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A model for oxygen consumption of Atlantic salmon (*Salmo salar*) based on measurements of individual fish in a tunnel respirometer

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Abstract

A model for oxygen consumption of Atlantic salmon (*Salmo salar*) including body-weight (BW, kg), temperature (T, °C) and swimming speed (U, bodylengths s^{-1}) was developed. A multiregression analysis of 157 measurement periods on six different fish gave the model: V_{O_2} (mg kg^{-1} h^{-1}) $= 61.6(\pm 6.6)\ BW^{-0.33(\pm 0.11)}\ 1.03(\pm 0.10)^{T} 1.79(\pm 0.10)^{U}$. The model is compared with earlier work on oxygen consumption of salmonids. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Oxygen consumption; *Salmo salar*; Model; Swimming respirometer

1. Introduction

Several workers have published data on the oxygen consumption of salmonids (Brett, 1964; Liao, 1971; Braaten, 1976; Kazakov and Khalyapina, 1981; Bergheim et al., 1991; Christiansen et al., 1991; Fivelstad and Smith, 1991; Berg et al., 1993). However, most of the data are presented in tables and are not very user-friendly for engineers, who are dependent on this information for the design and management of sea farms. The aim of this study was to create a comprehensive model that expresses the correlation between oxygen consumption and body-weight, temperature and swimming speed. The model was tested by oxygen consumption measurements of individual starved Atlantic salmon under controlled conditions.

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The relation between the effect of body-weight (BW) and oxygen consumption (V_{O_2}) can be expressed by using the allometric equation with the general form $y = ax^b$ (Schmidt-Nielsen 1984)

$$V_{O_2} = a'\mathrm{BW}^b \tag{1}$$

When considering the influence of temperature on the rate of a reaction, it is useful to obtain a temperature quotient by comparing the reaction rate at two different temperatures. A temperature difference of 10°C has become the standard. The Q_{10} is calculated by using the van't Hoff equation and is entirely an empirical value (Eckert et al. 1988). By rearranging the van't Hoff equation the influence of temperature on the metabolic rate is given by:

$$V_{O_2} = a''c^{\mathrm{T}} \tag{2}$$

The base c is called the temperature parameter (or Q_1) and a'' is V_{O_2} for a given animal at a temperature of 0°C.

Movement in water is met by hydrodynamic constraints, which are determined by the physical properties of water and the speed, size and shape of the fish moving through the water (Johnston and Altringham 1991). Examination of the effect of swimming speed in a respirometer (Brett, 1964) supports the idea that the metabolic relation can be described as an exponential equation:

$$V_{O_2} = a'''b^u \tag{3}$$

where u is the swimming speed in body-length per second (b s^{-1}), b is the activity parameter and a''' is the standard metabolic rate for a given fish.

By combining Eqs. (1)–(3), it is possible to construct a model that describes the metabolic rate for fish at a given body-weight, temperature and swimming speed:

$$V_{O_2} = a\mathrm{BW}^b c^t d^u \tag{4}$$

where a is the standard metabolic rate for a fish of 1 kg at 0°C. The model assumes that the different parameters are independent.

2. Materials and methods

Atlantic salmon from third-generation stock (Gjedrem et al. 1991) were used in these experiments. The fish (1.1–2.0 kg) were kept for 1 year in indoor rearing tanks, in continuous light and at natural temperature (range 7–9°C), before being netted from the tank and placed individually in the respirometer.

The fish were not fed for 24 h before the start of the experiment. Before transfer to the respirometer, each fish was sedated with benzocaine and its weight, length, width and thickness were measured. The transfer from the tank to the respirometer took 3–5 min. Before the oxygen consumption recordings were started, the fish were kept for 1 day in the respirometer in order to stabilize metabolic rate. Continuous light was used during the experiment.

