O₂ h⁻¹ (Huuskonen and Karjalainen 1997). The active metabolic rate models of Kitchell et al. (1977), Karås and Thoresson (1992) and Hanson et al. (1997) predicted similar values for given body masses and water temperatures (Fig. 2a). Predicted active metabolic rates at 14°C ranged from 0.50 to 0.55 mg O₂ h⁻¹ for a 4 g fish and from 2.38 to 2.57 mg O₂ h⁻¹ for a 25 g fish.

Comparison of the SMR model with published metabolic rate estimates

SMR obtained during this study at 14°C were 6.9- to 15.1-times lower than the metabolic rates reported by Solomon and Brafield (1972) for Eurasian perch of similar mass held at this water temperature (Fig. 2a). However, the perch metabolic rate values obtained by Huuskonen and Karjalainen (1997, Fig. 2b) and Karås (1990, Fig. 2c) were within the 95% C.I. of the predictions of the SMR model developed during the present study.

There were considerable differences between the predictions of the SMR model developed during this study and predictions of AMR models of Kitchell et al. (1977), Karås and Thoresson (1992), and Hanson et al. (1997) (Fig. 2a). The metabolic rates predicted by the SMR model of this study were 4.1- to 4.5-times lower than the

AMR predicted by published models for a 4 g fish. The difference increased with increasing body mass to 19.4- to 20.9-times lower metabolic rates predicted by the SMR model for a 25 g fish.

Discussion

The SMR model developed during the present study indicates that body mass and water temperature can explain up to 72% of the 3.4-fold variation in the standard metabolic rates observed among the experiments. SMR has been shown repeatedly to be related to body mass in a double logarithmic relationship (Beamish 1964; Brill 1987). Interestingly, body mass explained only a small proportion of the variation in SMR (0.9%) compared to water temperature (70.9%). This most likely related to the relatively small range of body mass between the juvenile yellow perch used in the present study. As we compared our results to SMR values of similar sized fish, the small range in body mass does not affect our ability to reach our objective of comparing our model with other models and to interpret the differences between models and their implications for bioenergetics models.

The present study confirmed the expectation that the metabolic rates published by Solomon and Brafield (1972) may overestimate the SMR of perch. Similarly, the models of Kitchell et al. (1977), Karås and Thoresson (1992), and Hanson et al. (1997) produced metabolic rates that were larger than predictions based on the SMR model developed during the present study. This finding is not surprising since these models were developed using the metabolic rates reported by Solomon and Brafield (1972). Part of the discrepancy between the SMR values obtained during this study and published estimates or models

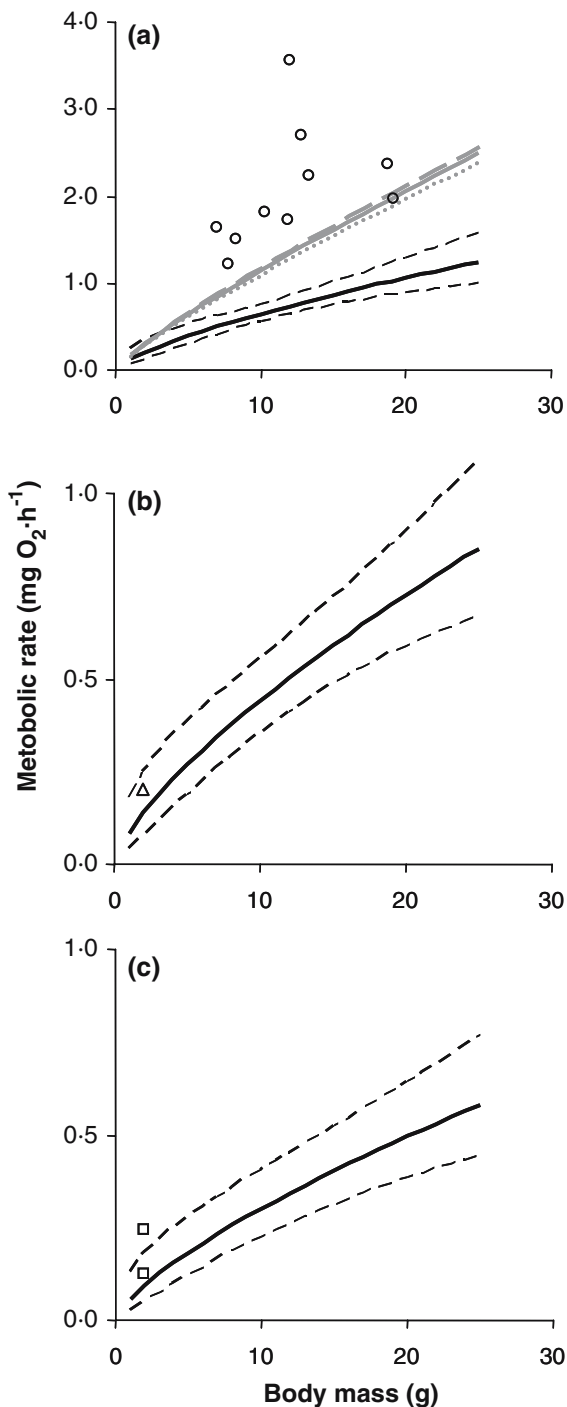
Table 3 Reported values for the metabolic rate of perch using different experimental approaches and metabolic models