Nine measuring periods at three different swimming speeds, in random order, were registered each day. The swimming speeds were 0.5, 1.0 and 1.5 body-lengths s^{-1} (bl s^{-1}), corrected for the blocking effect of the fish on the water speed according to Bell and Terhune (1970). Each experiment started at a water temperature of 10°C. After 2 days of experiments, the temperature was changed to either 15 or 5°C. After an acclimation period of 10–15 h, 2 days of measurements at the new temperature were started.

A total of 157 measurements on 6 individual fish, were carried out and used to test the model. Each period lasted for 5–20 min, depending on the behaviour of the fish and on the oxygen consumption. The oxygen level was kept $> 80\%$ saturation. The behaviour of the fish was observed by means of a video camera. Only measurements where the fish showed steady swimming movements were used in the calculations.

The respirometer had a total volume of 62 l and was made of stainless steel, except for the ellipsoidal-shaped 22 l transparent PVC swimming section. An electromagnetic flowmeter (Fischer and Porter) registered the water velocities through the swimming section. Readings from the temperature sensors (NTC, Radiometer) and the oxygen electrode (E5046, Radiometer) were made and aeration and temperature controlled by a computer-based system.

All statistical calculations and nonlinear regressions for fitting the results to the mathematical model were done by Systat v. 5.02.

3. Results

Fitting the data set to Eq. (4) gave the following equation, in which four variables were estimated, and which relates oxygen consumption to body weight, temperature and swimming speed ($\pm$SE):

$$V_{O_2} = 61.6(\pm 6.6)\ \mathrm{BW}^{-0.33(\pm 0.11)}\ 1.03(\pm 0.10)^{\mathrm{T}}\ 1.79(\pm 0.10)^{\mathrm{U}} \qquad (5)$$

The results of the non-linear regressions gave a value for a (Eq. (4)) equal to 61.6 mg l^{-1} h^{-1}, which represents the standard metabolism of a fish of 1 kg at 0°C. The mass exponent was estimated to be -0.33 (b in Eq. (4)) for the specific metabolic rate (V_{O_2} (mg O_2 kg^{-1} h^{-1}) $= a\mathrm{BW}^{-0.33}$), which is equal to 0.67 for the metabolic rate (V_{O_2} (mg O_2 h^{-1}) $= a\mathrm{BW}^{0.67}$). Q_1 (c in Eq. (4)) was found to be 1.03 and corresponded to a Q_{10} of 1.34. The regression analysis estimated the activity parameter (d in Eq. (4)) to be 1.79.

The probabilities plot of the distribution of the residuals (Fig. 1) shows an approximately normal distribution and no systematic tendencies can be observed.

Fig. 2 shows a scatterplot matrix (SPLOM), where weight, temperature and swimming speed are plotted against measured data, estimated data and residuals of each measurement period. The histograms show the relative numbers of measurements in each group. Comparing measured values with estimated value reveals a good correlation between the model and the registered value. The plot of residuals against temperature and swimming speed does not show any trends to suggest an unequal variance. On the contrary, analysis of the plot of residuals against body weight seems to show a correlation between the weight of the animal and the deviation from the model. However, the reason for these irregularities is not necessarily an effect of the body weight, but may be due to other individual differences.

The model assumes that the variables (body weight, temperature and swimming speed) in the model do not have any influence on each other. To test the independence of the variables used in the model, values for each variable were used to calculate the effects of the other two. For example, all measurements on fish with a bodyweight of 1.1 kg were used to calculate the effect of temperature and swimming speed on fish with this weight. The results of the multiregression analysis are given in Table 1, which presents values of the variables and calculated parameters with SE and numbers of replicates which presents.

Stability of oxygen consumption during the measurement periods and during the time the fish spent in the respirometer was evaluated by examining the deviation of measured oxygen consumption from the model against time. Linear regression analysis of the deviation against time did not give slopes significantly different from zero, neither for the effect of measurement periods nor for the time the fish spent in the respirometer.

4. Discussion

The model used to describe the results in this experiment resembles the model reported by Muller-Feuga et al. (1978) and Smirnov et al. (1986), except that these authors did not include the effect of swimming speed. In the equation used by Liao (1971) and Fivelstad and Smith (1991), the effect of temperature was described as an exponential, rather than a logarithmic function that corresponded to the definition

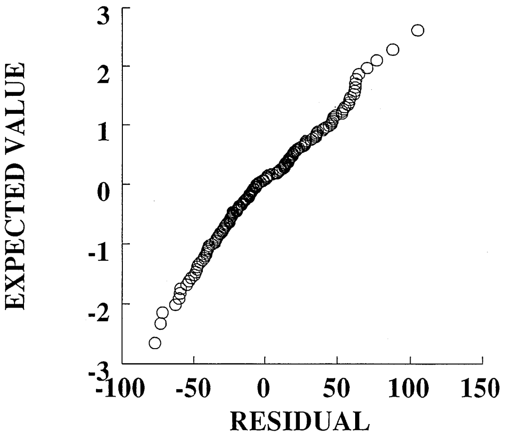

Fig. 1. Probabilities plot of the distribution of the residuals of the model.

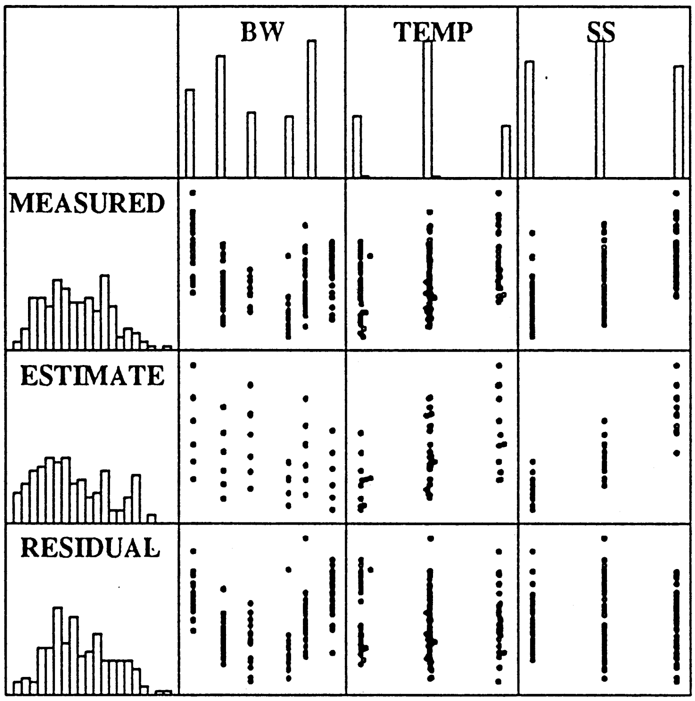

Fig. 2. A scatterplot matrix (SPLOM) of body weight, temperature and swimming speed plotted against measured, modelled and the residuals of the model. The histograms show the relative numbers of measurements in each group.

of Q_{10}. None of these works included the swimming speed in the model for oxygen consumption, because the model describes the routine metabolism of the fish.

The multiregression analysis gave a weight exponent of -0.33 (b in Eq. (4)). The SPLOM plot (Fig. 2) of the residuals against weight showed an unequal distribution, which indicated individual differences in oxygen consumption that cannot be explained by the weight exponential. On the basis of the plot of the oxygen consumption against weight, the two fish with highest body weight seemed to deviate from the other fish by not following the negative trend in oxygen consumption, as expected on the basis of the mass exponent in the model. This may be explained by a maladaptation to the respirometer because of the size of the fish. However, observations of the behaviour during the experimental period did not indicate such maladaptation. Other biological or environmental factors may also have influenced the oxygen consumption of the individual fish. Factors such as seasonal variation, sexual maturation and sex are known to influence the metabolism of the fish (Dickson and Kramer 1971).