Studies	Experiment/Model (Duration)	Species	n	Temperature (°C)	Photoperiod (L:D)	Respirometer volume (l)	Body mass (g)	Metabolic rate (mg O ₂ h ⁻¹)
Solomon and Brafield (1972) Karås (1990)	Respirometry (28 d)	<i>P. fluviatilis</i>	10	14	-	10	7.0–19.2	1.22–3.55
	Starvation (1 month)	<i>P. fluviatilis</i>	16	10	16L:8D	16	2.0	0.24
Huuskonen and Karjalainen (1997) Kitchell et al. (1977) Hanson et al. (1997) Karås and Thoreson (1992)	Respirometry (21–22 h)	<i>P. fluviatilis</i>	6	12	8L:16D	16	2.0	0.12
	Model	<i>P. fluviatilis</i>	-	14	18L:6D	0.158–0.167	2.0	0.20
	Model	<i>P. flavescens</i>	-	14	-	-	4.0–25.0	0.50–2.38
	Model	<i>P. flavescens</i>	-	14	-	-	4.0–25.0	0.53–2.50
	Model	<i>P. fluviatilis</i>	-	14	-	-	4.0–25.0	0.55–2.57

may be due to differences between the metabolic rate of the Eurasian perch studied by Solomon and Brafield (1972) and that of the North-American yellow perch used in the present study. Two lines of evidence do not support this hypothesis. First, Thorpe (1977) showed that the only difference between the two species is the position of the predorsal bone. No other significant difference could be identified between *P. fluviatilis* and *P. flavescens* in terms of the effect of the factors that may limit their distribution (temperature, flow velocity, oxygen concentration, salinity), reproductive development (spawning time, age of first maturation, fecundity), and feeding behavior (feeding periodicity, prey consumed, cannibalism). However, the comparison between *P. fluviatilis* and *P. flavescens* performed by Thorpe (1977) was based strictly on anatomical, morphological, and ecological variables and it must be recognized that no genetic comparison has been conducted to confirm these conclusions.

Second, the metabolic rates estimated by Karås (1990) and Huuskonen and Karjalainen (1997) for Eurasian perch were within the 95%-confidence interval of the predictions of the SMR model developed during this study for North-American yellow perch. This situation may seem a priori unexpected because, during the experiments performed by Karås (1990), perch were allowed to swim freely. It may therefore be anticipated that the metabolic rates obtained by Karås (1990) should overestimate SMR. However, it is important to note that during the study of Karås (1990), in contrast with that of Solomon and Brafield (1972), perch were not allowed to feed. As shown by Kerr (1982) and Boisclair (1992), activity and consumption rates are directly related. It is therefore plausible that activity rates were negligible during the prolonged starvation experiments performed by Karås (1990), and consequently, that the metabolic rates estimated under these conditions do represent SMR. These considerations suggest that the SMR difference between *P. fluviatilis* and *P. flavescens* may be negligible.

SMR has often been estimated as the intercept of the relationship between the respiration rate of unfed fish and swimming velocity (Brett 1964; Beamish 1978; Dewar and Graham 1994). This



method is generally accepted to provide reliable SMR estimates (Brett and Groves 1979; Leonard et al. 1999; Reidy et al. 2000). However, it implies an extrapolation (fish respiration at zero swimming velocity) that has been criticized because

Fig. 2 Comparison of the estimated standard metabolic rates at given water temperature and 95%-confidence interval (dashed lines) with data (a) from Solomon and Brafield (1972) at 14°C (open circles), (b) from Huuskonen and Karjalainen (1997) at 12°C (open triangles) and (c) from Karås (1990) at 10°C (open squares). At 14°C (panel a), the estimated SMR were also compared to metabolic rates predicted by the model of Kitchell et al. (1977) (. . .), the model of Karås and Thoreson (1992) (— —), and the model of Hanson et al. (1997) (—)

metabolic rates derived using this approach are not observed experimentally (Smit 1965; Forstner and Wieser 1990). Furthermore, Forstner and Wieser (1990) suggested that this approach would provide higher metabolic rates than would be measured in fish exhibiting increased spontaneous activity at low flow velocities. The similarity between the SMR values obtained during the present study and those published by Karås (1990) and Huuskonen and Karjalainen (1997) suggests that the problem of extrapolating fish respiration to zero swimming velocity may be negligible. The intercept of respiration-velocity relationships and long-term respiration rates during starvation experiments may therefore provide similar and reliable SMR values.

Calculations based on our SMR model, which is independent of swimming and digestive costs, suggest that only 24.1–60.8% of the metabolic rates (0.58–1.20 mg O₂ h⁻¹) presented by Solomon and Brafield (1972) were, in fact, imputable to SMR. The remaining 39.2–75.9% were due to costs related to digestion and activity. Similar calculations suggest that, for a 4 g fish, SMR accounts for only 55.2–62.8% of the active metabolic rate predicted by the models of Kitchell et al. (1977), Karås and Thoreson (1992), and Hanson et al. (1997). Corresponding values for a 25 g fish ranged from 44.1–49.8% suggesting that the use of a constant activity multiplier over such a range may be invalid.

Conclusion

The present study suggests that published metabolic rate models may overestimate SMR. Furthermore, they may confound the effects of

environmental conditions on SMR. An increase in body mass leads to both an increase SMR and activity costs. However, water temperature may increase SMR but not necessarily activity rates. Similarly, activity rates, in contrast to SMR, may be affected by prey abundance and fish density (Ware 1975, 1978; Boisclair and Sirois 1993). The magnitude and the variability of the proportion of digestion and activity expenditures in models presumed to represent SMR indicates that this problem is not negligible. The overestimation of SMR and the use of an activity multiplier may therefore lead to deficiencies in predictions as found in both field (Boisclair and Leggett 1989; Schaeffer et al. 1999) and laboratory evaluations (Bajer et al. 2003) of the Kitchell et al. (1977), the Karås and Thoreson (1992) and the Hanson et al. (1997) models. The present analysis underlines the utility of developing precise SMR models and the potential difficulties of using activity multipliers with metabolic models that are a composite of numerous physiological processes.

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