Winberg (1960) concluded that the general relationship between the specific metabolic rate and body weight of adult fish of different sizes is proportional to their weight raised to a power of approximately -0.2. This is the same result as

Table 1
Control of the independence between the variables in the model (Eq. (4))[a]

BW (kg)	T (°C)	SS (bl s^{-1})	*a*	SE	*b*	SE	*c*	SE	*d*	SE	*n*
1.13			74.5	10.2			1.05	0.01	1.52	0.10	23
1.33			33.9	5.3			1.06	0.02	1.95	1.17	32
1.50			46.0	7.1			1.06	0.01	1.22	0.08	17
1.75			28.4	17.1			0.96	0.04	4.27	2.68	16
1.86			61.5	12.6			1.02	0.01	1.75	0.16	36
2.04			74.0	9.7			1.00	0.01	1.83	0.15	33
	5		27.9	4.9	0.99	0.20			2.29	0.24	39
	10		82.5	9.3	−0.39	0.14			1.85	0.14	85
	15		166.2	16.8	−0.93	0.13			1.44	0.10	33
		0.50	59.7	8.5	−0.83	0.18	1.08	0.01			50
		1.00	118.3	19.9	−0.35	0.21	1.03	0.01			59
		1.50	157.4	19.0	−0.21	0.15	1.02	0.01			48

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[a] Values for each variable (body weight (BW), temperature (T) or swimming speed (SS)) were set into the model, and the parameters (*a*, *b*, *c*, *d*) (± SE) were calculated by using multiregression analysis. *n* Is the number of replicates.

was obtained when the relation of the metabolism of fish of different sizes of single species was examined. Kazakov and Khalyapina (1981) examined Atlantic salmon between 1.6–13.2 kg and found an exponential of -0.16. By using the model of Muller-Feuga et al. (1978) and Smirnov et al. (1986), Fivelstad and Smith (1991) found the exponential to be -0.38 for postsmolt Atlantic salmon (200–850 g). A multiregression analysis was carried out on the data from measurements of oxygen consumption on a population of Atlantic salmon (Berg et al., 1993). The fish were of the same genetic origin as the fish used in this experiment and were also kept in continuous light, but they were not starved. The analysis gave the equation $V_{O_2} = 62.5\mathrm{BW}^{-0.30}1.06^{\mathrm{T}}$, with a weight exponential of -0.30, not significantly different from the value obtained in this experiment.

By analysis of the effects of temperature, Q_1 was found to be 1.03, which corresponds to a Q_{10} of 1.34. Calculation of Q_{10} from the results from Berg et al. (1993) gave a Q_{10} of 1.71. Brett and Groves (1979) found a value of 2.3 as a general Q_{10} within the a range of ± 10°C. There is limited information available about the pattern and the degree of compensation in oxygen consumption for temperature change in salmonids. Acclimation occurs at different rates according to species and acclimation to cold is usually slower than to warmth (Prosser and Heath, 1991). One day of acclimation may be considered to be too short to achieve full acclimation to a new thermal regime (Jobling, 1982). The metabolic rate measured at 5 and 15°C may therefore reflect a short-time response to changing temperature, rather than full acclimation. There was no marked difference between the Q_{10} value found in these studies and the value found by Berg et al. (1993) during natural temperature changes between 6 and 16°C.

(The effect of activity level or swimming speed on oxygen consumption was found to give an activity parameter of 1.79. In his studies of the performance of sockeye salmon (*O. nerka)* Brett (1964)) found the base to be between 1.48 and 2.18. A base of 1.34 was found for juvenile coho salmon (*O. kisutch*) (Puckett and Dill, 1984). For Atlantic salmon Braaten (1976) found a value of 1.51. These works are all based on measurements of smaller fish (< 0.2 kg), and to our knowledge no work on Atlantic salmon or other salmonids exists in the 1–3 kg class for comparison with the experiment reported here.

The probability plot of the distribution of the residuals shows an approximately normal distribution, and does not reveal skewness, kurtosis or a mixture of two distributions. The SPLOM plot does not show a tendency that indicates trends or systematic deviation from the model, except for the effect of the body weight. In Table 1 the model was used to calculate the effect of temperature and swimming speed on oxygen consumption at different body weights. The effects of temperature on oxygen consumption seemed to decrease with increasing body weight. However, a linear regression of the temperature parameter (*c*, Eq. (4)) against body weights (Table 1) does not give a slope significantly different from zero. The effect of swimming speed appears to be independent of body weight.

The effect of temperature on body weight and swimming speed parameters showed a large variation. This variation may be explained by the fact that we used only three fish for the registrations at 5°C and three fish at 15°C.

Evaluation of the effect of swimming speed at oxygen consumption at various body weights showed that the measurements of oxygen consumption at 0.5 bl s^{-1} varied more than the data from measurements made at 1.0 and 1.5 bl s^{-1}. Restlessness (spontaneous activity) and excitement are reported to elevate metabolism at low velocities (Brett, 1964; Evans, 1972). Although registration periods during which the fish did not show steady swimming activity were eliminated from the data set, undesirable behaviour could have influenced the results.

Experiments performed on smaller fish have shown variations in oxygen consumption during fasting (Dickson and Kramer, 1971; Jobling and Davies, 1980; Wiggs et al., 1989). Our results did not show any significant trends in deviation from the model during experimental periods, indicating that fasting did not influence the results. Netting, sedation and transfer to the respirometer may also have caused a short-term rise in the metabolic rate (Smart, 1981). Diurnal rhythms in metabolic rate are known to exist in salmonids, but usually as a consequence of diurnal fluctuations in light (Bergheim et al., 1993). Lack of significant trends in deviations from the model during the experimental period, both within and between days, shows that these environmental factors had no major influence on the results.

In order to compare the measured oxygen consumption in this study with previously published data on salmonids, values from the literature were plotted against the model values. In Fig. 3, oxygen consumption measurements of sockeye

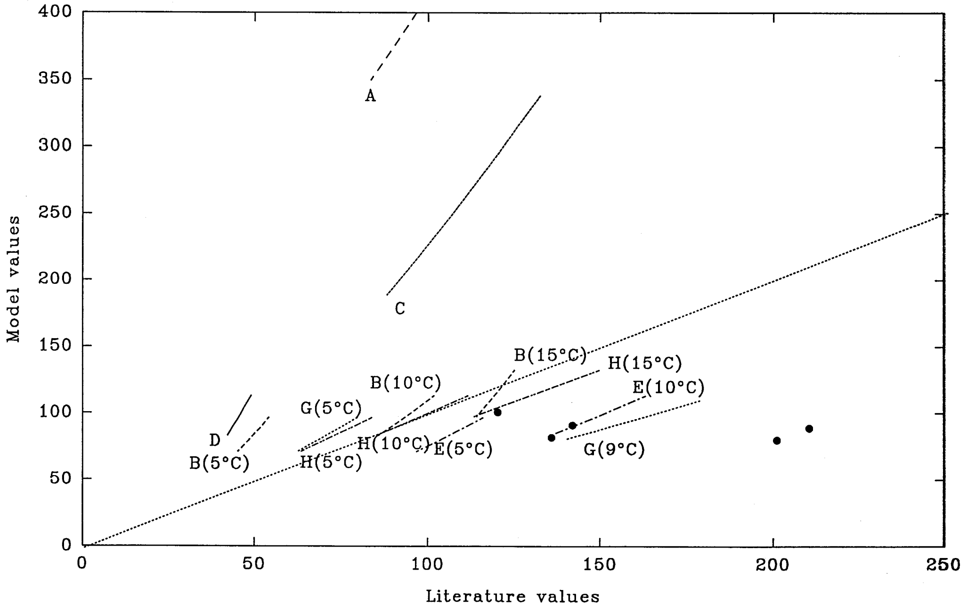

Fig. 3. Comparison of literature data with results obtained in this study. The letters refer to references given in Table 2 and symbols are from the work of Bergheim et al. (1991).

Table 2
Literature data on oxygen consumption of salmonids

Publication	Model	Species	Weight (kg)	T (°C)	Exp. Setup	Feeding
Brett, 1964	$V_{O_2} = 60.3 \times 1.91^{\mathrm{u}}$	*Oncorhyncus nerka*	0.03	10	Swimming respirometer	Starved
Liao, 1971	$V_{O_2} = (60 \times 7.7 \times 10^{-7}/0.144) \times (32 + 1.8 \times t)^{3.2.} (0.454 \times w)^{-0.194}$	Salmonids	—	—	Tank	—
Braaten, 1976	$V_{O_2} = 71.62.1.51^{u}$	*Salmo salar*	0.18	8	Tank	Starved
Kazakov and Khalyapina, 1981	$V_{O_2} = 49 \times w^{-0.16}$	*Salmo salar*	1–13	—	Respirometer	—
Christiansen et al., 1991	$V_{O_2} = 82.9 \times w^{-0.2.} \times 1.07^{t}$	Salmonids	—	—	Tank	Fed
Bergheim et al., 1991	—	*Salmo salar*	1.0–2.1	6.8–7.5	Tank	Fed
Fivelstad and Smith, 1991	$V_{O_2} = 8.65 \times w^{-0.261.} \times t^{1.378}$	*Salmo salar*	0.20–0.85	5–9	Tank	Fed
Berg et al., 1993	$V_{O_2} = 62.5 \times w^{-0.3.} \times 1.06^{t}$	*Salmo salar*	0.2–3.3	6–16	Tank	Fed

Symbols used are $V_{O_2,}$ oxygen consumption (mg kg^{-1} h^{-1}); w, bodyweight (kg); t, temperature (°C); u, swimming speed (bodylength $second^{-1}$).

salmon (0.032 kg, 10°C, 0–1.5 bl s^{-1}, measured in respirometer) from Brett (1964) show considerably higher oxygen consumption than estimated by our model. A direct comparison is not possible since our model is based on larger fish. This was confirmed by Braaten (1976) on Atlantic salmon (0.180 kg, 8.25°C, 0.5–1.5 bl s^{-1}, measured on fed fish in tanks). In order to compare our results with those of Liao (1971) (1–2.5 kg), Kazakov and Khalyapina (1981) (1–2.5 kg), Christiansen et al. (1991), Fivelstad and Smith (1991)and Berg et al. (1993), a swimming speed of 0.5 bl s^{-1} was used in the model. This swimming speed is assumed to correspond to the routine activity of Atlantic salmon in rearing tanks. The temperature was not stated in the work of Kazakov and Khalyapina (1981), and 10°C is used in the figure. Comparisons with Liao (1971), Christiansen et al. (1991), Fivelstad and Smith (1991) and Berg et al. (1993), suggests that the model presented underestimates the effect of temperature on metabolism. The results of Kazakov and Khalyapina (1981) and Liao (1971) deviated more from the model with increasing weight. However, the studies of Christiansen et al. (1991), Fivelstad and Smith (1991) and Berg et al. (1993) showed approximately the same effect of body weight on the metabolism as would be predicted from the results of our work. Fig. 3 shows that there is a variation in the magnitude of deviation from the model presented (see Table 2). Compared to the model presented in this paper, the results of other studies show both higher (Kazakov and Khalyapina, 1981) and lower (Christiansen et al., 1991) metabolic rates. The effects of temperature in the model are underestimated in comparison with the work of Liao (1971). The expected effect of temperature and body weight on oxygen consumption does not seem to appear in the population studies of Bergheim et al. (1991). Comparing the results with those of Berg et al. (1993) it appears that the metabolism of individual fish in the respirometer is higher than in landbased seafarms, although these fish were fed. A higher stress level in fish placed in a respirometer may explain this, which would raise their metabolic rate

Although the presented model can not be used directly in aquaculture design and management, it may be a valuable tool in development of operational criteria for Atlantic salmon oxygen consumption.

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